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# Heteroderinae, Cyst- and Non-Cyst-Forming Nematodes

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## I. INTRODUCTION

### A. Biology

#### 1. Distribution

Heteroderinae Filipjev and Schuurmans Stekhoven, *sensu* Luc et al. 1988, are of worldwide concern because they include some of the most important nematode pathogens of agriculture, the cyst nematodes. New reports including discovery of new species underscore the worldwide distribution of Heteroderinae, challenging earlier views that the group is nearly restricted to cool climates. Indeed, the first descriptions were of pathogens in temperate Europe and North America and these continue to be among the greatest menaces to agriculture. *Heterodera* was first recognized as *H. schachtii* on sugar beet in Europe in the late 1800s; today the range extends to wherever sugar beets are grown and beyond, including Europe, USSR, USA, Mexico, and Africa, even becoming established in hot deserts and tropics. In the early years following description of *H. schachtii* the diversity of the cyst nematodes was recognized by many "races." Today nearly 60 species of *Heterodera* extend throughout the world. These include species limited to hot climates such as *H. sacchari* on sugar cane and rice and *H. oryzae* on rice and banana. *Heterodera zea* while occurring on corn in both India and Maryland seems to be better adapted and more pathogenic in warm climates of India. About one-third of the species, including *H. amygdali* on almonds and other *Prunus* in Tajik, USSR, seem highly restricted in distribution, some with only a single known site. Others, including *H. avenae*, *H. cruciferae*, *H. glycines*, and *H. trifolii*, are widely distributed. *Heterodera avenae* occurs in Europe, USSR, North America, South America, the Middle East, Africa, Asia, and Australia; although it generally attacks cool weather cereals, it persists in the tropics where cultivars, seasons, or altitudes allow suitable hosts to be grown. *Heterodera cruciferae* is widely distributed in Europe and USSR; it also extends to California and South Australia. *Heterodera glycines* occurs from Asia to the eastern USA with reports in Egypt and South America; it is not known in Europe.



The golden potato cyst nematode was first considered a race of *H. schachtii*. It is now recognized as *Globodera rostochiensis*, the type species of a genus with about 12 species including a second potato cyst nematode, *G. pallida*. Several species, including *G. zelandica* on *Fuchsia* in New Zealand, are restricted in distribution. However, the potato cyst nematodes *G. rostochiensis* and *G. pallida* occur worldwide, extending from South and Central America to Europe, USSR, Mediterranean region, Asia, India, Africa, Australia, New Zealand, Iceland, Philippines, and restricted regions of Canada and the USA. Although the potato cyst nematodes have been reported in tropics, they are typically found at high elevations. However, rare reports suggest occurrences in hot tropics of Mozambique and southern India.

*Heterodera* (= *Punctodera*) *punctata* was among the first cyst nematodes known in North America and was described only 5 years after the golden potato cyst nematode was recognized as a species distinct from *H. schachtii*. This parasite of cereals is of little economic concern, although it is widespread in Europe, USSR, and USA. In contrast, *Punctodera chaltoensis* is highly destructive to *Zea mays*, and it is apparently restricted to Mexico. *Cactodera* is abundant in the warm lower elevations of Mexico and Cuba as well as the hot desert regions of the western USA. The type species *C. cacti* occurs on cacti and *Euphorbia*; widespread reports outside the New World may be the result of exported ornamental plants. While some species are subtropical, others, such as *C. weissi*, extend from southern Virginia to the cooler climates of the USA and Canada, and *C. aquatica* and *C. estonica* are described from the USSR.

