Chapter 1

Morphology, Anatomy and Biology of Plant Parasitic Nematodes – a Synopsis

Michel LUC[1], David J. HUNT[2] and Janet E. MACHON[2]

1. Nematologist ORSTOM, Muséum national d'Histoire naturelle, Laboratoire des Vers, 61 rue de Buffon, 75005 Paris, France and 2. CAB International Institute of Parasitology, 395a Hatfield Road, St. Albans, Herts, AL4 0XU, UK.

Nematodes successfully colonize a greater variety of habitats than any other group of multicellular animals. They are found in all oceans; from the polar regions to the equator, from the litoral zone to the abyssal depths; they colonize freshwater lakes, rivers and marshes and all types of soil from the antarctic to the tropics; they parasitize most groups of animals, including other nematodes, and a wide variety of algae, fungi and higher plants. However, despite such ecological diversity they are surprisingly similar in structure.

A very brief, simplified account[1] of the basic morphology, anatomy and bionomics of plant parasitic nematodes forms the first part of this chapter and is followed by illustrated descriptions concentrating on the diagnostic features of the most commonly occurring and/or most important plant parasitic genera referred to in the corpus of the book, together with other pertinent data.

Morpho-Anatomy of the Plant Parasitic Nematodes

Plant parasitic nematodes can be divided into three major groups: the tylenchs (including tylenchids and aphelenchids); the longidorids; and the trichodorids (see: Outline Classification, p. 9). The tylenchs are the most numerous and the most important on a world scale and so will be dealt with in greatest detail.

Tylenchs (Fig. 1 A-J)

Tylenchs are vermiform animals, usually ranging from 0.2 to 1 mm long, but occasionally over 3mm. In some genera the female loses the vermiform shape and becomes obese or even globose.

The head end or **labial region**, when seen *en face* (Fig. 1C), is typically hexaradiate and has a central orifice, the mouth, through which the **stylet** is protruded. Various sensory structures, including

ormation on nematode morpho-anatomy and biology can be found in: Dropkin, V. H. (1980) *Introduction to plant* New York, John Wiley & Sons, XIV + 293 p. Maggenti, A. M. (1981) *General nematology*. New York, Springer + 372 p.

n, excellent illustrated descriptions of various plant and insect parasitic nematodes, together with data on biology, d classification can be found in: Siddiqi, M. R. (1986) *Tylenchida Parasites of Plants and Insects*. Farnham Royal, nwealth Agricultural Bureaux, ix + 645 p.

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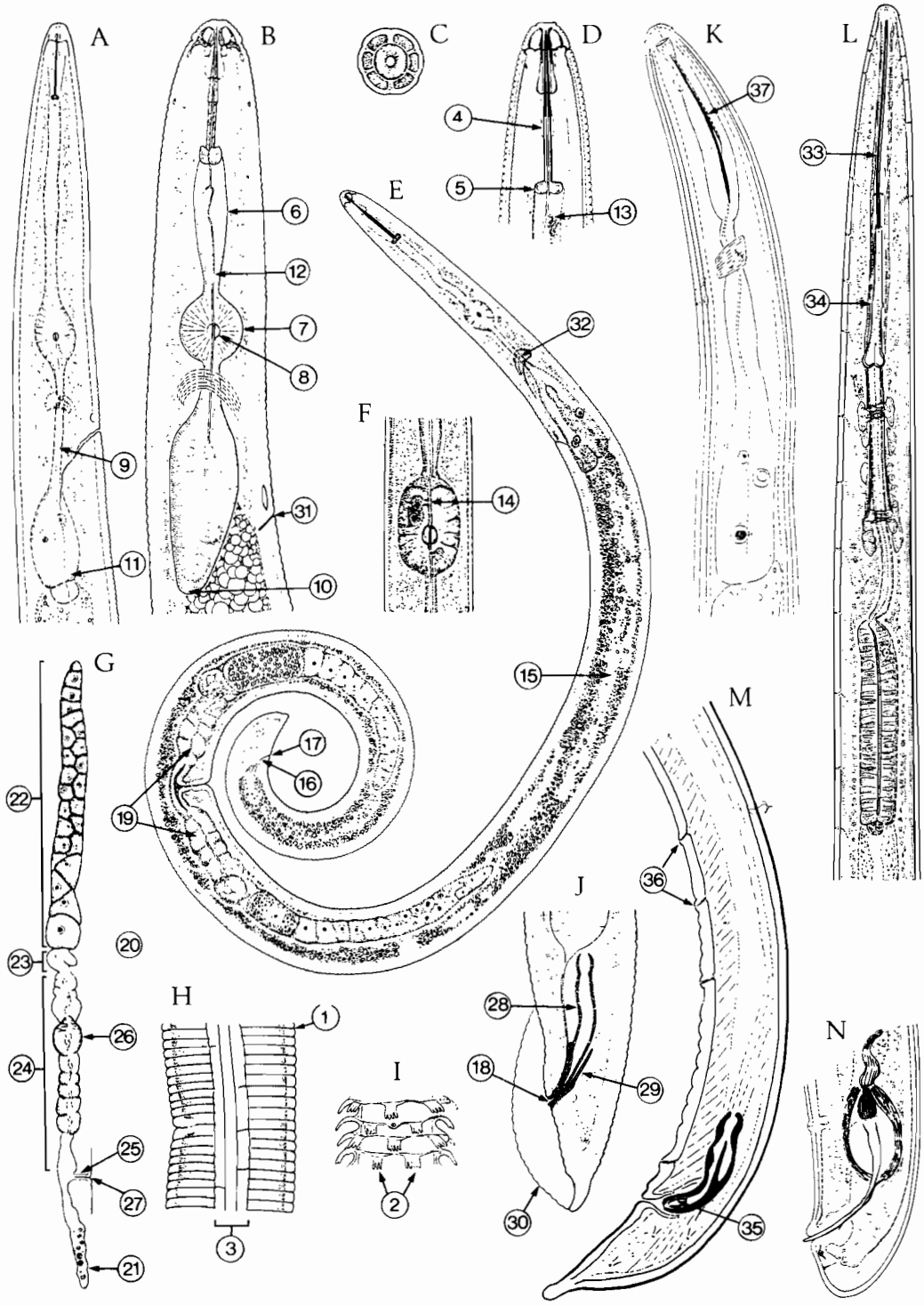


Fig. 1. Major diagnostic features of plant parasitic nematodes.

the **amphids**, occur on the head which is often transversely annulated and usually separated from the body by a constriction. Internally the head contains a sclerotized **framework** (or skeleton) to support the structure and for attachment of the stylet protractor muscles.

The body is enclosed in a **cuticle** which is usually transversely annulated (H1) and may be ornamented with a variety of processes in the criconematid forms (I2). Longitudinal ridges occur in some species. Beneath the cuticle is the **hypodermis** and the **muscles** which are attached to four **chords** – longitudinal thickening of the cuticle and hypodermis. The lateral chords are better developed than the ventral and dorsal ones and correspond externally to the **lateral field** which is marked by a number of **longitudinal lines** (H3) or **incisures**. The central cavity of the nematode, the **pseudocoelom**, contains a viscous fluid which acts as an **hydrostatic skeleton**. Suspended within the fluid are the three major organs – digestive, reproductive and excretory.

The digestive system comprises: **stylet; oesophagus; intestine** and **rectum**. The stylet (D4) is a protrusible cuticular tube, pointed anteriorly and with a subterminal aperture and generally swelling posteriorly to form three **basal knobs** (D5). Protractor muscles run from the knobs to the cephalic (labial) skeleton.

The **oesophagus** (or pharynx) comprises a narrow cylinder or **procorpus** (B6) which expands to form the **median bulb** (B7) a muscular swelling containing refringent **valve plates** (B8) and then narrows to form the **isthmus** (A9) before expanding into the **oesophageal glands** (B10, A11). There are three glands, one dorsal and two subventral, which may form a bulb-like structure (A11) abutting the intestine or be extended into an overlapping lobe (B10). Between the stylet and the oesophago-intestinal junction runs a central tube, the **oesophageal lumen** (B12), through which glandular secretions and food passes. In tylenchids, the dorsal oesophageal gland opens into the oesophageal lumen near the stylet base (D13) and the two subventral glands open within the median bulb. In aphelenchids, all three glands open within the median bulb (F14). The **intestine** (E15) is a largely undifferentiated tube which opens via the **rectum** (E16) at the **anus** (E17) or, in adult males, the **cloaca** (J18). In the males of certain genera the digestive system is degenerate and non-functional.

The reproductive system in both sexes is tubular. The female genital system may be composed of two (E19), usually opposed, branches (**didelphic**) or reduced to one (**monodelphic**). In monodelphy (G20) the posterior branch is reduced to a **post-uterine sac** (G21) or entirely absent. Each branch has four major parts: **ovary**; (G22) **oviduct** (G23); **uterus** (G24) and **vagina** (G25). A specialized uterine structure for storing sperm, the **spermatheca** (G26), may be present. The vagina opens to the exterior via the **vulva** (G27), a ventrally situated transverse slit in the middle or posterior section of the body. The male system is less variable. The single genital tube consists of a **testis, seminal vesicle** and **vas deferens** opening to the exterior via a common pore with the rectum, the **cloaca** (J18). The copulatory organ consists of the paired **spicules** (J28) with a guiding piece, the **gubernaculum** (J29). The protrusible spicules are heavily cuticularized and serve to open the female vulva and channel sperm. The male tail often has cuticular expansions, the caudal alae (J30) or **bursa**, which aid in copulation.

The excretory system consists of a uninucleate **gland cell** connected via an **excretory canal** to the ventrally situated **excretory pore** (B31). This pore is usually in the oesophageal region but may be posteriorly located (e.g. *Tylenchulus*).

The nervous system consists of a circumoesophageal commisure – the **nerve ring** (E32) – and a network of nerves connected to body organs and various sensory structures. These sense organs are mostly on the head (**sensillae** and **amphids**), in the oesophageal region (**cephalids, deirids, hemizonid** and **hemizonion**) and on the tail (**phasmids**).

Longidorids (Fig. 1 L, M)

Compared with tylenchs these are much longer and range from 0.9–12mm in size. The cuticle is smooth and lateral fields are absent. The stylet is more properly called an **odontostylet** and is up to 300 μm long. It consists of needle-like **odontostyle** (L33) attached posteriorly to a cuticular extension – the **odontophore** (L34). The oesophagus consists of a narrow anterior section and a posterior bulb

which is both muscular and glandular. The female reproductive system is didelphic or monodelphic, the anterior branch regressing in the latter case. The male spicules are well-developed and have **lateral guiding pieces** (M35). There is no gubernaculum or bursa but a series of sensory **ventral supplements** (M36) run anteriorly from the cloaca. Some morphological features of tylenchs are missing (e.g. excretory pore, phasmids, deirids, cephalids).

Trichodorids (Fig. 1 K, N)

Short (0.5–1.1mm) cigar-shaped nematodes with bluntly rounded head and tail. The cuticle is smooth and may swell with acid fixatives. The stylet or **onchiostyle** (K37) is curved and the oesophagus comprises a narrow cylindrical anterior section and a posterior bulboid expansion. The female genital system is usually didelphic. The male spicules are slightly curved and a weak bursa may be present. Ventral supplements occur.

Bionomics of Plant Parasitic Nematodes

Reproduction and development

Reproduction is either **amphimictic** (separate males and females) or **parthenogenetic** (males absent, non-functional, or very rare). Eggs are either laid singly or stuck together in masses in a **gelatinous matrix** which is secreted by the female. Such egg-masses are associated with species where the females swell and become sedentary, although some obese genera retain all the eggs within the body, the cuticle tanning on the death of the female to form a **cyst**. Egg-sacs and cysts serve to protect the eggs.

Nematodes typically have four juvenile stages between the egg and adult with intervening moults allowing an increase in size. In tylenchs the first stage juvenile, J1, moults to the J2 within the egg, but in longidorids and trichodorids it is the J1 which emerges.

Environmental conditions

Although occupying many different ecological niches, nematodes are essentially aquatic animals. Plant parasitic nematodes require at least a film of water to enable locomotion and, as all species spend a greater or lesser proportion of their life within soil, the soil water content is a primary ecological factor. Many species die in dry soils whilst others may survive in an anhydrobiotic state. Conversely, too much soil water results in an oxygen deficit and many nematodes succumb – although certain genera, such as *Hirschmanniella*, thrive in such conditions.

Soil temperature is not a particularly important factor as it tends to remain reasonably stable. Most tropical nematodes do not survive prolonged periods below 10°C and some are able to survive soil temperatures of 50°C if they have sufficient time to enter anhydrobiosis.

Soil structure has an important effect on nematodes as the pore size affects the ease with which they can move through the soil. In general, sandy soils provide the best environment – soils with a high clay content or those with an excessively open texture inhibit movement. However, saturated clay soils can be colonized successfully by certain specialised nematodes, including *Hirschmanniella* and some *Paralongidorus*. Soil pH may influence nematodes, but few data are available for tropical and subtropical species.

The maxim that 'where a plant is able to live, a nematode is able to attack it' is a good one. Nematodes are even able to attack the aerial parts of plants provided that the humidity is high enough to facilitate movement. Such conditions are provided in flooded rice fields where foliar species such as *Aphelenchoides besseyi* and *Ditylenchus angustus* can be very damaging.

Hatching, host location and penetration

The eggs of many plant parasitic nematodes are deposited singly, either in the soil or within the plant tissues, and hatch irrespective of the presence of a host plant, provided that other factors are favourable.

In the more advanced parasites, however, the eggs may be embedded in a gelatinous matrix to form an egg-mass (e.g. *Meloidogyne*) or retained within the swollen female body, the cuticle of which tans to form a protective cyst (e.g. *Heterodera, Globodera*). The eggs of cyst nematodes require the presence of root exudates from the host to promote hatching and this is associated with a restricted host range.

Nematodes are attracted to plant roots by a variety of factors which have yet to be fully elucidated. Such attractive factors can operate over considerable distances – up to one metre in *Meloidogyne*. Having found a host there are three main types of parasitism (Fig. 2):

1. **ectoparasitic** – the nematode does not enter the plant tissues, but feeds by using the stylet to puncture plant cells – the longer the stylet the deeper it can feed.

2. **semi-endoparasitic** – only the anterior section of the nematode penetrates the root, the posterior section remaining in the soil.

3. **endoparasitic** – the entire nematode penetrates the root. Migrating endoparasites retain their mobility and move through the tissues feeding as they go. Sedentary endoparasites, on the other hand, have a fixed feeding site (nurse cells), lose their mobility and become obese.

The above categories are not mutually exclusive as some genera may be semi-endoparasitic or migratory ectoparasitic depending on the host e.g. *Helicotylenchus*, whilst some sedentary parasites have only the anterior section embedded in the root (= sedentary semi-endoparasites) e.g. *Rotylenchulus, Tylenchulus*.

In *Meloidogyne* and *Heterodera/Globodera* the J2 is the infective stage, but in ectoparasites and most migratory endoparasites all stages may feed on or penetrate the root (Fig. 3). Rarely, as in *Rotylenchulus*, the immature female is the infective stage, the juveniles and males remaining in the soil and not feeding.

Host reactions

As ectoparasites do not enter the plant, the damage they cause is usually limited to necrosis of those cells penetrated by the stylet e.g. *Tylenchorhynchus*. However, those species with longer stylets (e.g. *Xiphinema, Hemicycliophora*, etc) penetrate the tissues more deeply thus killing more cells. As such nematodes tend to feed on meristematic tissue near the root tips, galling or hooked roots result and secondary root proliferation may occur if the growing point is destroyed.

Endoparasites not only kill the cells they feed upon but, by burrowing through the root tissues, they cause extensive destruction leading to cavitation and secondary infection. Successive generations of nematodes compound the damage and it is not surprising that some of the most pathogenic nematodes belong to this group (*Pratylenchus, Radopholus, Hirschmanniella*).

Sedentary endoparasites have a sophisticated relationship with the host involving transformation of root cells into a trophic system of nurse or transfer cells. The function of these nurse cells is to act as a nutrient sink so that the sedentary nematode enjoys a continuous supply of nutrients, thus enabling it to enlarge enormously and produce a large number of eggs. In *Meloidogyne* multiplication of the root cells is also stimulated leading to the characteristic galls.

Plants with the root system damaged by nematodes often show above-ground symptoms such as retarded growth, chlorosis and reduced yield. These symptoms are a direct result of the impaired ability of the root system to deliver water and nutrients and thus may be confused with similar symptoms resulting from poor soil conditions and/or nutrient deficiencies.

The exact ways in which nematodes affect plants have yet to be fully elucidated and besides impairing root function by physical damage, toxins may also be involved. An interesting case involves 'Ontario peach-decline' where a very low population of *Pratylenchus* can kill young trees. The nematodes metabolize the sugar part of cyanosides in the plant tissue and thus liberate the CNH radical which is highly toxic to the tree.

In nematology the following terms are used to describe the inter-relationships of host and parasite. Plants can be divided into **hosts** or **non-hosts** depending on whether nematode reproduction occurs. Non-hosts may be **immune** i.e. no nematode penetration or reproduction, or **resistant** i.e. allowing

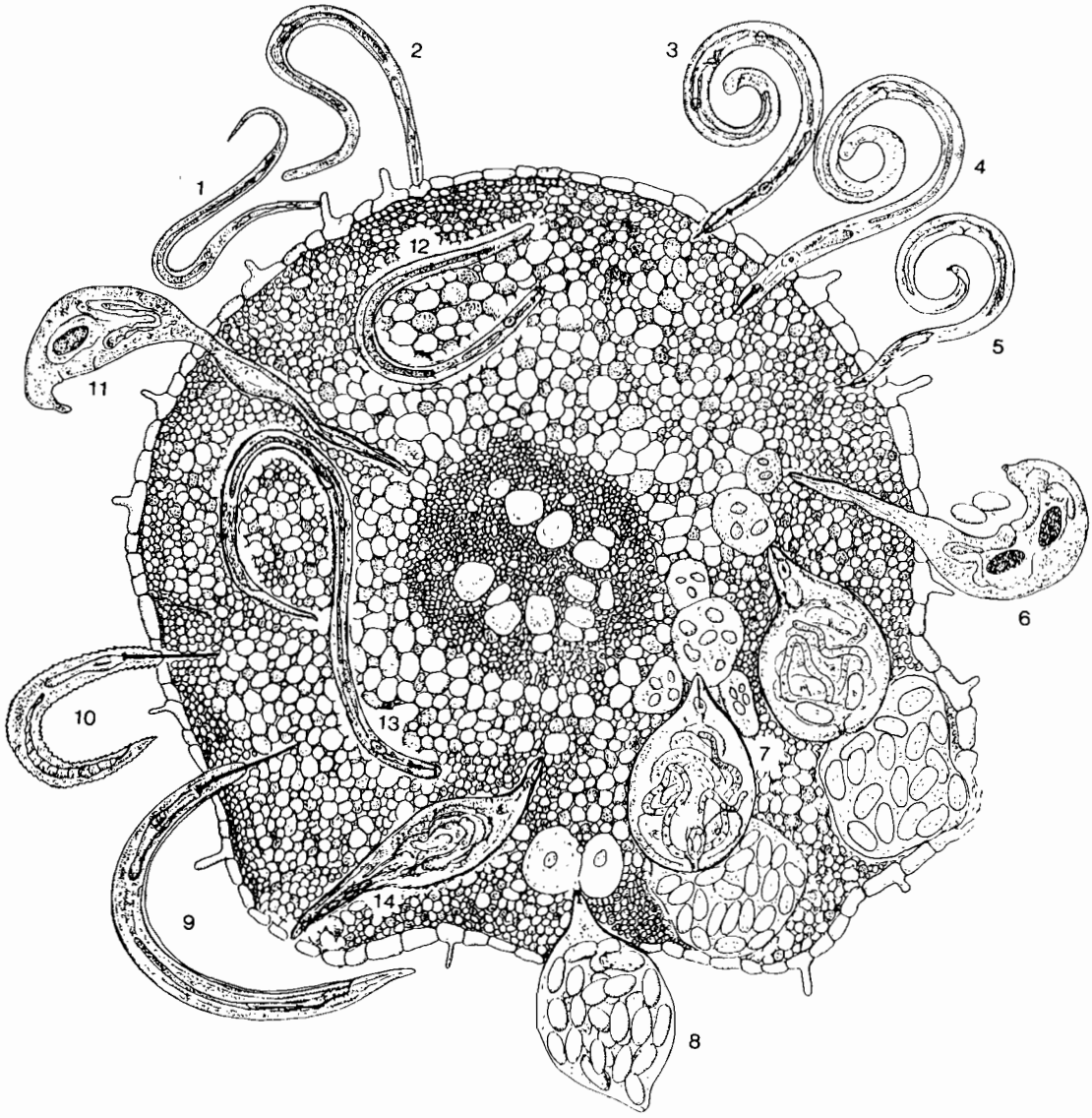


Fig. 2. Diagrammatic presentation of various types of tylenchid feeding on root tissue. 1. *Ditylenchus*. 2. *Tylenchorhynchus*. 3. *Rotylenchus*. 4. *Hoplolaimus*. 5. *Helicotylenchus*. 6. *Rotylenchulus*. 7. *Meloidogyne*. 8. *Heterodera*. 9. *Hemicycliophora*. 10. *Criconemella*. 11. *Tylenchulus*. 12. *Pratylenchus*. 13. *Hirschmanniella*. 14. *Nacobbus*. (Modified after Siddiqi, 1986).

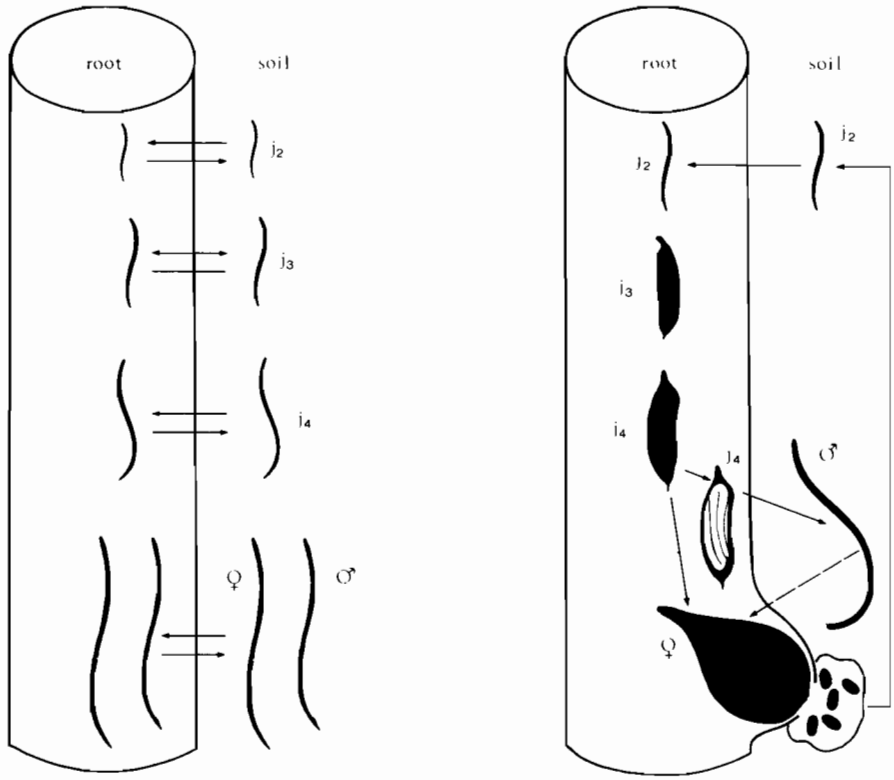


Fig. 3. Diagrammatic comparison of the life-cycle of a migratory endoparasite (left) and a sedentary endoparasite (right). (Modified after Merny, 1972).

nematode penetration/parasitism but not reproduction. Host plants are **non-resistant** or **susceptible** and can be **good hosts** or **poor hosts** depending on whether reproduction is high or low. Susceptible plants which support the lowest levels of reproduction within a dataset have been referred to as partially resistant or even, in some cases, as 'resistant'.

Variations in the ability of nematodes to reproduce on given plant species or cultivars are of great agricultural significance and are of two principal types. Nematode populations, distinguished by their ability or inability to reproduce on designated plant species are known as **host races. Pathotypes** are variants of a host race or species which are distinguished by their ability to reproduce on a designated host plant genotype (e.g. cultivar, line, etc).

Tolerance refers to the amount of damage caused by the nematode to the plant and should not be confused with resistance (q.v.). A **tolerant host** suffers little damage even when heavily infected whilst an **intolerant host** may be severely damaged, even if only lightly infested.

Survival

In the absence of a live host nematodes may survive in the soil or in plant residues. Provided that the environment dries slowly, many nematodes are able to enter a reversible anhydrobiotic state when they are less susceptible to desiccation, temperature and chemicals. In a number of genera

the eggs are the survival stage and are protected in a gelatinous matrix (*Meloidogyne, Tylenchulus, Rotylenchulus*) or within the hardened cyst-like body of the female (*Heterodera, Globodera*). In the later case, infective J2 nematodes may emerge several years after being laid. Anhydrobiosis is probably more common in tropical and subtropical areas than is currently realized and enables the nematode to survive the dry season and also some non-chemical control methods such as dry-fallow. The record for longevity in the anhydrobiotic state is held by seed nematodes, such as *Anguina*, where they have been recorded surviving for 39 years. A practical consequence of anyhydrobiosis is that when extracting dry soil a sufficient period of soaking should be allowed to re-activate the nematodes.

Identification of the Major Genera

This section is intended to serve as a basic guide to the identification of the major parasitic genera of tropical and subtropical agriculture. Each generic diagnosis has the major characters printed in bold and numerically cross-referenced, where appropriate to the illustrations. The descriptions are designed to be multi-level and should be of benefit to both the novice and the more experienced user. The systematic arrangement used is outlined in Table 1 although the descriptions are arranged according to the mode of parasitism – stem or foliar parasites (p. 10), ectoparasites (p. 14), migratory endoparasites (p. 24), sedentary endoparasites (p. 34) – in order to facilitate rapid comparison between genera which are systematically distant, yet share a similar biotope.

TABLE 1 Outline classification.

Order/Sub-order	Family	Genus	Page
TYLENCHIDA			
Tylenchina	Anguinidae	*Anguina*	12
		Ditylenchus	12
	Belonolaimidae	*Tylenchorhynchus*	14
	Pratylenchidae	*Hirschmanniella*	30
		Nacobbus	38
		Pratylenchus	28
		Radopholus	32
	Hoplolaimidae	*Aorolaimus*	26
		Helicotylenchus	24
		Hoplolaimus	26
		Rotylenchulus	40
		Scutellonema	26
	Heteroderidae	*Globodera*	34
		Heterodera	34
		Meloidogyne	36
	Criconematidae	*Criconemella*	16
		Hemicriconemoides	18
		Hemicycliophora	18
	Tylenchulidae	*Tylenchulus*	42
Aphelenchina	Aphelenchoididae	*Aphelenchoides*	10
		Rhadinaphelenchus	10
DORYLAIMIDA			
Dorylaimina	Longidoridae	*Longidorus*	22
		Paralongidorus	22
		Xiphinema	22
Diphtherophorina	Trichodoridae	*Paratrichodorus*	20
		Trichodorus	20

Aphelenchoides Fischer, 1894

Systematic position: Aphelenchina, Aphelenchoididae

Morphology: Small to medium sized (0.4–1.2 mm), slender nematodes. Females die straight or ventrally arcuate on heat relaxation while the **male tail curls ventrally to produce a 'walking-stick' shape** (1). Head region weakly sclerotized; stylet weak, with or without basal swellings. **Oesophageal bulb well-developed, spherical to rounded-rectangular in shape and more or less filling the body width** (2). **Dorsal oesophageal gland duct opening within bulb** (3), just anterior to the valve plates. Oesophageal gland lobe overlapping intestine dorsally. Female: **vulva posterior** (60–75%) (4); **genital tract single**, anteriorly directed. Tail medium conoid, with or without terminal mucron(s). Male: tail medium conoid, **spicules well-developed, thorn shaped** (5). No bursa.

Biology: Ecto-parasitic on leaves, stems and other parts of higher plants. Most species can also be readily cultured on various fungal hyphae. *A. besseyi* can withstand desiccation for several years. The life-cycle is rapid and can be completed in as little as a week.

Major species: *A. arachidis, A. besseyi, A. fragariae, A. ritzemabosi.*

Distribution: *A. arachidis* is only recorded from groundnut in northern Nigeria but the other species are well-distributed with *A. besseyi* being found in most rice-growing areas.

Rhadinaphelenchus J. B. Goodey, 1960

Morphology: Similar in general respects to *Aphelenchoides* but both sexes are **very slender (body length/body width = about 100)**. In addition, the female has a **very long post-vulval sac, a very long, slightly tapering tail with a rounded tip** (6), and **a vulval flap** (7). The **male tail tip bears a small cuticular flap** (8) ('bursa') visible most easily in ventral view. **Dorsal limb of spicule elongate** (9).

Biology: Parasitic in cortical tissues of coconut roots but mainly found in the stem where 10 g of tissue may contain 50,000 nematodes. Infection often causes the development of a red or orange-red ring of tissue within the stem (hence the common name of 'red-ring' for the nematode). The nematode is believed to be vectored by the palm-weevil during oviposition and death of the palm occurs in 2–4 months.

Major species: *R. cocophilus* (no other species described).

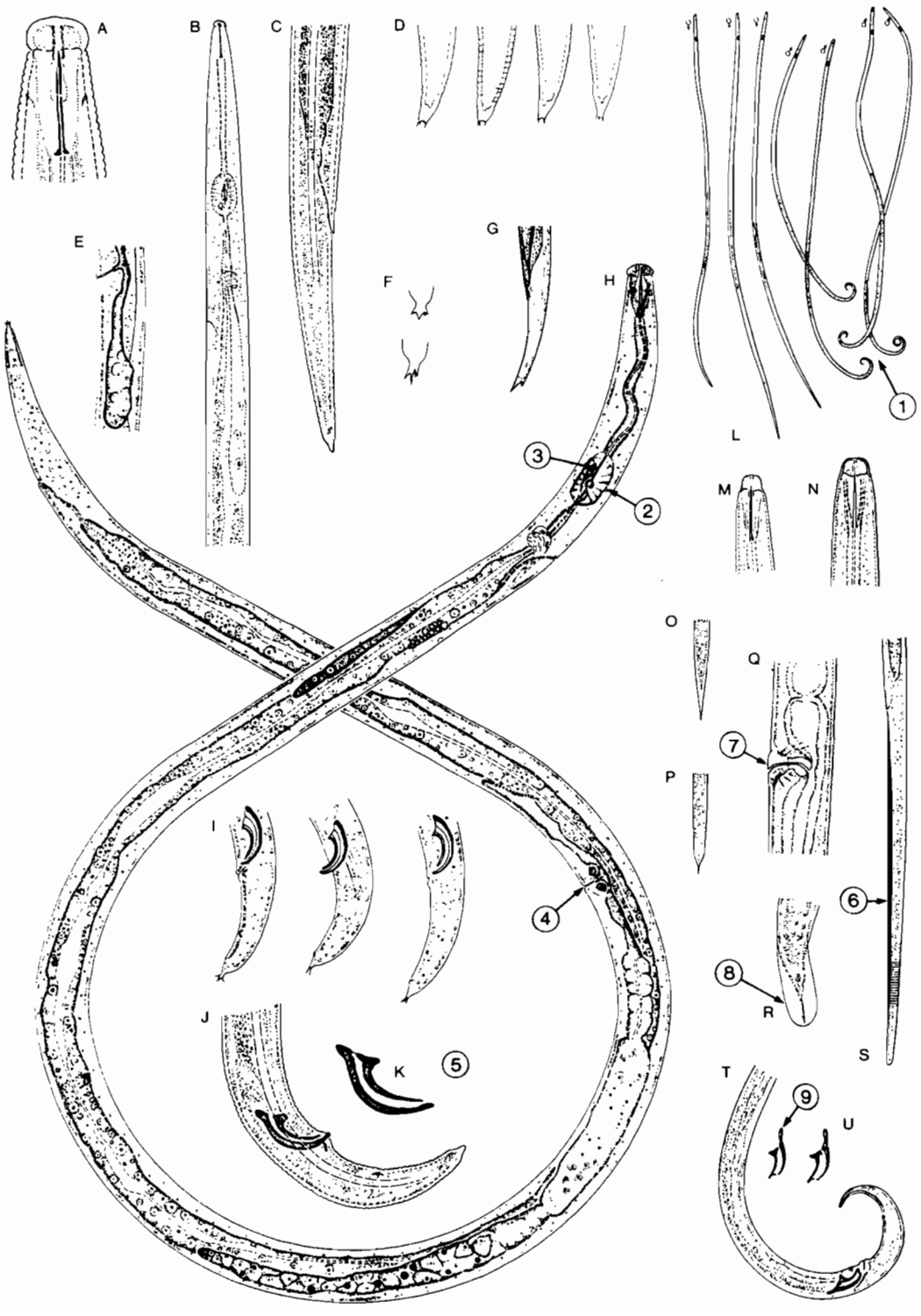
Distribution: Widespread in the Caribbean, Central and South America.

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 4; Set 3, No. 32; Set 5, No. 72; Set 8, No. 116).

Dean, C. G. (1979) Red ring disease of *Cocos nucifera* L. caused by *Rhadinaphelenchus cocophilus* (Cobb, 1919) Goodey 1960. An annotated bibliography and review. *Technical Communication No. 47.* CAB International, Wallingford, UK.