*Afenestrata* is a cyst nematode with only a single known species, *A. africana*, of very limited distribution, on a woody host in tropical Africa. Records suggest that species and most genera of non-cyst-forming heteroderines have restricted distributions. However, they are often not known to be economically important, so that their presence may go unnoticed and the breadth of their distribution may yet be unknown. Collectively, the six species of *Meloidodera* are particularly widely distributed including the USSR, Alaska, and mild climates of the southeastern USA. *Verutus* spp. occur at restricted sites in the southeastern and southwestern USA as well as Japan and Europe. *Cryphodera* apparently occurs only in Australia and New Zealand, *Hylonema* in Africa, and *Camelodera* in central Asia of the USSR. Most sarisoderines (*Sarisodera*, *Rhizonema*, *Bellodera*, *Ekphymatodera*) are limited to the western USA and perhaps subtropical and tropical Mexico and South America (unpublished observations). Ataloderines (*Atalodera*, *Thecavermiculatus*) extend from Alaska through the western USA to South America. The potential of *Meloidodera charis* on corn (*Zea mays*) in Nebraska and *Thecavermiculatus* n. sp. on potato (*Solanum tuberosum*) in Alaska suggests that non-cyst-forming heteroderines may yet prove important to agriculture.

The distribution of Heteroderinae is largely determined by the evolutionary history of the taxa and the history of the areas of the earth in which they live (Ferris, 1979). However, superimposed on these patterns is the effect of dispersal, particularly of agricultural pests, by man. Several authors have speculated on the introduction of potato cyst nematodes from the Andean region of South America to Europe and then throughout the world (Mia, 1977); new infestations can sometimes be traced to the introduction of contaminated potato seed pieces. Containment in the case of the potato cyst nematode in the USA is often attributed to rigorous quarantine enforcement. Conversely, spread suggests failure of quarantine, as in the case of soybean cyst nematode in the USA. Occurrence of the soybean cyst nematode in the USA has been linked to importation from Japan (Riggs, 1977), a hypothesis which may be testable by molecular biology methods which analyze genealogical relationships among geographic isolates (Ferris et al., 1985; Radice et al.,



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1988; Sandall and Powers, 1988). Whereas interpretation of results of these methods are not yet conclusive, they nevertheless point to the promising new approach to understanding dispersal of Heteroderinae and other nematodes.

## 2. Life History

The basic life history is consistent within Heteroderinae, including four molts and four juvenile stages plus adults (Fig. 1). The first and part of the second stage occur within the egg, and the emerging infective second-stage juvenile establishes a sedentary feeding site in a host where the final three molts occur.

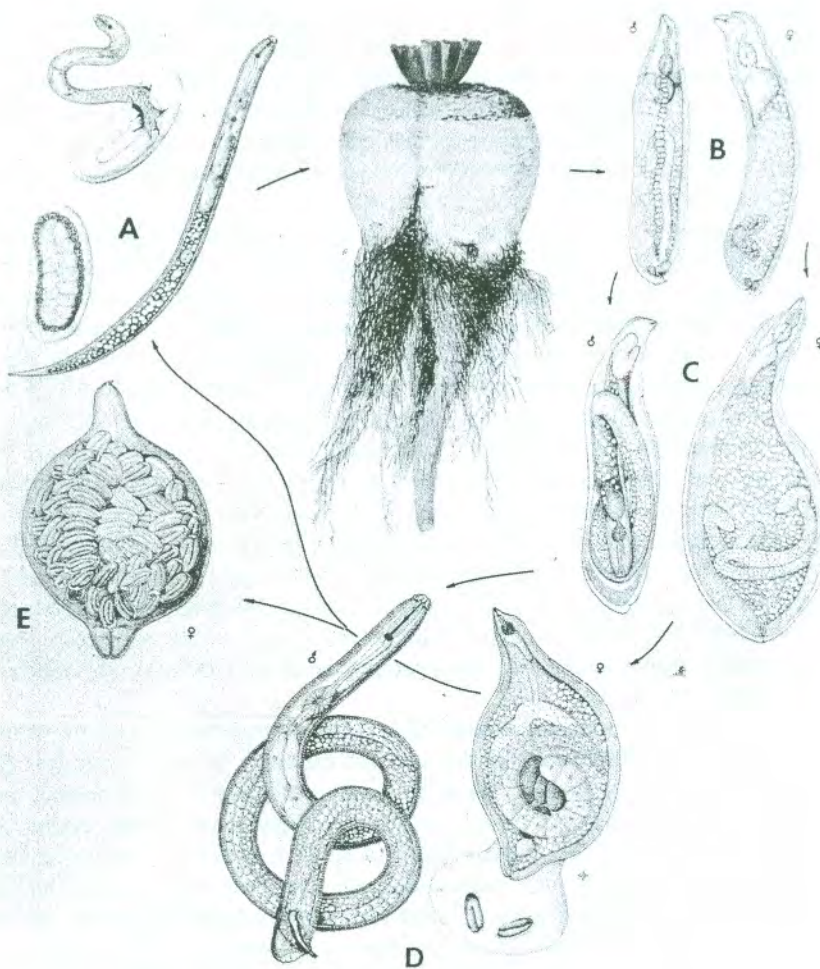


FIGURE 1 Life cycle of *Heterodera schachtii* on sugar beet. (A) Egg and second-stage juvenile. (B) Third-stage juveniles. (C) Fourth-stage juveniles. (D) Adults. (E) Cyst. (Illustrated by C. Papp.)



In most *Heterodera* spp. egg hatching as well as attraction to hosts is stimulated by host root exudates (Stone, 1974; Williams and Siddiqi, 1972; Brown, 1958; Perry and Clarke, 1981; Perry, 1986; Perry et al., 1989). However, other factors such as soil moisture, aeration, and temperature as well as nematode diapause are also responsible for seasonal emergence of juveniles in many species of *Heterodera* (Oostenbrink, 1967, Mulvey and Anderson, 1974; Mankau and Lindford, 1960; Franklin, 1972; Stone, 1974). In the absence of a host, cysts usually decompose slowly. Even where a host is present, hatching is often delayed over a period of years, with most second-stage juveniles released by the fifth or sixth year (e.g., Thorne, 1961). A few cyst nematode species, including *H. schachtii* and *H. trifolii*, apparently do not have a strong and consistent response to host exudates. Although there are many exceptions, little response to host exudates might be expected in species with relatively low host specificity and a wide host range.

Freshly hatched second-stage juveniles move toward roots of a potential host searching with movements of the head and lips and continuous stylet probing (Doncaster and Seymour, 1973). Once the nematode reaches the root tip surface, it makes quick, intermittent probes on the epidermis until a favorable site is found (Fig. 2B). Then it penetrates the cell wall (Fig. 2C). Penetration of the host occurs mostly at the growing tip of roots or at sites where lateral roots emerge; however, in some cases penetration may occur at any available site including wounds (Wyss and Zunke, 1986). Once the nematode penetrates epidermal cells, it moves intracellularly in the cortex toward the vascular cylinder, frequently in tissue adjacent to the protoxylem poles (Jones, 1981). Here probing occurs on cells that surround the head region until a feeding site is selected, stylet penetration takes place, and material from the esophageal gland lobe is injected (Endo, 1987).

After the infective juvenile establishes a suitable feeding site and nurse cells, the nematode enlarges rapidly and the final molts are completed (Figs. 2D, 3). Adults include sedentary obese egg-producing females and in most cases vermiform migratory males. Unbalanced sex ratios in amphimitic cyst-forming heteroderines are probably due to differential rates of death in unfavorable conditions. Females often die where there is reduced food availability and competition for feeding sites is high. Conversely, males require less food than females and are more tolerant of crowding (Koliopanos and Triantaphyllou, 1972). Some dispute that differential death rate alone can account for unbalanced sex ratios and consider sex reversal, as occurs in *Meloidogyne*, to also occur in some heteroderines (Müller, 1986). Environmentally controlled sex expression has indeed been demonstrated for *Meloidodera floridensis* (Triantaphyllou and Hirschmann, 1973).