Fig. 4. *Aphelenchoides besseyi.* A: head; E: postvulval sac; F: tail tips; H: entire female; I: male tails. *A. bicaudatus.* G: female tail. *A. fragariae.* C: female tail; J: male tail; K: spicule. *A. ritzemabosi.* B: oesophagus; D: female tail tips. *Rhadinaphelenchus cocophilus.* L: adults; M: male head. N: female head; O,P: juvenile tail tips; Q: vulva; R: male tail tip; S: female tail; T: male tail; U: spicules.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Ditylenchus Filipjev, 1936

Systematic position: Tylenchina, Anguinidae

Morphology: Slender nematodes dying straight or slightly curved ventrally on heat relaxation. **Head skeleton weakly sclerotized** (1), stylet of moderate strength and with small basal knobs. Oesophagus with a muscular median bulb and **isthmus gradually expanding to form the basal bulb** (2) which may extend as a lobe over the intestine. Female: **vulva well posterior** (3). **Genital tract single, anteriorly outstretched. Post-uterine sac present** (4). **Tail elongate, conoid** (5). Male: **bursa adanal** (6), not reaching tail tip. **Tail elongate, conoid** (7).

Biology: Ectoparasites of plant stems and leaves but also found within the tissues. Infected stems and leaves are often stunted and deformed.

Major species: *D. angustus, D. dipsaci.*

Distribution: *D. angustus* is found in rice-growing areas of Bangladesh, Vietnam and other areas of Asia. *D. dipsaci* is restricted to the cooler regions of the tropics and subtropics.

Confusable genus: *Aphelenchoides*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, U.K. (Set 1, No. 14; Set 5, No. 64).

Fortuner, R. (1982). On the genus *Ditylenchus* Filipjev, 1936 (Nematoda: Tylenchida). *Revue de Nématologie, 5*: 17–38.

Anguina Scopoli, 1777

Morphology: Sexually dimorphic. Adult stages found only in plant galls, juveniles found in galls, plant tissue or soil depending on stage of life cycle. General morphology similar to *Ditylenchus*. Female: **obese**, medium to large nematodes (1.5–5mm) **dying spirally coiled** (8) on heat relaxation. **Vulva very posterior with a single, anteriorly directed genital tract** which is **reflexed two or more times** (9). **Numerous oocytes** (10). Male: small to medium sized (1–2.5mm) dying ventrally or dorsally (e.g. as in *A. tritici*) arcuate. **Testis well developed with one or more flexures** (11). **Bursa adanal** (12).

Biology: Forming galls on stems, leaves or flowers of various plants. The J2 stage is found in the soil and feeds ecto-parasitically on the plant tissues. The final moult takes place after gall formation, each female laying one to two thousand eggs. As the gall matures and dries, the J2 infectives slowly desiccate and in this anhydrobiotic state can survive many years.

Major species: *A. agrostis, A. tritici*

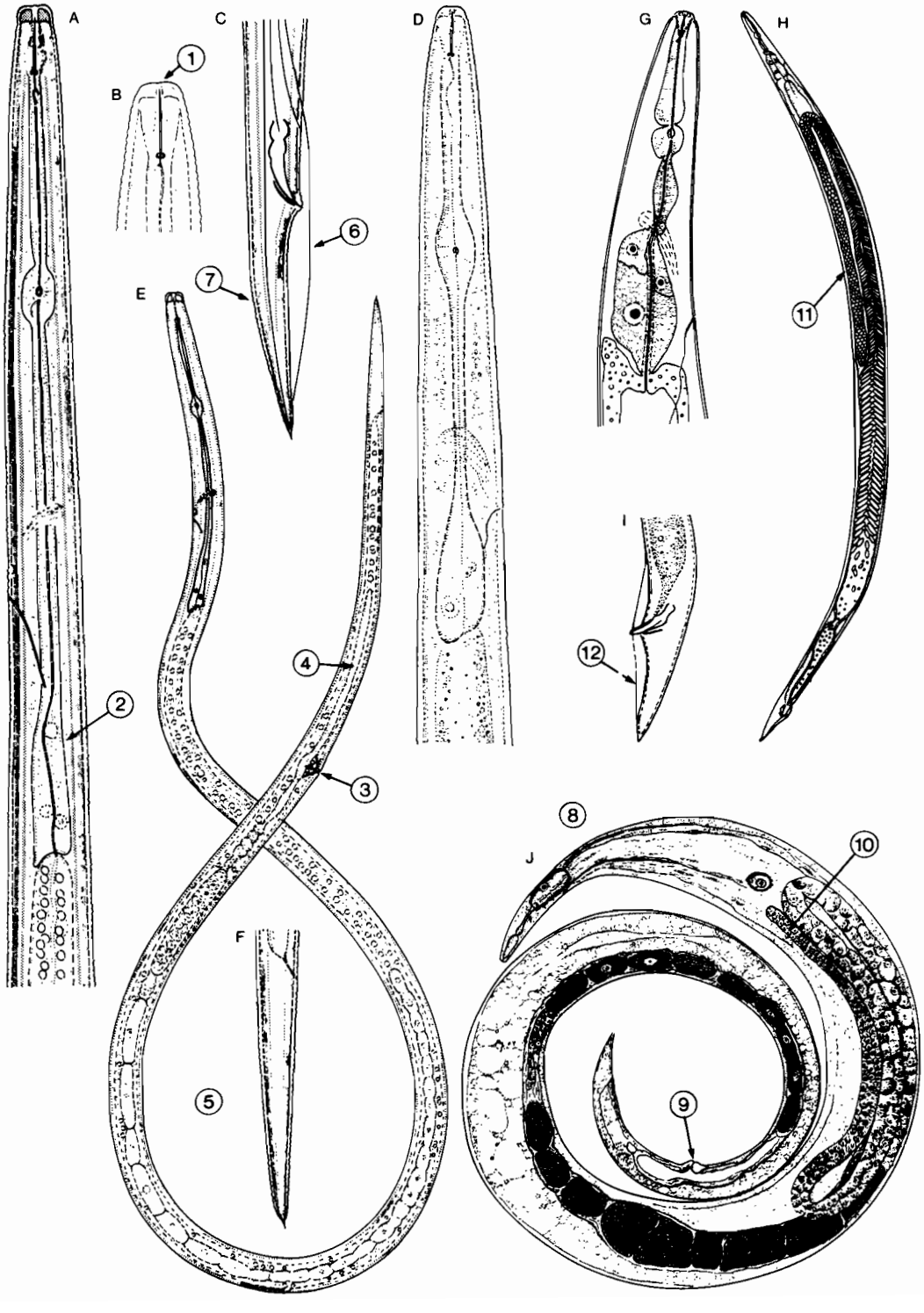
Confusable genus: juveniles in soil very similar to juvenile *Ditylenchus*.

Useful Literature

CIH Descriptions of Plant-Parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK (Set 1, No. 13; Set 2, No. 20).

Brzeski, M. W. (1981). The genera of Anguinidae (Nematoda, Tylenchida). *Revue de Nématologie, 4*: 23–34.

Fig. 5. *Anguina agrostis*. I: male tail. *A. tritici*. G: female oesophagus; H: entire male; J: entire female. *Ditylenchus angustus*. A: female oesophagus; C: male tail; E: entire female; F: female tail. *D. myceliophagus*. B: head region; D: oesophagus.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Tylenchorhynchus Cobb, 1913

Systematic position: Tylenchina, Belonolaimidae

Morphology: Small nematodes (rarely over 1 mm long), dying more or less straight or slightly curved ventrally on application of gentle heat. **No marked sexual dimorphism in form of anterior region**. Head region rounded, continuous with body contour or slightly offset, with thin annules, and **weak sclerotization** (1). **Stylet slender, 15–30 µm long, moderately sclerotized with rounded, backwardly sloping knobs** (2). Lateral field with 2, 3, 4 or 5 lines; cuticle sometimes divided into blocks. Oesophagus equally developed in both sexes; median bulb fusiform, moderately developed; oesophageal glands abutting the intestine (3) or, very rarely, overlapping. Female: **vulva median with two equally developed genital tracts** (4); one directed anteriorly, one posteriorly. Spermatheca rounded. **Tail about three anal body diameters long, conoid to subcylindrical, with rounded tip** (5). Male: tail elongate, conical-pointed, bursa extending to tail tip (6), trilobed in some species. Spicules slightly curved.

Biology: Migratory ecto-, semi-ecto- or endo-parasites. Most species bisexual. Polyphagous. Not considered as being very important parasites. Well distributed in all climatic areas.

Major species: *T. annulatus, T. brassicae, T. mashoodi*

Synonyms: *Telotylenchus, Quinisulcius, Dolichorhynchus, Trilineellus, Divittus, Morasinema, Tessellus, Neodolichorhynchus, Mulkorhynchus.*

Confusable genera: *Trichotylenchus, Merlinius, Amplimerlinius*

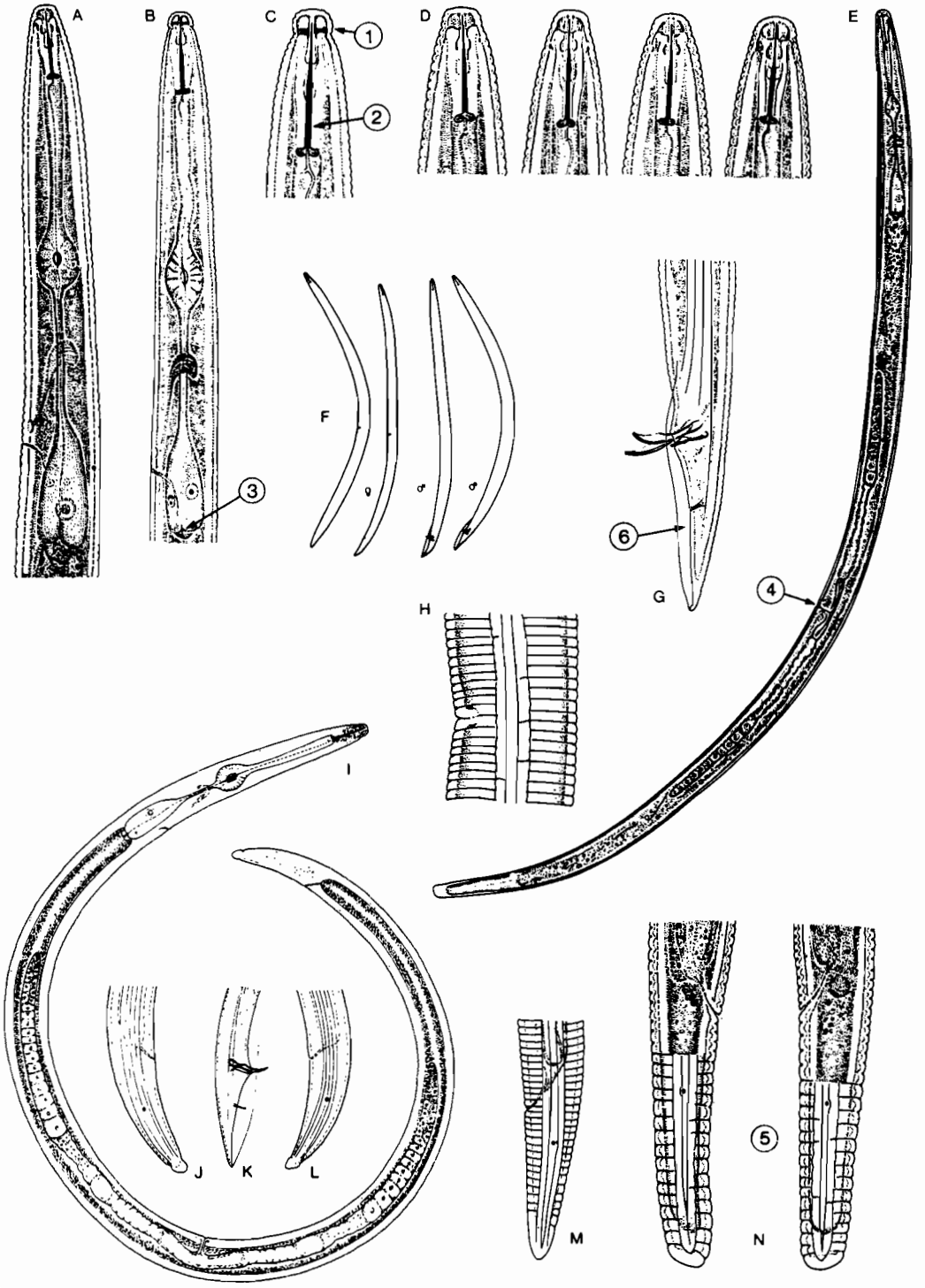
Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK (Set 6, No. 85).

Fortuner, R. & Luc, M. (1987). A reappraisal of Tylenchina (Nemata). 6. The family Belonolaimidae Whitehead, 1960. *Revue de Nématologie, 10*: 183–202.

Siddiqi, M. R. (1986). *Tylenchida Parasites of Plants and Insects*. CAB International, Wallingford, UK. 645 pp. [see pp. 172–221].

Fig. 6. *Tylenchorhynchus annulatus*. A: oesophagus; D: head ends; E: entire female; H: lateral field; N: female tails. *T. capitatus*. I: entire female; K: male tail; J,L: female tails. *T. claytoni*. F: adults. *T. cylindricus*. B: oesophagus. C: head; G: male tail; M: female tail.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Criconemella De Grisse & Loof, 1965

Systematic position: Tylenchina, Criconematidae

Morphology: Sexually dimorphic. Female: body 0.20–1mm long, stout, dying straight or slightly curved, with rounded anterior end, and rounded to conical posterior part. **Cuticle provided with 42–200 prominent, retrorse annules** (1), with a **smooth** (2) **or finely crenate posterior margin** (3). Labial area not well separated from rest of body, marked by one or two thinner annules. **Stylet strong, basal knobs with a forwardly directed process** (4) (= anchor shaped). Oesophagus with a strong median bulb which is fused with the procorpus; glands forming a small posterior bulb. Vulva posterior. **One genital tract, extending anteriorly** (5). Spermatheca laterally situated. Male: Body slender and short (6). Anterior end rounded. No stylet; oesophagus degenerate. Spicule short, slightly curved. **Bursa weakly developed**, exceptionally absent. Tail pointed. Juveniles: Resembling female. **Annules smooth to finely crenate** (exceptionally with a row of scales) on posterior margin.

Biology: Migratory ectoparasites on perennial crops, trees and vines. Males non-feeding. Most species are parthenogenetic. Only a few species have been proved to be harmful. Found in all geographic areas.

Major species: *C. axestis, C. onoensis, C. sphaerocephala, C. xenoplax*

Synonyms: *Xenocriconemella, Mesocriconema, Madinema, Seshadriella, Neobakernema, Crossonemoides. Macroposthonia* and *Criconemoides*, two generic names often found in the literature, could also be regarded as synonyms of *Criconemella* but are better considered as *genera dubia*.

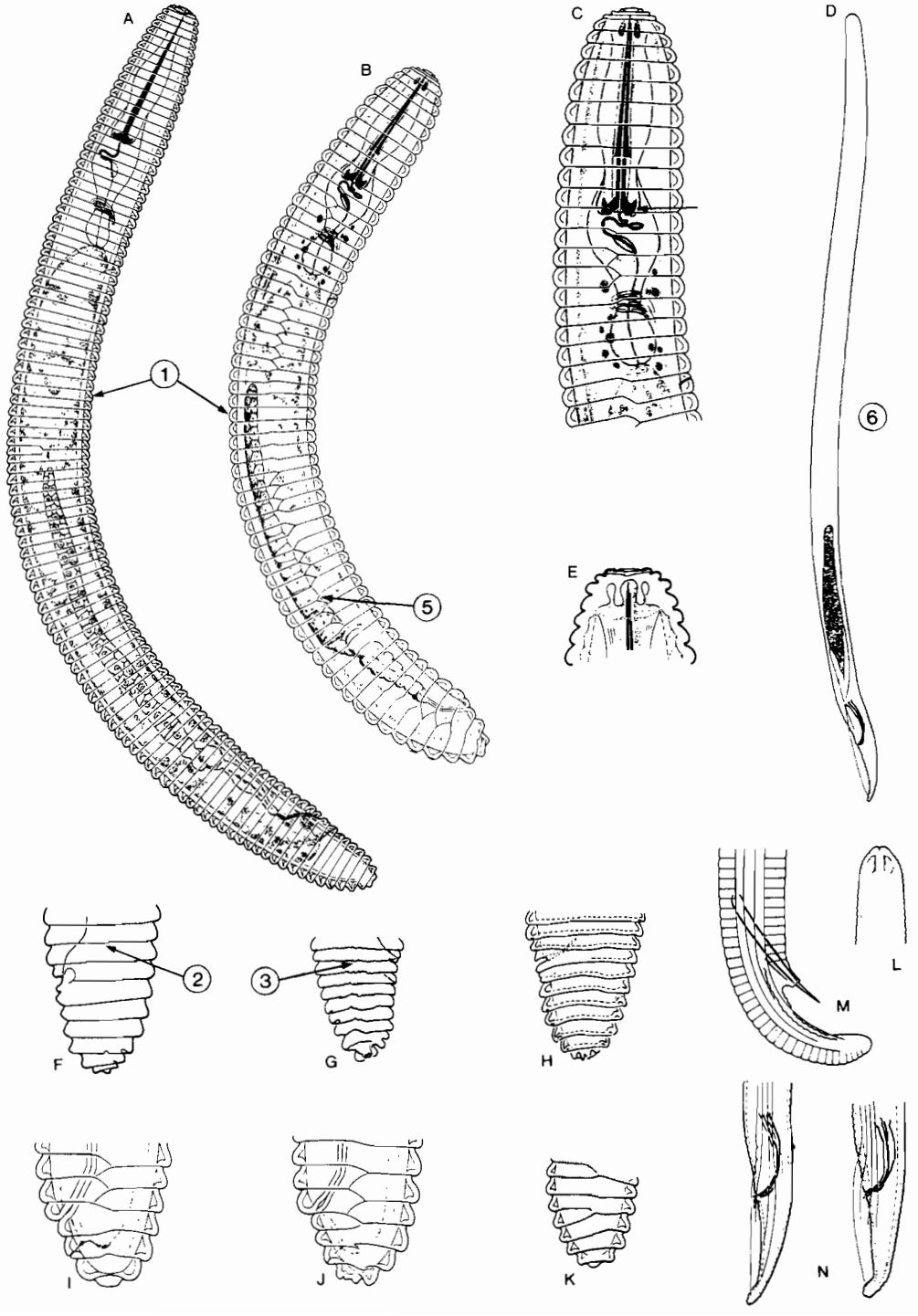
Confusable genera: *Criconema, Discocriconemella, Hemicriconemoides*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 127; Set 2, No. 28).