Males of amphimitic species are apparently attracted to pheromones which may occur in exudates secreted through the vulva of females often into a clear gelatinous matrix (Green, 1971a; Cordero, 1989) (Fig. 4). Several males may be attracted to a single female, and copulation may occur more than once. After copulation, the clear matrix changes in color and intensity; subsequently fertilized eggs begin embryogenesis and may be laid or retained within the uterus. In many genera of heteroderines, females, full of eggs, may be transformed into tanned cysts upon death. These cysts typically have posterior fenestration, areas in the cuticle of loose fibrous mesh (see "Morphology" below). Fenestrae are eventually ruptured by second-stage juveniles hatching from eggs retained within the cysts (Fig. 2A). The first juveniles to hatch thrust their stylets against the fibrous areas creating rows of perforations. With pressure of these first juveniles against the fenestrae, the fibrous tissue is broken and infective juveniles emerge from the cyst (Cordero, 1989). Non-cyst-forming heteroderines, including *Thecavermiculatus*, may also retain eggs which hatch within the female, and they emerge as second-stage juveniles (Robbins, 1978) (Fig.



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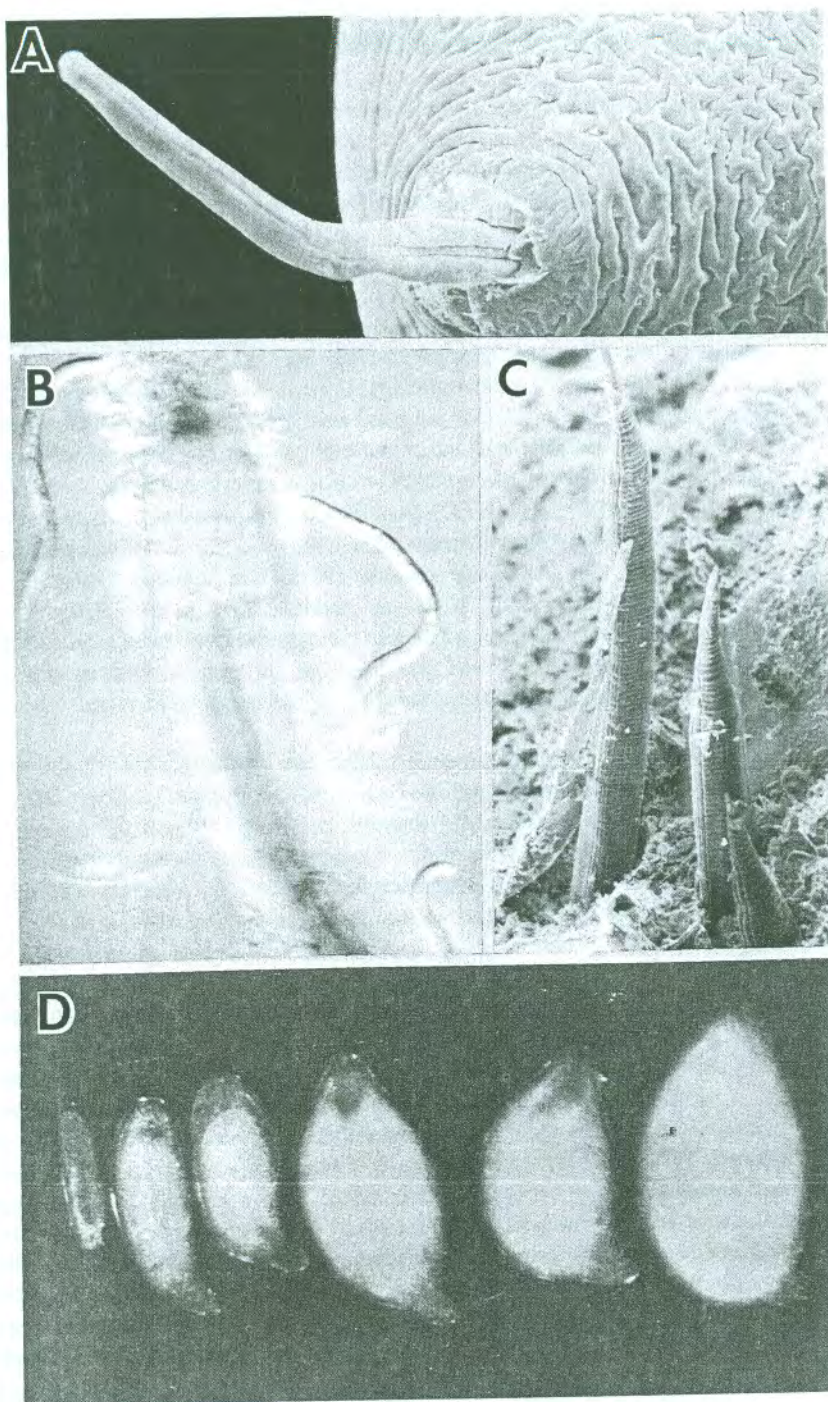


FIGURE 2 Biology of *Heterodera schachtii*. (A) Second-stage juvenile (J2) emerging from fenestrae of cyst (SEM). (B) J2s probing surface of sugar beet root prior to penetration. (C) Tail end of J2s protruding from root following penetration (SEM). Development of the female from the saccate second (left), third, fourth stages, as well as the young adult, mature adult, and cyst (right). (A, B, C courtesy D. Cordero Clark.)



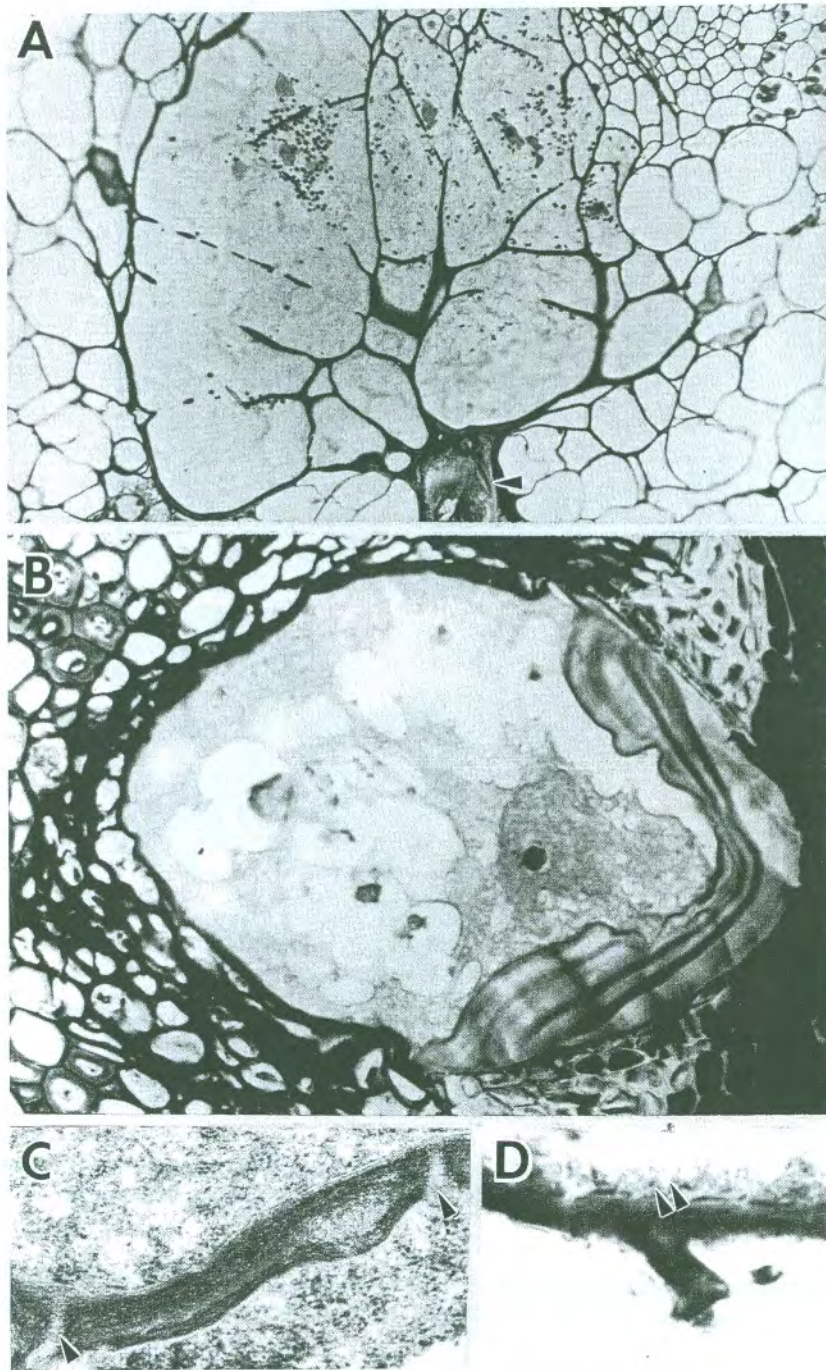