Raski, D. J. & Luc, M. (1987). A reappraisal of Tylenchina (Nemata). 10. The superfamily Criconematoidea Taylor, 1956. *Revue de Nématologie, 10*: 409–444.

Fig. 7. *Criconemella pseudohercyniensis*. D: entire male; E: head region; G: female tail; N: male tails. *C. onoensis*. H: female tail. *C. sphaerocephala*. B: entire female; C: head region female; I,J: female tails. *C. xenoplax*. A: entire female; F: female tail; K: juvenile tail. L: male head; M: male tail.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Hemicycliophora de Man, 1921

Systematic position: Tylenchina, Criconematidae

Morphology: Sexually dimorphic. Female: Body straight, or slightly ventrally curved, 0.6–1.9 mm long, stout. Anterior end rounded. Posterior end pointed, more rarely rounded. **Cuticle** (1) **with two detached layers** (= 'double' cuticle); external layer marked by **numerous (up to 400) prominent, but not retrorse annules**. No true lateral field, but cuticle may be variously ornamented (longitudinal lines, squares, dots, scratches, etc.). Labial area not separated from body, marked by 2–3 annules. **Stylet strong** (2), long, with **rounded basal knobs** (3). Oesophagus with strong median bulb fused with the procorpus (4); glands forming a small terminal bulb. Vulva posteriorly situated. **One anteriorly directed genital tract**; spermatheca lateral. **Vestigial anus and rectum**. Postvulval part generally conical, with pointed terminus, more rarely cylindrical with rounded extremity. Male: Slender, with simple cuticle. **No stylet**. Oesophagus degenerate. **Spicule strong, semi-circular to hook-shaped** (5). **Bursa adanal, well developed. Tail long** (6), conical, often presenting a ventral angle to the body axis. Juveniles: resembling female.

Biology: As for *Criconemella*

Major species: *H. arenaria, H. parvana, H. typica*

Confusable genus: *Hemicriconemoides*

Synonyms: *Aulosphora, Colbranium, Loofia*

Useful Literature

Brzeski, M. W. (1974). Taxonomy of Hemicycliophorinae (Nematoda, Tylenchida). *Zesz. probl. Postep. Nauk robn. 154*: 237–330.

Hemicriconemoides Chitwood & Birchfield, 1957

Systematic position: Tylenchina, Criconematidae

Morphology: Sexually dimorphic (7). Female: Similar in many ways to *Hemicycliophora*, but shorter (usually around 0.5 mm long) with fewer annules and very **closely adpressed 'double' cuticle** (8). **Stylet knobs with anteriorly directed processes** (9). Tail short, conoid (10).

Biology: Similar to *Criconemella*.

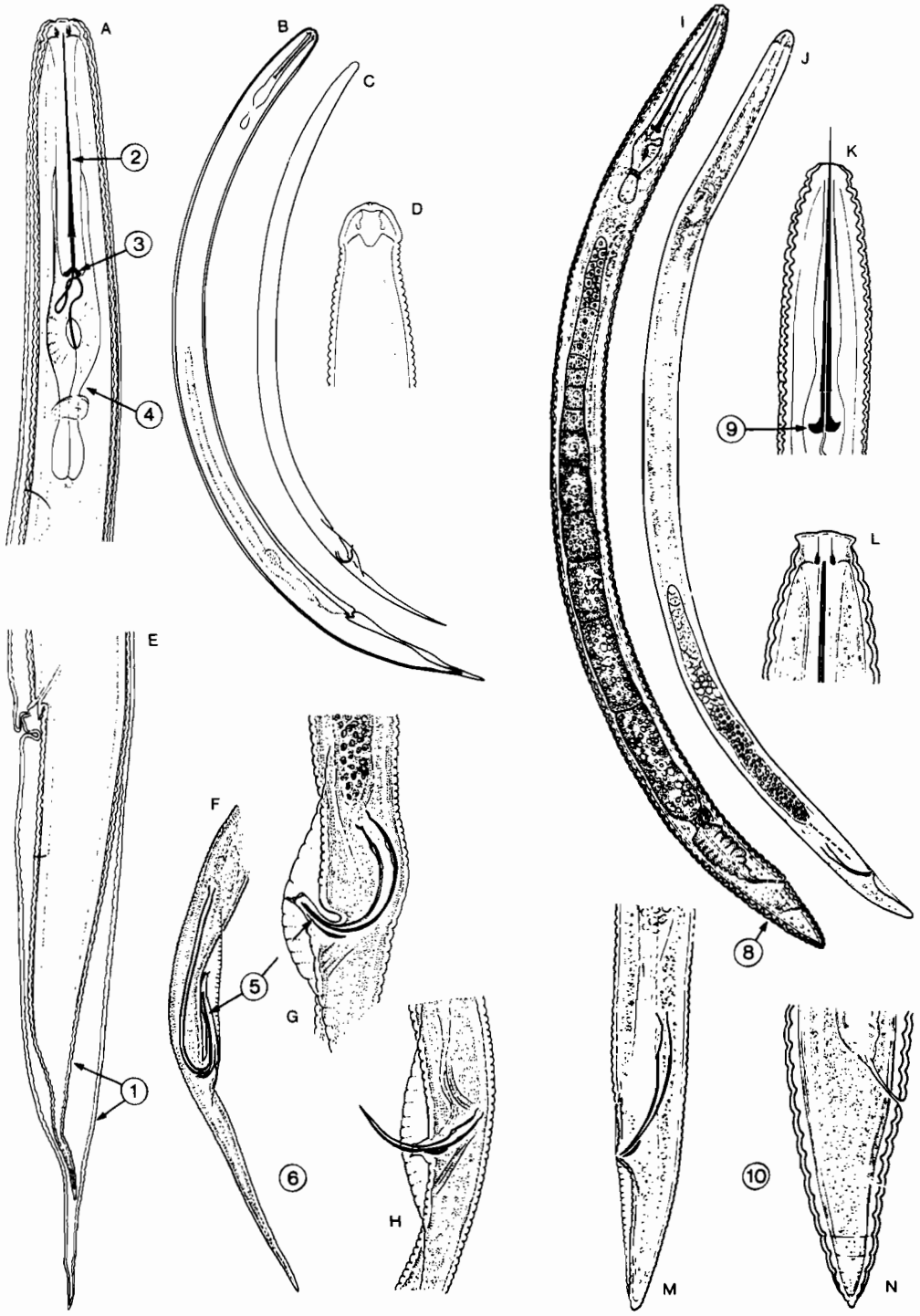
Major species: *H. cocophillus, H. mangiferae*

Confusable genera: *Caloosia, Hemicycliophora*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK (Set 7, No. 99).

Fig. 8. *Hemicycliophora chathami*. A: female oesophagus; B: entire female; C: entire male; D: male head; E: female posterior region; G: male tail. *H. penetrans*. F: male tail. *H. thienemanni*. H: male tail. *Hemicriconemoides mangiferae*. I: entire female; J: entire male; L: female head; M: male tail; N: female tail. *H. chitwoodi*. K: female stylet.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Trichodorus Cobb, 1913

Systematic position: Diphtherophorina, Trichodoridae

Morphology: Body stout, 0.8–1.2 mm long, **cigar shaped** (1). Cuticle smooth. Head continuous with body contour; papillae prominent. **Onchiostyle** (= stylet) **tripartite, curved** (2). **Oesophagus anteriorly slender with a posterior bulboid expansion** (3). Female: vulva median with **strong vaginal sclerotization** (4), **one pair of lateral body pores present within one body width of vulva** (5). Typically two genital tracts present, but very rarely only one is present (= '*Monotrichodorus*'). **Tail rounded, very short** (6) with anus almost terminal (7). Male: spicules arcuate, gubernaculum present. **Protractor muscles conspicuous, of unusual form** (8) and encapsulating the spicule shafts. Ventral supplements present, **bursa** usually **absent or very small** if present.

Synonym: *Monotrichodorus*

Paratrichodorus Siddiqi, 1974

Morphology: Very similar to *Trichodorus* but **cuticle markedly swelling with acid fixation** (9). Female: **vulva with weak vaginal sclerotization** (10). **No lateral body pores within one body width of vulva** (11). Male: **spicule protractor muscles inconspicuous. Bursa present** (12).

Synonyms: *Atlantadorus, Nanidorus*

Biology: Ectoparasitic on the roots of perennial and woody plants. The main area of attack is just behind the root tip, restricting root elongation. The root tip is then attacked as are lateral root initials as they form. The characteristic 'stubby-root' syndrome results. Both genera are more common in light or sandy soils and highest densities tend to occur at depths of 30–40 cm. Some species are known to be virus vectors and it is likely that the other species are potential vectors.

Major species: *T. primitivus, T. similis, T. viruliferus, P. minor, P. pachydermus.*

Distribution: Worldwide. *Trichodorus* tends to be more temperate whilst *Paratrichodorus* is more tropical.

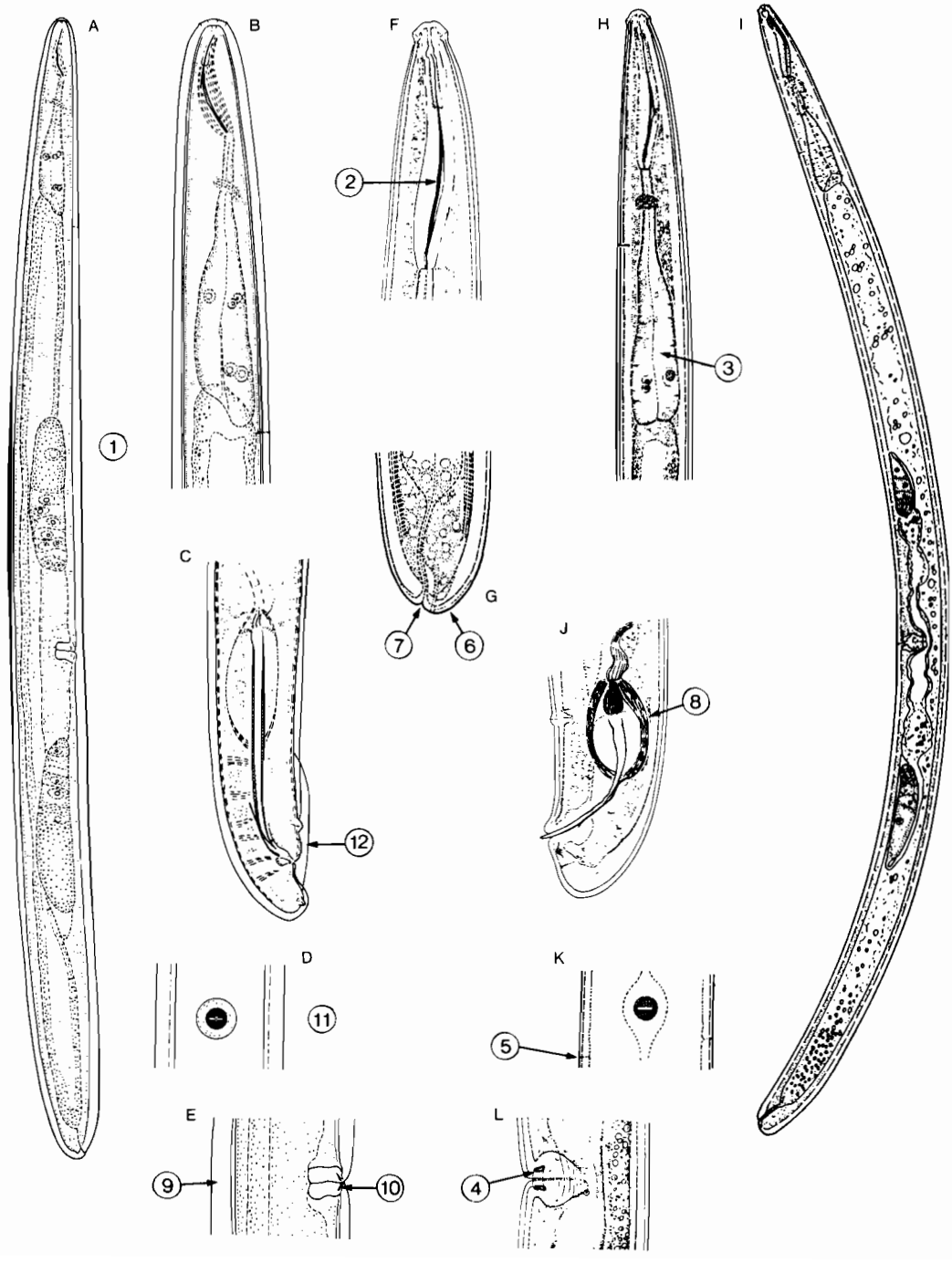
Confusable genera: each other

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes. Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 15; Set 4, No. 59; Set 6, No. 86; Set 7, No. 103; Set 8, No. 112

Decraemer, W. (1980) Systematics of the Trichodoridae (Nematoda) with keys to their species. *Revue de Nématologie 3*: 81–99.

Fig. 9. *Paratrichodorus minor*. A: entire female; B: oesophagus; C: male tail; D: vulva, ventral view; E: vulva, lateral view. *Trichodorus primitivus*. F: head region; H: oesophagus; J: male tail; L: vulva lateral view. *T. similis*. G: female tail; K: vulva, ventral view. *T. viruliferus*. I: entire female.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Xiphinema Cobb, 1913

Systematic position: Dorylaimina, Longidoridae

Morphology: Slender nematodes, 1.5–5 mm long. Head region continuous or offset. **Amphidial apertures a broad slit** (1) leading back to a **funnel-shaped pouch** (2). **Stylet very long** (60–250 μm) consisting of an anterior **odontostyle** (3) which is **needle-like** and has a **forked base** (4) and a posterior **odontophore** (5) with **three prominent basal flanges** (6). **Stylet guiding ring located in posterior half of odontostyle** (7). Oesophagus consisting of a long, narrow, procorpus and a short, glandular, bulb. Female: vulva usually at 40–50% but may be more anterior. Usually two genital tracts, but when the vulva is more anterior only the posterior tract remains. Tail very variable from short and rounded to long filiform. Male: spicules very powerful, arcuate. Ventral supplements form a pre-cloacal row.

Longidorus Micoletzky, 1922

Morphology: Similar to *Xiphinema* but body thinner and may be up to 11 mm long. **Amphids pouch-like** (8) and **opening via a minute, inconspicuous pore. Odontostyle/odontophore junction not forked** (9), **odontophore lacks flanges** (10) and both parts are less strongly cuticularized. **Guide ring in anterior half of odontostyle** (11).

Paralongidorus Siddiqi, Hooper & Khan, 1963

Morphology: Similar to *Longidorus*, but amphids and amphidial aperture (12) as for *Xiphinema*.

Synonym: *Siddiqia*

Biology: Long lived migratory ectoparasites attacking a wide variety of hosts. The favoured point of attack is at or near the root tip leading to hooked root-tips and/or terminal galls. Attacked root systems are stunted, lack developed laterals and show necrosis at the feeding sites. *Xiphinema* tends to be more abundant under woody hosts whereas *Longidorus* and *Paralongidorus* are more common under non-woody plants, particularly grasses and cereals. Greatest populations are found below 30 cm. With few exceptions, sandy soils support higher populations than heavier clays. Some species have been shown to be virus vectors. Reproduction is amphimictic or parthenogenetic.

Major species: *X. americanum* sensu lato, *X. index, X. elongatum, L. africanus, L. laevicapitatus, P. australis*

Distribution: *Longidorus* is mainly found in cooler areas whilst *Xiphinema* and *Paralongidorus* are more tropical.