FIGURE 3 Host responses to Heteroderinae. (A) Syncytium. Arrowhead indicates head of female. (B) Single uniculate giant cell (SUGC). (C) Cell wall of SUGC with plasmodesmata (arrowheads). (D) Cell wall with wall ingrowths (double arrowheads). (A–C after Mundo-Ocampo and Baldwin, 1983a,b; reprinted by permission *J. Nematol.*)



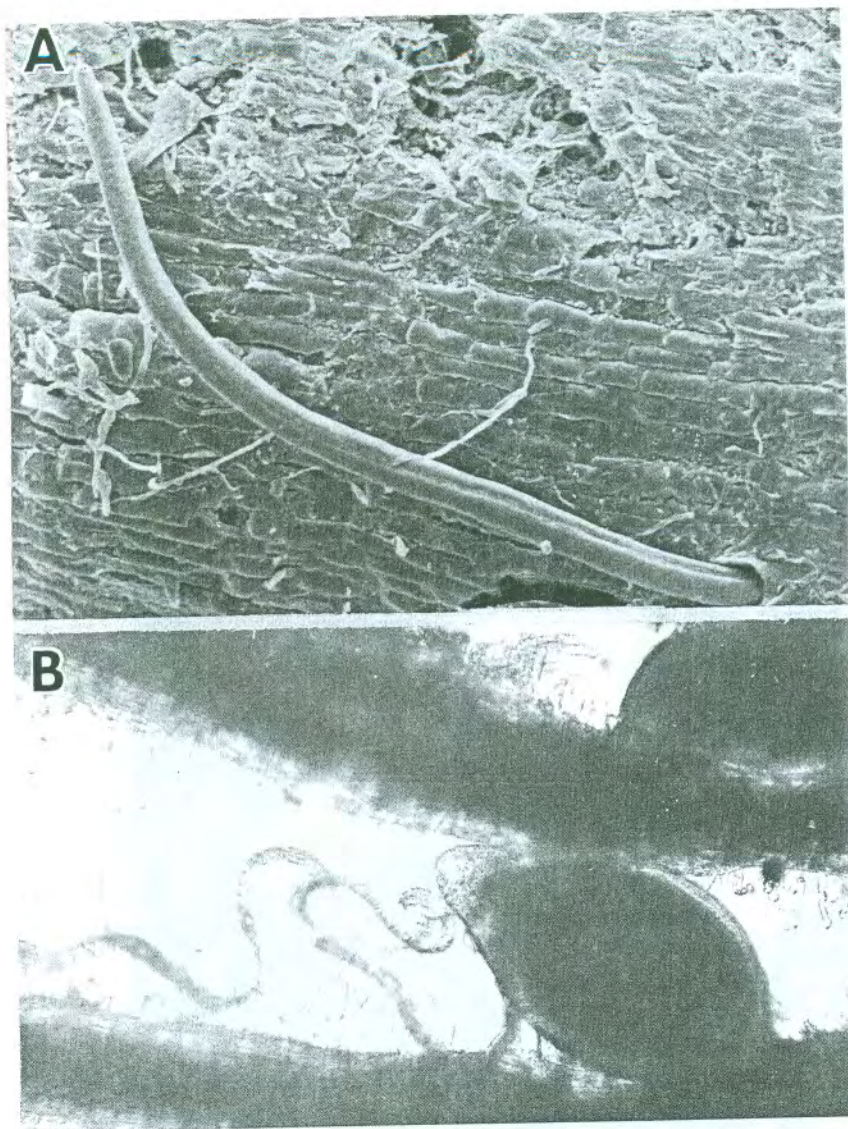


FIGURE 4 Males of *Heterodera schachtii*. (A) Male emerging from host root (SEM) (B) Males attracted to posterior terminus of newly hatched female. (B courtesy of D. Cordero Clark.)