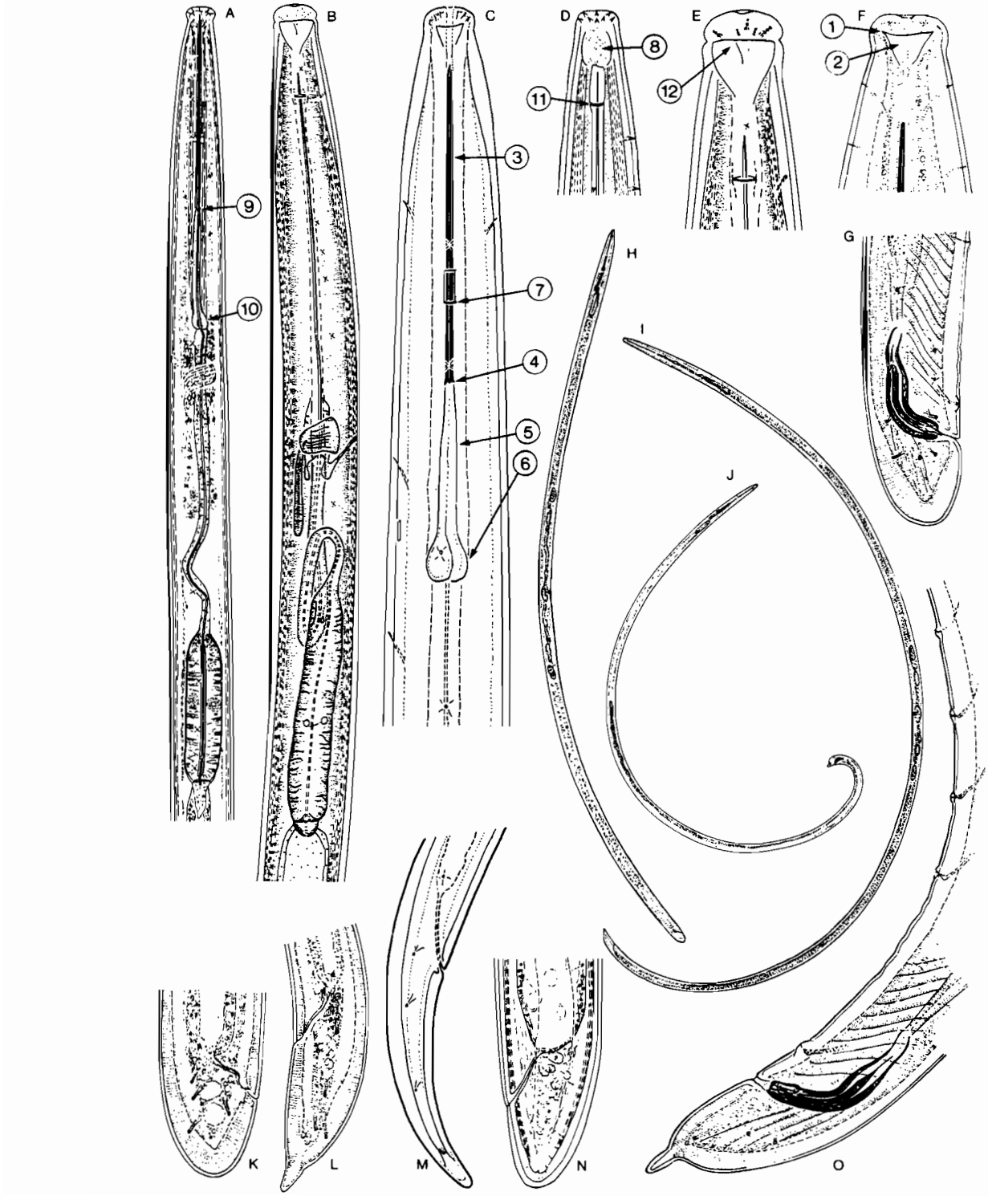
Confusable genera: each other

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes. Sets 1–8. CAB International, Wallingford, UK (Set 2, No. 29; Set 3, No. 45; Set 8, No. 117).

Loof, P. A. A. & Luc, M. A revised polytomous key for the identification of species of the genus *Xiphinema*, Cobb, 1913 (Nematoda: Longidoridae) with exclusion of *X. americanum* group. *Systematic Parasitology* (in press).

Fig. 10. *Longidorus fursti*. A: oesophagus; N. female tail. *L. elongatus*. D: head region. *Paralongidorus natalensis*. B: oesophagus; E: head region. *Xiphinema diversicaudatum*. J: entire male *X. heynsi*. G. male tail; H: entire female; K: female tail. *X. mammatum*. O: male tail. *X. neobasiri*. F: head region; I: entire female; L. female tail. *X. savanicola*. C: oesophagus; M: female tail.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Helicotylenchus Steiner, 1945

Systematic position: Tylenchina, Hoplolaimidae.

Morphology: Small to medium-sized nematodes (0.4–1.2 mm) **usually dying in a spiral** (1) (rarely C-shaped) on heat relaxation. Head region conoid-rounded, rarely truncate, sclerotization moderate. **Stylet well-developed, usually 3–4 times the lip width in length** (2) and with rounded or cup shaped knobs. **Opening of dorsal oesophageal gland duct 25–50% of stylet length posterior to knobs** (3). **Oesophageal gland lobe overlapping intestine mainly ventrally** (4). Female: **vulva posterior** (5) (60–70%), **both genital tracts usually fully developed**, posterior branch rarely reduced and non-functional (= "*Rotylenchoides*") . Tail short, usually dorsally convex-conoid or hemispherical. A terminal projection may be present. **Phasmids small, dot-like** (7). Male: Tail short (8), spicules well developed, arcuate. Bursa reaching tail tip.

Biology: Ecto-parasitic, semi-endoparasitic or endoparasitic nematodes of roots. All stages can be found in the root cortex but migration through the tissues has not been reported. Small lesions are formed which become necrotic as secondary invasion proceeds. Polyphagous. Most species are parthenogenetic but one of the commonest and most damaging species, *H. multicinctus*, is bisexual.

Major species: *H. dihystera, H. erythrinae, H. mucronatus, H. multicinctus, H. pseudorobustus.*

Distribution: Throughout the tropical and subtropical areas.

Synonym: *Rotylenchoides*

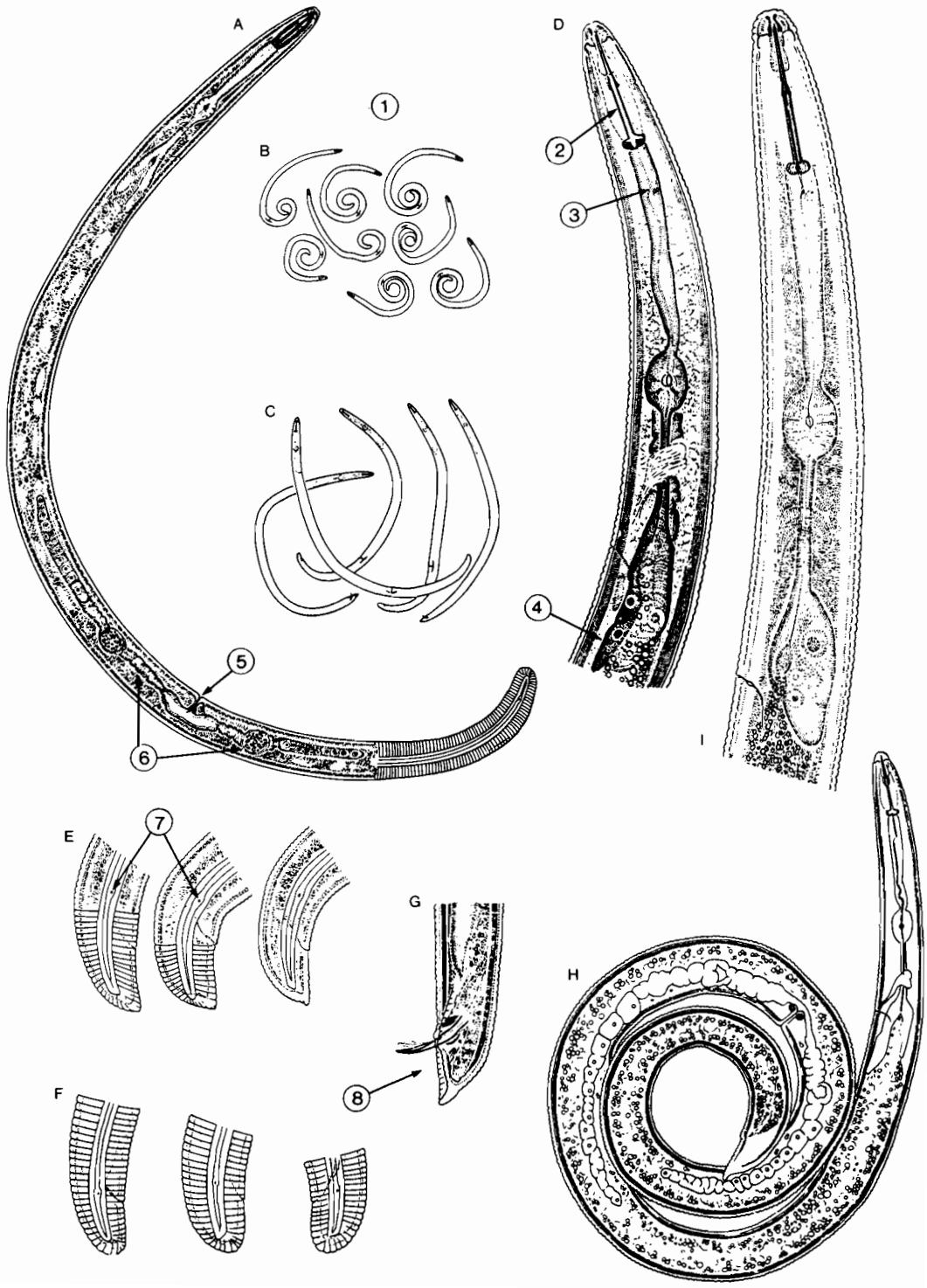
Confusable genus: *Rotylenchus* (has dorsal oesophageal gland duct opening more anterior and dorsal overlap of gland lobe).

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 9; Set 2, No. 23; Set 8, No. 109).

Boag, B. & Jairajpuri, M. S. (1985). *Helicotylenchus scoticus* n.sp. and a conspectus of the genus *Helicotylenchus* Steiner, 1945 (Tylenchida: Nematoda). *Systematic Parasitology* 7: 47–58.

Fig. 11. *Helicotylenchus dihystera*. B: females; E: female tails. *H. multicinctus*. A: entire female; C: males and females. F: female tails; G: male tail. *H. pseudorobustus*. D: oesophagus; H: entire female. *Rotylenchus buxophilus*. I: oesophagus.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Hoplolaimus von Daday, 1905

Systematic position: Tylenchina, Hoplolaimidae

Morphology: Nematodes of medium length (1–2 mm) dying slightly curved ventrally on application of gentle heat. **Head region high, offset, rounded and with massive sclerotization** (1). Basal lip annule may be divided into small squares. **Stylet massive, 40–50 µm long, with well developed basal knobs bearing anterior tooth-like projections** (2). **Oesophagus** well-developed **with a dorsally overlapping gland lobe** (3) containing 3 or 6 nuclei. Female: vulva median, genital system consisting of two opposed tracts. Tail short, bluntly rounded. **Phasmids enlarged to form scutellae, one being between the anus and the vulva** (4) **and the other anterior to the vulva** (5). Male: tail short, spicules well-developed, arcuate. Bursa extending to tail tip. **Scutellae situated at similar relative positions to the female.**

Major species: *H. columbus, H. indicus, H. pararobustus, H. seinhorsti*

Synonyms: *Basirolaimus, Hoplolaimoides*

Scutellonema Andrássy, 1958

Morphology: Small to medium sized nematodes (0.3–1.5 mm) usually dying in a C-shape or open spiral, **Head region with moderate sclerotization** (6). **Stylet of medium development with rounded knobs** (7). **Oesophagus with dorsal overlap**. Female: vulva median with two opposed genital tracts. Tail short, bluntly rounded. Phasmids enlarged to form **scutellae which are opposite one another and either on or very near to the tail** (8). Male: tail short, spicules well-developed, arcuate. Bursa extending to tail tip. **Scutellae opposite one another on tail region.**

Major species: *S. brachyurus, S. bradys, S. cavenessi*

Aorolaimus Sher, 1964

Morphology: Similar to *Scutellonema* in general characters but females differ in having the **scutellae well anterior to the anus (yet posterior to the vulva)** (9) and **not opposite one another**. Males have a similar arrangement of the scutellae and the **bursa is large, often extending beyond the tail tip as two lobes** (10).

Major species: *A. luci*

Synonym: *Peltamigratus* Sher, 1964

Biology: All three genera are migratory endoparasites of roots and/or tubers. Most species are polyphagous. Reproduction can be amphimictic or parthenogenetic. *Scutellonema bradys* causes a serious dry rot of yam tubers.

Distribution: Widespread in tropical and subtropical areas although *Aorolaimus* is more restricted to S. America and parts of Africa.

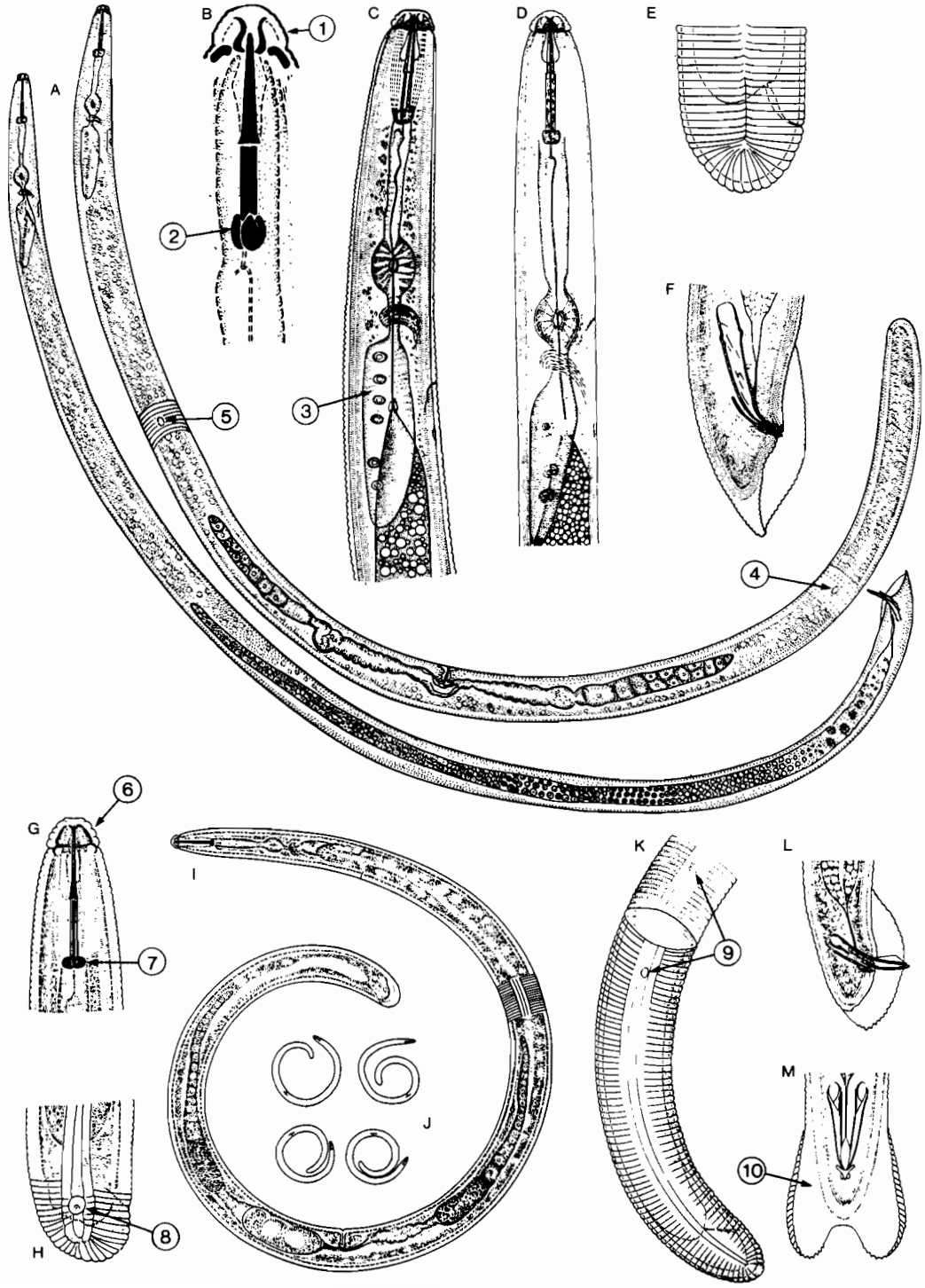
Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 10; Set 3, No. 33; Set 4, No. 54; Set 5, No. 66; Set 6, Nos. 76, 81).

Bittencourt, C. & Huang, C. S. (1986) Brazilian *Peltamigratus* Sher, 1964 (Nematoda: Hoplolaimidae), with descriptions of six new species. *Revue de Nématologie 9*: 3–24.

Germani, G., Baldwin, J. G., Bell, A. H. & Wu, X. Y. (1985). Revision of the genus *Scutellonema* Andrássy, 1958 (Nematoda: Tylenchida). *Revue de Nématologie 8*: 289–320.

Fig. 12. *Aorolaimus luci*. K: posterior region; L,M: male tails. *Hoplolaimus indicus*. A: adults; C: oesophagus. *H. pararobustus*. D: oesophagus; E: female tail; F: male tail. *H. seinhorsti*. B: stylet. *Scutellonema brachyurus*. G: head region; H: female tail; I,J: adult females.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Pratylenchus Filipjev, 1936

Systematic position: Tylenchina, Pratylenchidae

Morphology: Small nematodes (less than 1 mm long) dying slightly curved ventrally on application of gentle heat. **No marked sexual dimorphism in form of anterior region** (1). **Head region low, flattened** (2), usually appearing as a flat, black cap under the stereomicroscope. Lip region divided into 2, 3 or 4 annules and continuous with the body contour; strongly sclerotized. Stylet 20 µm or less in length (i.e. about twice the head width) moderately sclerotized and with rounded or anteriorly concave knobs. Oesophagus equally developed in both sexes, median bulb well-developed; **oesophageal gland lobes overlapping the intestine ventrally** (3). Female: **vulva well posterior at 70–80% of body length** (4); genital system with a single anteriorly directed tract and a variable post-vulval section which may show some differentiation but is never functional (5) (**mono-prodelphic**); spermatheca oval or round and usually filled with sperm in bisexual species; **tail sub-cylindrical or more or less conoid with a broad to narrowly rounded** (6) **or truncate terminus** (7) which may be smooth (8) or annulated (9). Male: tail short, dorsally convex-conoid; **bursa extending to tail tip** (10); spicules slender, arcuate.

Biology: Migratory endoparasites with all stages found in the root cortex. Low soil populations can be associated with high root populations. The nematodes feed mainly on cortex cells and form cavities containing 'nests' or colonies of nematodes of all stages. Discolouration of affected tissues is usually pronounced. Above ground symptoms of attack include chlorosis and stunting.
Some species reproduce sexually while others are parthenogenetic. The life-cycle can be completed in three to four weeks and the nematodes can survive in the absence of host plants for several months. Most important species are polyphagous, although *P. goodeyi* may be restricted to banana.

Major species: *P. brachyurus, P. coffeae, P. goodeyi, P. penetrans, P. zeae*

Distribution: *P. brachyurus, P. coffeae* and *P. zeae* are widely distributed in tropical and subtropical areas; *P. penetrans* mainly in cooler regions of the tropics; *P. goodeyi* on banana in Crete and the Canary Islands and in the cooler areas of Ethiopia, Kenya, Tanzania, Uganda and Burundi.

Confusable genus: *Radopholus*

Useful Literature

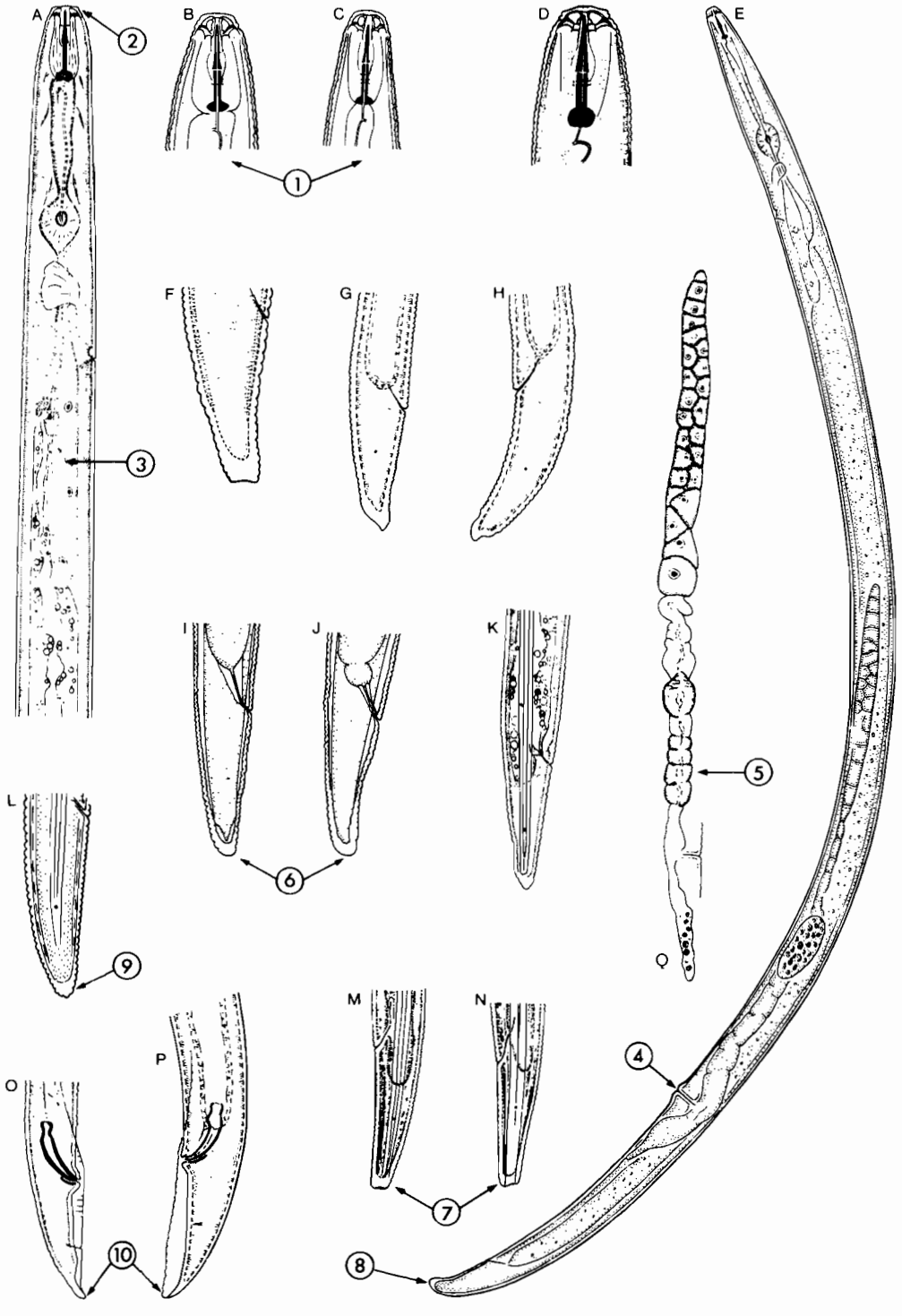
CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 6; Set 2, No. 25; Set 6, Nos. 77, 89; Set 8, No. 120).

Café Filho, A. C. & Huang, C. S. (1989) Description of *Pratylenchus pseudofallax* n.sp. with a key to species of the genus *Pratylenchus* Filipjev, 1936 (Nematoda: Pratylenchidae) *Revue de Nématologie, 12*: 7–15.

Handoo, Z. A. & Golden, A. M. (1989). A key and diagnostic compendium to the species of the genus *Pratylenchus* Filipjev, 1936 (Lesion nematodes). *Journal of Nematology, 21*: 202–218.

Loof, P. A. A. (1978). The genus *Pratylenchus* Filipjev, 1936 (Nematoda: Pratylenchidae): a review of its anatomy, morphology, distribution, systematics and identification. *Vaxskyddsrapporter, Jordbruk 5* Uppsala. Sweden, 50 pp.

Fig. 13. *Pratylenchus zeae*. A: oesophagus; K: female tail; O: male tail; Q: female genital tract. *P. vulnus*. B: female head; C: male head. *P. brachyurus*. D: female head; F: female tail. *P. pratensis*. E: entire female; L: female tail. *P. goodeyi*. G,H: female tail. *P. coffeae*. M,N: female tail. *P. penetrans*. I, J: female tail.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Hirschmanniella Luc & Goodey, 1963

Systematic position: Tylenchina, Pratylenchidae

Morphology: Medium-sized to long, slender nematodes (1–4 mm) dying more or less straight or ventrally arcuate (1) on application of gentle heat. No marked sexual dimorphism in form of anterior region (2). **Head region** continuous with body contour, **hemispherical** (3) **or anteriorly flattened** (4). Stylet strongly developed (15–46 μm) with rounded basal knobs. **Oesophageal glands elongate and overlapping the intestine in a long ventral lobe** (5). Female: **vulva median** (6); **genital system with two functional and equally developed genital tracts** (7), one anteriorly and one posteriorly, directed; **tail elongate, conoid** (8), **terminal mucron often present** (9). **Male tail similar to female** (10); **bursa not reaching to tail tip** (11), spicules slender, arcuate.

Biology: Migratory endo-parasites, mainly of roots, but also corms and rhizomes, where they move freely through the tissues. Eggs are laid within the root and development to the adult takes about 5–6 weeks. The genus is associated with aquatic environments – marsh, freshwater and marine. Most species are bisexual.

Major species: *H. mexicana (= caudacrena), H. imamuri, H. miticausa, H. mucronata, H. oryzae, H. spinicaudata*

Distribution: The genus is distributed worldwide in suitable habitats. *H. oryzae* is the major species and is well-distributed in the rice-growing areas of India, Bangladesh, Malaysia, Indonesia, Philippines, Japan. It is also found in parts of Africa and South America.

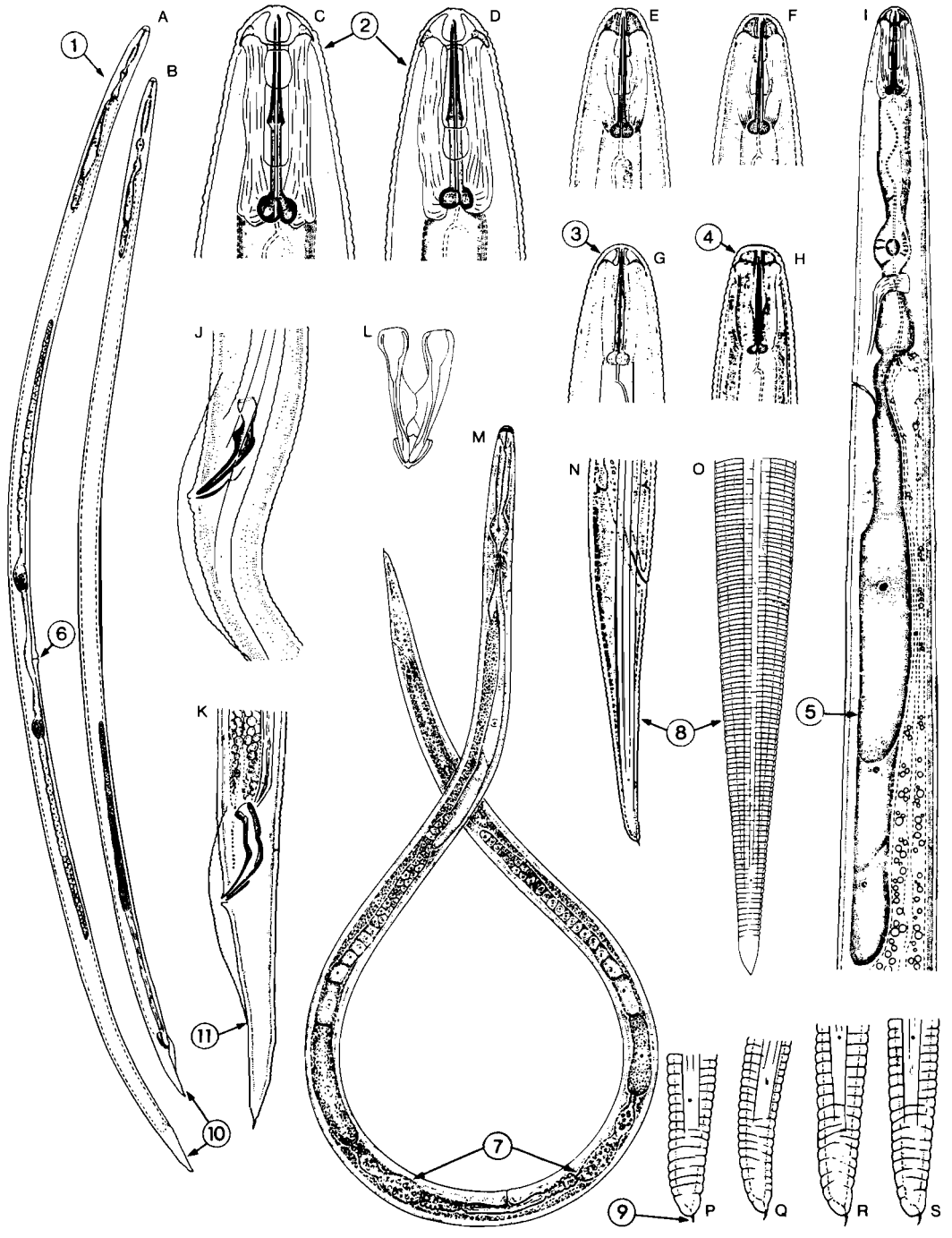
Confusable genus: *Radopholus*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 2, No. 26; Set 5, No. 68).

Ebsary, B. A. & Anderson, R. V. (1982). Two new species of *Hirschmanniella* Luc & Goodey, 1963 (Nematoda: Pratylenchidae) with a key to nominal species. *Canadian Journal of Zoology, 60*: 530–535.

Fig. 14. *Hirschmanniella spinicaudata*. A: entire female; B: entire male; C: female head; D: male head; I: oesophagus; K: male tail; L: spicules. *H. oryzae*. H: female head; N: female tail; P-S; female tail terminus. *H. magna*. E: female head; F: male head; J: male cloacal region. *H. mucronata*: female head. *H. nana*. (= *H. oryzae*). M: entire female. *H. diversa*. O: female tail.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Radopholus Thorne, 1949

Systematic position: Tylenchina, Pratylenchidae

Morphology: Small nematodes (less than 1 mm long) dying more or less straight or slightly curved ventrally on application of gentle heat. **Marked sexual dimorphism in form of anterior region** (1): female head region low, rounded, continuous or slightly offset from body contour; male head region higher, often knob-like and more offset. **Male cephalic sclerotization, stylet and oesophagus reduced** (2); female cephalic sclerotization strong, stylet and oesophagus well-developed (3). Median bulb in female oesophagus well-developed and **oesophageal glands overlapping the intestine mostly dorsally** (4). Female: **vulva median** (5), **usually with two functional and equally developed genital tracts** (6) but posterior tract may be reduced, spermathecae rounded and with sperm in bisexual species; **tail elongate** (7), conoid (about 60 µm long in *R. similis*). Male: **tail elongate** (8), conoid, ventrally arcuate; **bursa not reaching to tail tip** (9) in *R. similis* and most other species; spicules slender, arcuate.

Biology: Migratory endoparasites of root and corm/tuber tissues. In roots the feeding activities are restricted to the cortex causing cavitation, discolouration and severe damage allowing secondary invasion by other micro-organisms. The adult male is non-feeding. The major species is *R. similis* which has two recognised host races or biotypes. *R. similis similis* attacks banana and many other plants, but not citrus, whereas *R. similis citrophilus* (recognised as a separate species by some authorities on differing chromosome count and minor morphological details) attacks both citrus and banana as well as a variety of other plants. However, it is possible that *R. similis similis* includes a range of host races.

Major species: *R. similis similis, R. similis citrophilus*

Distribution: The majority of species have been described from Australasia. However, *R. similis similis* is found worldwide in tropical regions and occurs virtually everywhere that banana is grown. *R. similis citrophilus* is only recorded from Florida at present.

Synonyms: *Neoradopholus, Radopholoides*

Confusable genera: *Achlysiella, Pratylenchus, Hirschmanniella.*

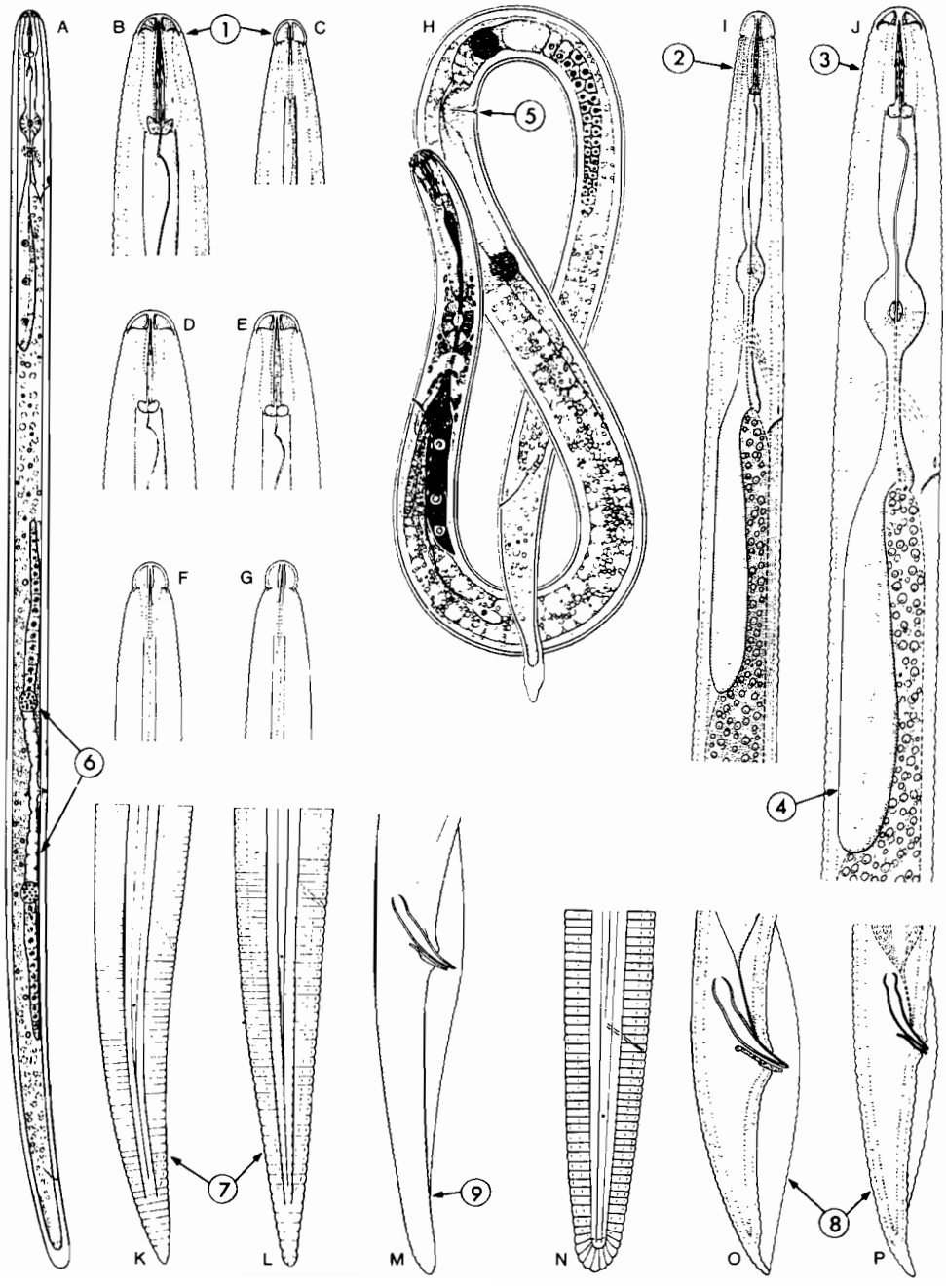
Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 2, No. 27).