26A). Comparisons among genera of cyst nematodes suggest that whether or not eggs are retained or laid is correlated with the degree of development of vaginal musculature in the adult (Cordero, 1989).

Although the entire life cycle of a heteroderine may be completed in less than 30 days, generation time varies with the heteroderine species and is greatly affected by environmental conditions.

Cytogenetically the heteroderines constitute a uniform group (Triantaphyllou, 1975a, 1983). Most of them are bisexual, cross-fertilizing species with a haploid



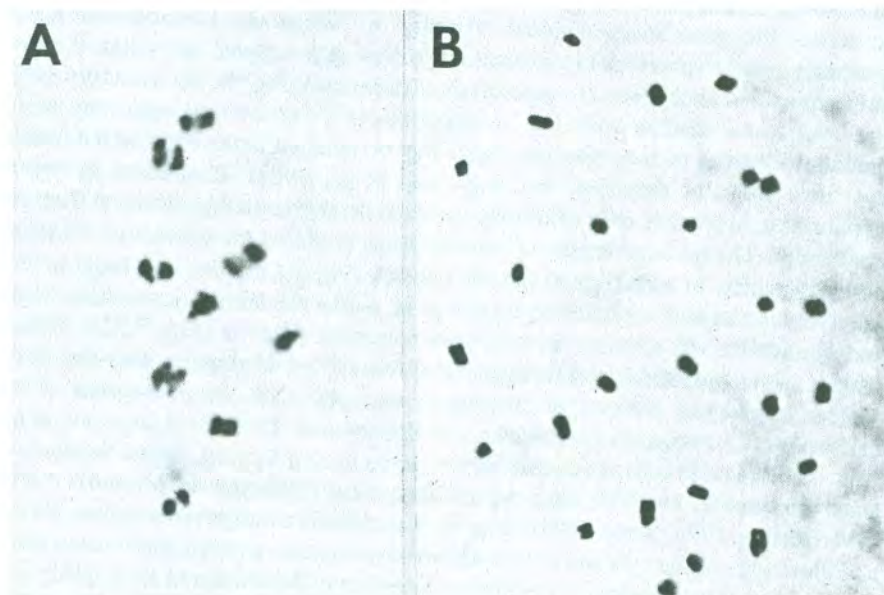


FIGURE 5 Chromosomes of oocytes of *Heterodera* spp. (A) Late prophase I of *Heterodera trifolii* with nine chromosomes. (B) Metaphase I of *H. trifolii* with 26 chromosomes. (Courtesy A. C. Triantaphyllou; after Triantaphyllou and Hirschmann, 1962, 1978.)

complement of nine chromosomes (Fig. 5A). *Cactodera betulae* deviates slightly from the normal cytogenetic status of the group in that it reproduces by meiotic parthenogenesis and has  $n = 12$  or 13 chromosomes (Triantaphyllou, 1970). Also, members of the *Heterodera trifolii* species complex have no males and reproduce exclusively by mitotic parthenogenesis (Triantaphyllou and Hirschmann, 1978). They represent polyploid forms with somatic chromosome numbers of 24 – 35 (Fig. 5B).

### 3. Morphology

The specialized morphology of Heteroderinae reflects a complex life history including sedentary parasitism. The morphology is varied, accommodating diverse adaptations to a wide range of hosts and habitats. Investigations of morphology are the most reasonable place to begin unraveling questions of biology and physiology of heteroderines. Comparative morphology is presently the most important approach for investigating phylogenetic relationships and for identification. At the most practical level morphological identification is used to predict pathogenicity and host specificity; this is an essential first step for efficient application of every control strategy.