Colbran, R. C. (1970) Studies of plant and soil nematodes. 15. Eleven new species of *Radopholus* Thorne and a new species of *Radopholoides* de Guiran (Nematoda: Tylenchoidea) from Australia. *Queensland Journal of Agricultural and Animal Sciences, 27*: 437–460.

Sher, S. A. (1968) Revision of the genus *Radopholus* Thorne, 1949 (Nematoda: Tylenchoidea). *Proceedings of the Helminthological Society of Washington, 35*: 219–237.

Fig. 15. *Radopholus similis*. D,E: female head; F,G: male head; H: entire female; K,L: female tails; M: male tail. *R. rotundisemenus*. A: entire female. *R. inaequalis*. B: female head; C: male head; N: female tail; O: male tail. *R. vangundyi*. I: male oesophagus; J: female oesophagus; P: male tail.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Heterodera Schmidt, 1871

Systematic position: Tylenchina, Heteroderidae

Morphology: Sexually dimorphic. Female: obese, **lemon-shaped**, 300–600 µm, in diameter with a distinct neck (1) and either partially enclosed in root tissue or in the soil. **Vulva subterminal, near anus. Cuticle thick**, whitish at first but **tanning** to a **brownish-black colour** as the **cyst matures. Eggs retained within the protective cyst. Vulva and anus located** on a **terminal cone** with **two** translucent areas, the **fenestrae**, on **either side of the vulval slit** (2). Two convoluted genital tracts. In young females the excretory pore can be seen at the level of, or posterior to, the median bulb valve plates (3). **Male: vermiform** with the **body often twisted through 180° on heat relaxation**; found free in soil. Stylet and head skeleton robust. **Tail short**, hemispherical. **Spicules opening subterminally** (4). **No bursa**. Juvenile (J2): vermiform, 450–600 µm long. **Stylet and head skeleton robust** (5), **tail** conical **with hyaline area starting well before tail terminus** (6).

Synonym: *Bidera*.

Globodera Skarbilovich, 1959

Morphology: Similar to *Heterodera* but the **cyst is globose** (7) (i.e. the vulva and anus are not on a terminal cone) and the **vulval slit** is **surrounded by a single, circular, fenestra** (8).

Biology: In most species all the eggs are retained within the mature cyst, although in some a few eggs are also held in an external gelatinous matrix. Eggs often hatch in response to root exudates from a host plant, although other hatching factors can be involved. The J2 emerges from the egg, invades a root and induces a feeding site composed of syncitial nurse cells. Root galling is not induced. The J2 swells and moults three times to form the adult female which enlarges rapidly, the posterior region bursting through the root epidermis. Males are more commonly produced when food is in short supply. They assume a vermiform state within the J4 cuticle before burrowing out of the root into the soil. Females produce several hundred eggs, and after death, the cuticle of the female tans to form a protective cyst.

Major species: *H. avenae, H. cajani, H. ciceri, H. glycines, H. latipons, H. sacchari, G. pallida, G. rostochiensis*

Distribution: Most *Heterodera* species are more tropical or subtropical whereas *Globodera* species tend to be confined to the cooler areas.

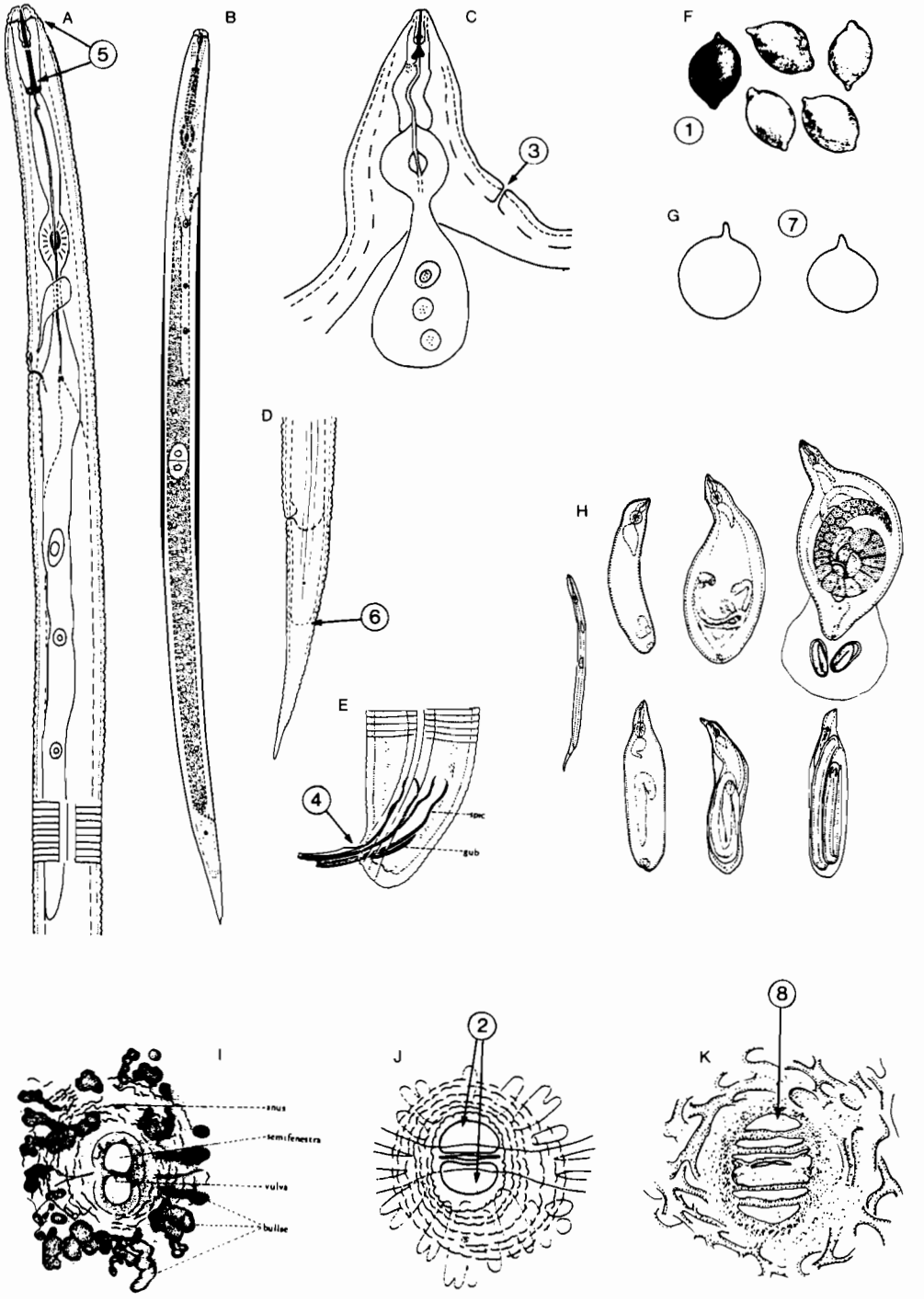
Confusable genera: *Cactodera, Punctodera*. J2 infectives can be confused with those of *Meloidogyne*.

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes. Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 2; Set 2, Nos 16, 17; Set 4, No. 48; Set 8, No. 118).

Golden, A. M. (1986). Morphology and identification of cyst nematodes. In: *Cyst Nematodes*. Ed. Lamberti & Taylor, NATO ASI Series, Plenum Press, London, pp. 23–46.

Fig. 16. *Globodera rostochiensis*. C: female anterior region; G: entire cysts; K: perivulval area. *Heterodera avenae*. E: male tail; F: cysts; I: perivulval area. *H. glycines*. J: perivulval area. *H. oryzae*. D: juvenile tail. *H. sacchari*. A: J2 oesophagus; B: juvenile (J2 infective). *H. schachtii*. H: developmental stages.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Meloidogyne Goeldi, 1887

Systematic position: Tylenchina, Heteroderidae

Morphology: Sexually dimorphic. **Female: embedded in root tissue, globose**, 0.5–0.7 mm in diameter **with a slender neck** (1). **Vulva subterminal near anus** (2). Cuticle whitish, thin, annulated. Stylet short, moderately sclerotized. Head skeleton weak. **Excretory pore anterior to median bulb valve plates** (3) and often near stylet base. Two convoluted genital tracts. **Eggs deposited outside the body in a gelatinous matrix. Male: vermiform** (4), free-living in soil, 1–2 mm long. **Body usually twisted through 180° along its length on heat relaxation. Stylet and head skeleton robust. Tail short** (5), hemispherical. Spicules robust. **Bursa absent**. Juveniles (J2): Slender, vermiform (6), about 450 µm long. **Stylet and head skeleton weakly sclerotized. Tail conical with hyaline portion starting near the tail tip** (7).

Biology: In most species the eggs are retained within a gelatinous matrix outside the swollen female body. On hatching the J2 invades a host root and induces a trophic system of giant cells. Cortical cells are also induced to multiply and so form the characteristic gall. The remainder of the life cycle is similar to *Heterodera/Globodera* except that, in most species, the females do not normally burst out of the root as they are surrounded by the gall tissue.

Major species: *M. arenaria, M. exigua, M. graminicola, M. incognita, M. javanica.*

Distribution: Widely distributed throughout the tropical and subtropical regions.

Synonym: *Hypsoperine*

Confusable genera: *Nacobbus, Heterodera/Globodera.* J2 infectives can be confused with those of *Heterodera/Globodera.*

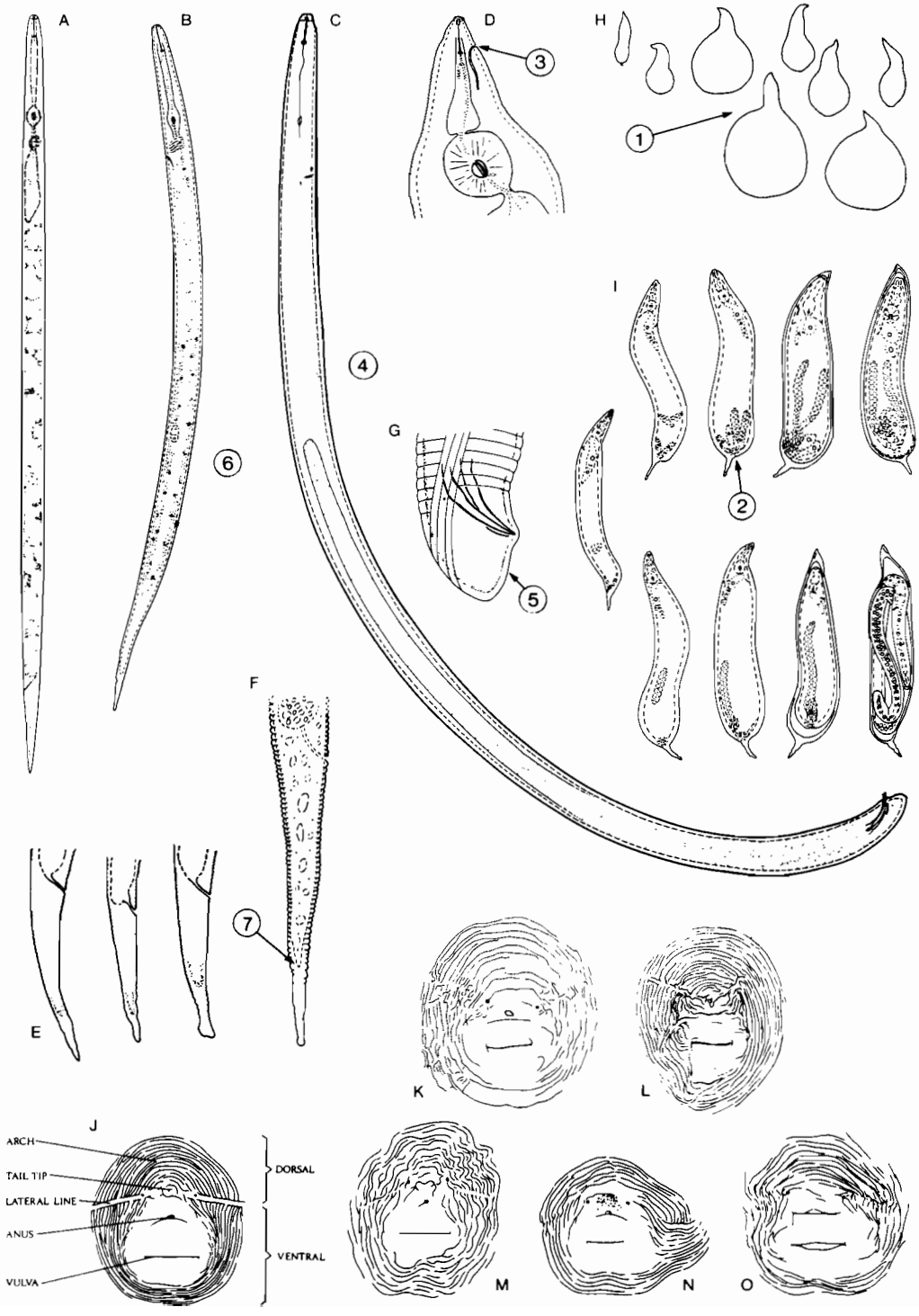
Useful Literature

CIH Descriptions of Plant-parasitic Nematodes. Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 3; Set 2, No. 18; Set 4, No. 49; Set 5, No. 62; Set 6, No. 87).

Jepson, S. B. (1987). *Identification of root-knot nematodes* (Meloidogyne *species*). CAB International, Wallingford, UK. 252pp.

Sasser, J. N. & Carter, C. C. (Editors) (1985). *An advanced treatise on* Meloidogyne. Vols. I & II. North Carolina State University, Raleigh, USA.

Fig. 17. *Meloidogyne arenaria*. O: perineal pattern. *M. chitwoodi*. C: male *M. exigua*. K: perineal pattern. *M. graminicola*. F: juvenile tail; L: perineal pattern. *M. hapla*. E: juvenile tails; N: perineal pattern. *M. incognita*. I: developmental stages of male and female; M: perineal pattern. *M. javanica*. A: J2 infective; H: development of female; J: perineal pattern. *M. naasi*. B: J2 infective; D: female oesophageal region.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Nacobbus Thorne & Allen, 1944

Systematic position: Tylenchina, Pratylenchidae

Morphology: Sexually dimorphic. Immature female (in soil or in roots). Vermiform, slender (1), 0.6–1 mm long. Labial area rounded, continuous with body contour. **Cephalic sclerotization strong** (2); **stylet robust, with rounded basal knobs** (3). Oesophagus with strong median bulb and strong valves; oesophageal glands long, dorsally overlapping the intestine (4). **Vulva posteriorly situated** (5) (V = 90–95%); vulval lips not protruding. **One anterior genital tract**. Tail short, rounded. Mature females: (in roots). **Body saccate; anterior and posterior portions tapering** (6). Genital tract convoluted, spermatheca axial, generally filled with sperm. Tail short. Male: Similar to immature female, except for sexual characters. Spicules curved. Tail short; **bursa reaching tail tip** (7). Juveniles: Resembling immature female.

Biology: The eggs are laid within a gelatinous matrix formed by the female. On hatching, the J2 invades a root, but does not form a fixed feeding site. Instead the juveniles migrate through the tissue and may even leave the root and enter another. The J3 and J4 stages are less mobile. After the final moult the immature female may leave the root and enter another before taking up a position near the vascular tissue and initiating a syncitial trophic system and gall formation. As the female develops, the posterior section extends towards the epidermis and an opening in the gall is formed through which the gelatinous matrix and eggs are extruded.

Major species: *N. aberrans, N. dorsalis*

Distribution: Known only from the Americas.

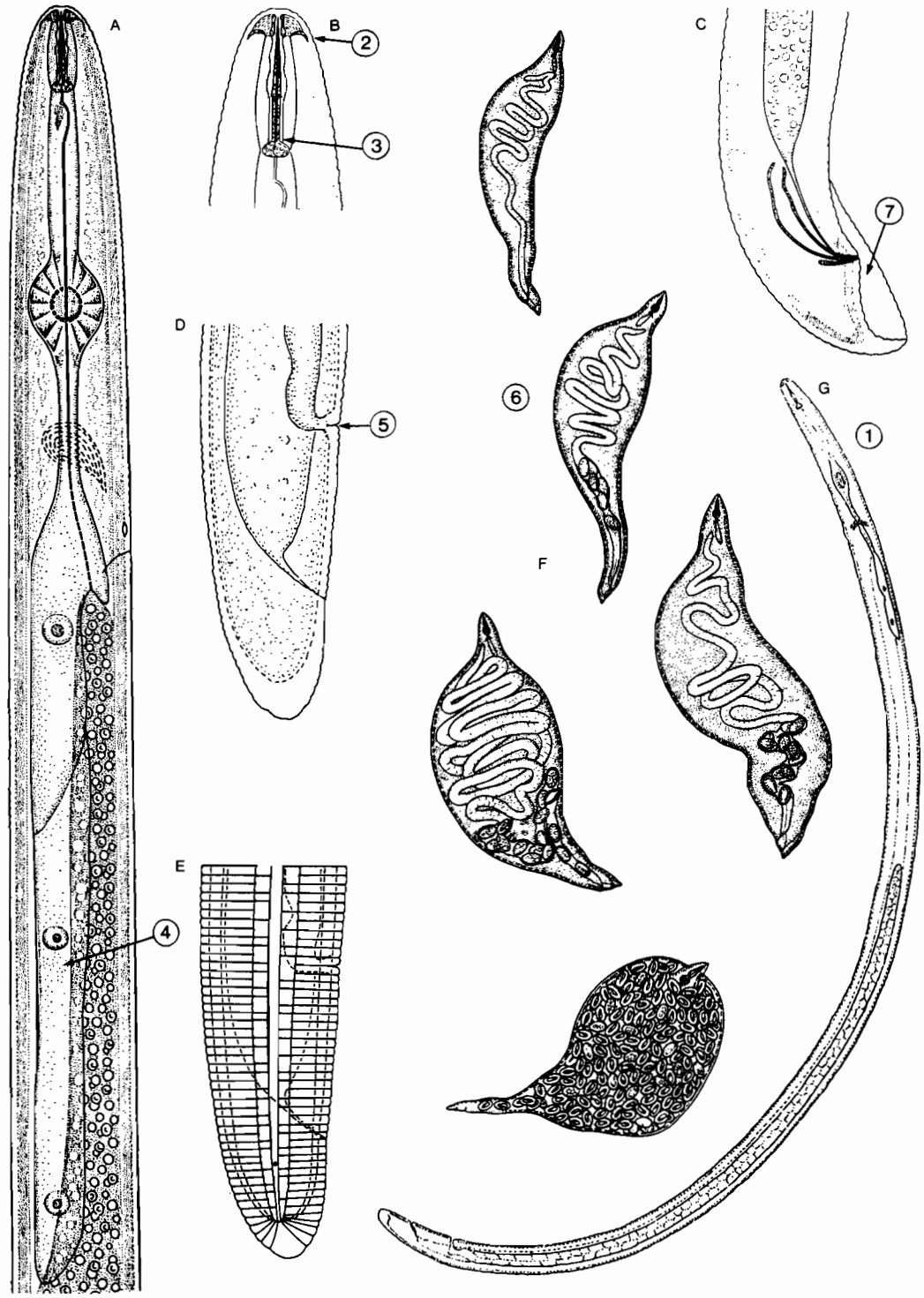
Confusable genus: *Meloidogyne*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 8, No. 119).

Doucet, M. E. (1989). The genus *Nacobbus* Thorne & Allen, 1944 in Argentina. 1. Study of a population of *N. aberrans* (Thorne, 1935) Thorne & Allen, 1944 on *Chenopodium album* L. from Rio Cuarto, Province of Cordoba. *Revue de Nématologie, 12*: 17–26.

Fig. 18. *Nacobbus aberrans*: Immature female. A: oesophagus; B: head; D,E: posterior region; G: entire. Male. C: tail. Mature female. F: developmental stages.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Rotylenchulus Linford & Oliveira, 1940

Systematic position: Tylenchina, Hoplolaimidae

Morphology: Sexually dimorphic. Immature female (free in soil): Body vermiform, small (0.23–0.64 mm), dying ventrally arcuate on application of gentle heat. **Head region** rounded to conoid, **continuous with body contour** (1), striated. Cephalic sclerotization of medium development. Stylet of medium strength, with rounded basal knobs. Oesophagus with well-developed median bulb and valves; dorsal oesophageal gland opening well posterior to stylet base (2) (0.6–1.9 times the stylet length); glands well developed with a long lateral overlap. **Vulva posteriorly situated** (V = 58–72); **vulval lips not protuberant** (3). **Two genital tracts**, each with a double flexure. Tail conoid, with rounded terminus. Mature female (on roots): **Swollen to kidney shaped body** (4). Anterior part irregular. **Vulval lips protruding** (5). Genital tracts convoluted. Male: Vermiform. Cephalic sclerotization, stylet and oesophagus reduced (median oesophageal bulb weak, without valves) but conspicuous. Spicules curved. **Tail pointed. Bursa not reaching tail tip**. Juvenile: Resembling immature female, but shorter, and lacking vulva and genital tracts.

Biology: The eggs are laid in a gelatinous matrix. On hatching the juveniles moult to the immature female or male without feeding. The immature female is the invasive stage, but only the anterior section penetrates the root tissue, the posterior part remaining in the soil and becoming obese (i.e. a sedentary semi-endoparasite). About 50 eggs are deposited in a gelatinous matrix which is secreted by specialized vaginal cells.

Major species: *R. borealis, R. parvus, R. reniformis*

Distribution: *R. reniformis* is almost ubiquitous in tropical and subtropical soils, but the other species are more restricted in their distribution.

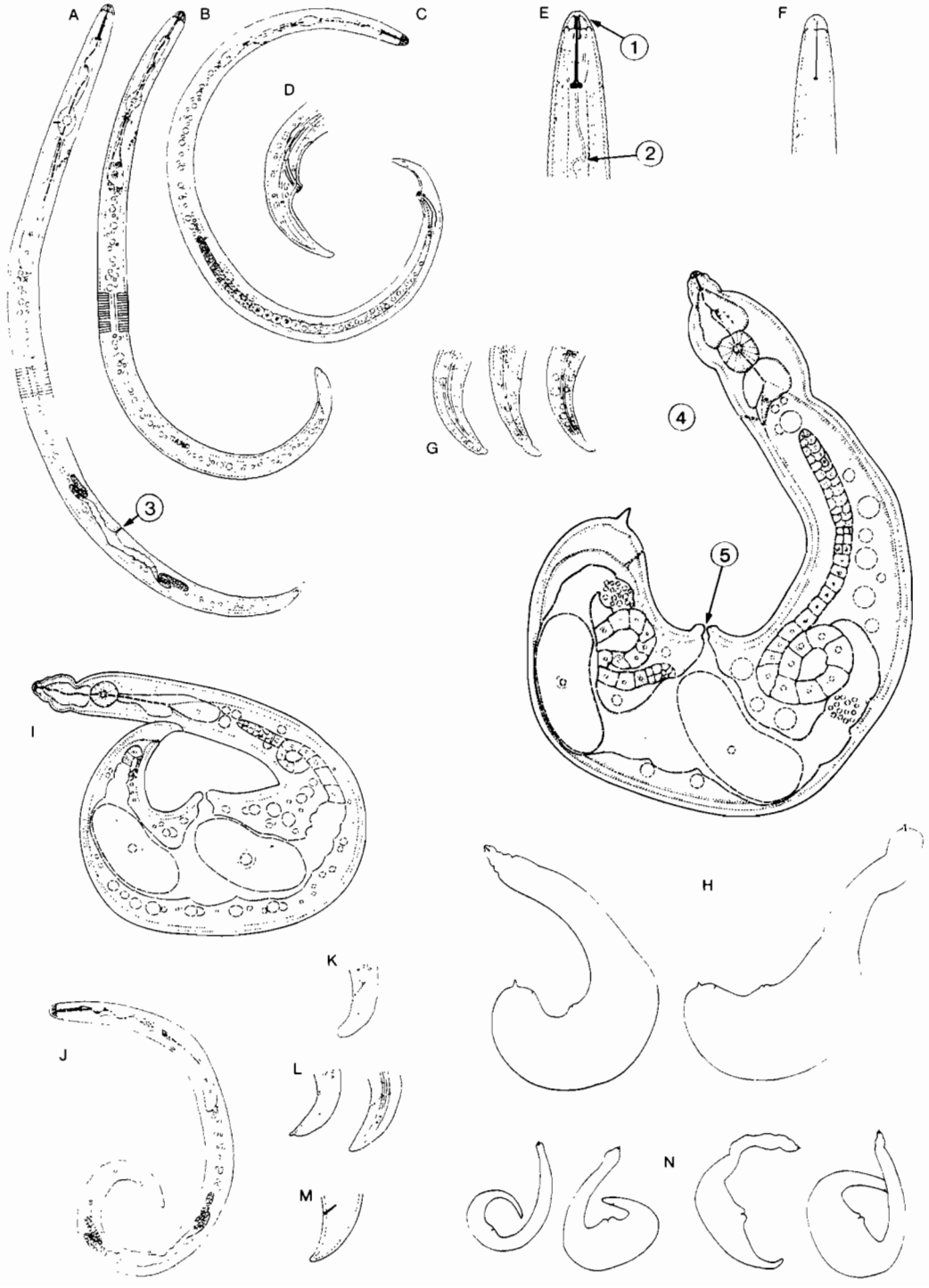
Confusable genus: *Senegalonema*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 5; Set 6, No. 83).

Dasgupta, D. R., Raski, D. J. & Sher, S. A. (1968). A revision of the genus *Rotylenchulus* Linford & Oliveira, 1940 (Nematoda: Tylenchidae) *Proceedings of the Helminthological Society of Washington. 35*: 169–192.

Fig. 19. *Rotylenchulus parvus*. I,N: mature females; J: immature female; K: juvenile tail; L,M: immature female tails. *R. reniformis*. A: immature female; B: juvenile; C: male; D: male tail; E: female head; F: male head; G: female tail development; H: mature females.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Tylenchulus Cobb, 1913

Systematic position: Tylenchina, Tylenchulidae

Morphology: Sexually dimorphic. Immature female (free in soil): Body vermiform, ventrally curved posteriorly, small (under 0.5 mm). Head region rounded, continuous with body contour. Cephalic sclerotization weak. **Stylet of medium development** (1) with rounded basal knobs. **Oesophagus with strong median bulb which is not well separated from the procorpus** (2); **glands forming a basal bulb** (3). **Vulva very posteriorly situated** (4); **genital tract single, anteriorly outstretched. Excretory pore very posteriorly situated** (5), slightly anterior to the vulva. Tail conical. **No anus or rectum.** Mature female: **Anterior part embedded in root tissue** (6), **irregular**, slender, **with thin cuticle** (7). **Posterior part**, bursting out of root, **swollen with very thick cuticle** (8) and a pointed postvulvar section; **excretory pore and vulva very posterior** (9). **Excretory cell well developed**, and producing a gelatinous matrix. Genital tract convoluted, with several eggs. **No anus, or rectum.** Male: Body vermiform, short and slender. **Cephalic sclerotization, stylet and oesophagus reduced** (10). Spicules slightly curved. **No bursa.** Tail conical, pointed. Juvenile: Body vermiform. Cephalic sclerotization, stylet and oesophagus similar to those of immature females. Tail long, pointed. Genital primordium differently shaped in male and female juveniles from J2 onwards.

Biology: The eggs are contained in a gelatinous matrix which is produced by the excretory cell. After hatching, male juveniles moult to the adult without feeding whilst female juveniles feed on cortical cells. The immature female penetrates deeper into the root, the anterior end reaching deep into the cortex whilst the posterior section remains in the soil and becomes obese. A highly sophisticated system of trophic nurse cells is initiated around the female head. [Note: a heavily infested citrus root, when carefully rinsed in water, retains a collar of earth adhering to the gelatinous egg-sacs underneath].

Major species: *T. semipenetrans*

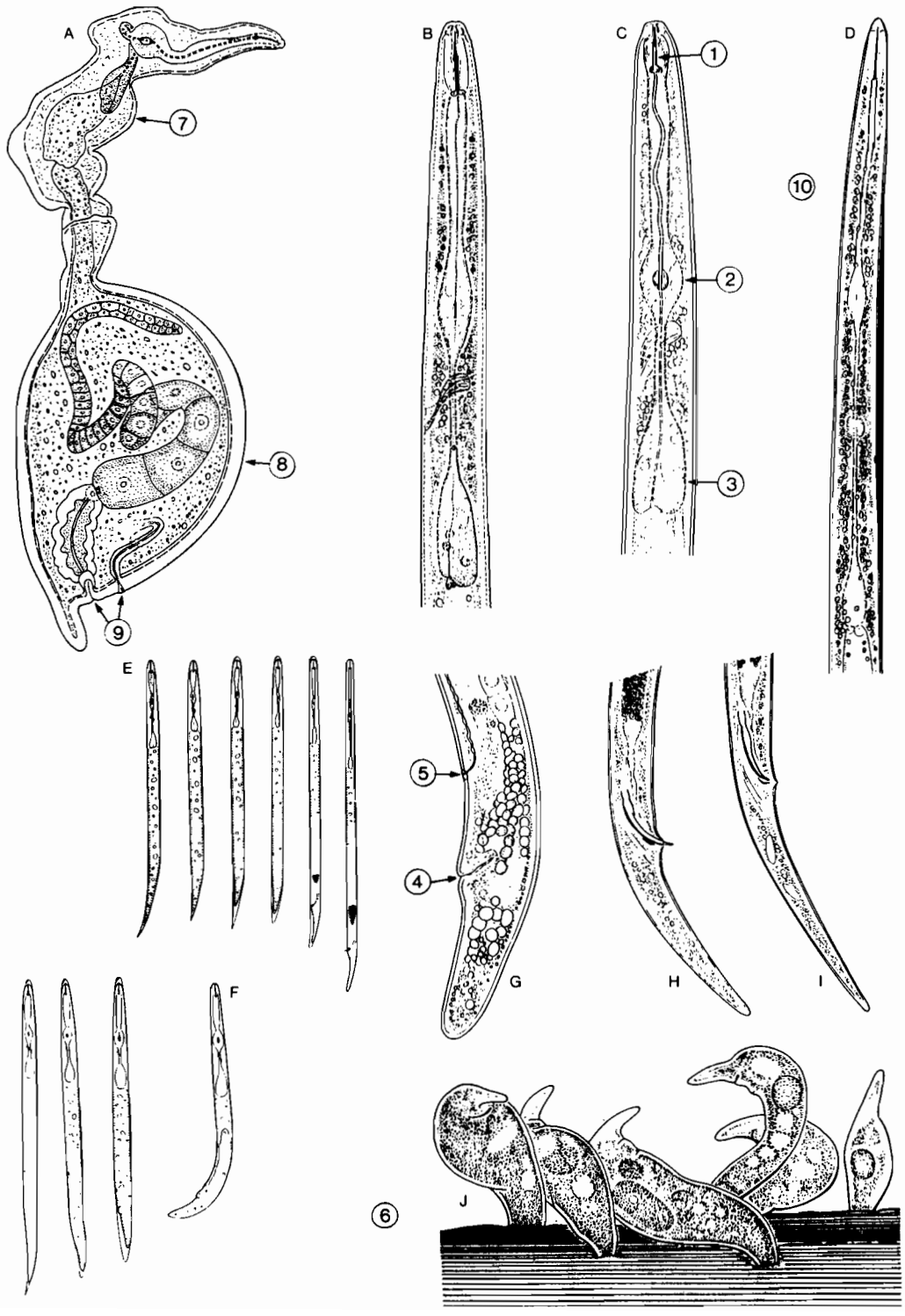
Distribution: Found almost everywhere that citrus is grown on any scale.

Confusable genus: *Trophotylenchulus*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 3, No. 34).

Fig. 20. *Tylenchulus semipenetrans*. A: mature female; B: juvenile oesophagus; C: immature female oesophagus; D: male oesophagus; E: development of male; F: development of female; G: immature female vulval region: H,I: male tails; J: mature females on root.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In : Luc Michel (ed.), Sikora R.A. (ed.), Bridge J. (ed.). Plant parasitic nematodes in subtropical and tropical agriculture.

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