Those morphological characters that diagnose heteroderines from other Tylenchida have become more complex, yielding a broader understanding of the group. In 1934, Filipjev diagnosed *Heterodera*, which then included all cyst and root-knot nematodes, on the basis of sexual dimorphism and infective vermiform juveniles. Chitwood (1949) reinstated root-knot nematodes as a separate genus and distinguished *Heterodera* as distinct from root-knot nematodes primarily by the presence of a cyst with a complex nonstriated cuticular surface pattern as well as at least partial retention of eggs. Subsequent description



of non-cyst-forming as well as striated heteroderines has required a more complex diagnosis to reflect the great morphological diversity of this group. Heteroderine females are generally nearly spherical but exceptions are sausage-shaped; the vulva is terminal or subterminal but exceptions are equatorial (subterminal) (Fig. 6); the excretory pore is near the level of the median bulb, but in exceptions it is far anterior; eggs may be laid in a gelatinous matrix, or they may not (e.g., Luc et al., 1988). Regardless of heteroderine variabilities, in practice only a little experience is needed to distinguish them from root-knot nematodes. The perineal region of heteroderines is unlike the distinctive fingerprint-like perineal pattern in root-knot nematode females (Fig. 7A,B). Second-stage juveniles are relatively robust with a hyaline terminal region, unlike the delicate appearance, weak stylet, and nonhyaline tail terminus of root-knot nematode juvenile (Fig. 7C,D). Heteroderine males lack the distinctive lateral amphidial cheeks of root-knot males; they also have a long, slender esophageal isthmus in contrast to the very short, broad isthmus of root-knot nematodes (Chitwood, 1949; Baldwin and Hirschmann, 1973, 1975; Baldwin et al., 1977) (Fig. 7E,F). The first heteroderines described were cyst forming. Since the cyst is the life stage most readily available from the soil, taxonomic characters are primarily related to the cyst (Hesling, 1978; Stone, 1986) (Fig. 8). Yet, there is a disagreement about the definition and homology of the cyst and even whether or not genera which acquire some color but do not retain eggs after death of the female have a cyst (Baldwin and Bell, 1985; Luc et al., 1986; Wouts, 1985). Luc et al. (1986) defined a heteroderine cysts as a persistent tanned sac which retains eggs and is derived from some or all components of the mature female body

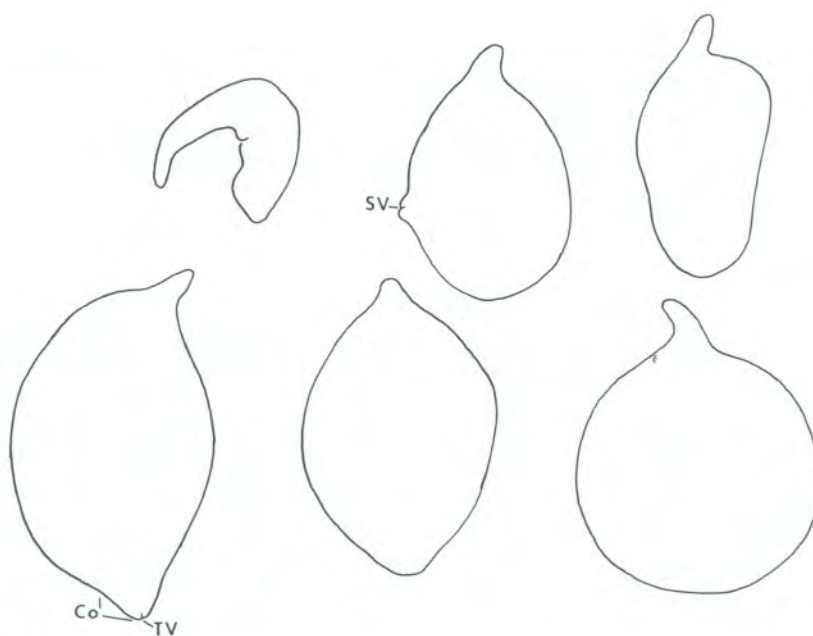


FIGURE 6 Shapes of females of Heteroderinae genera ranging from reniform to saccate and with a rounded terminus or cone (Co). Vulva may be subterminal (SV) or terminal (TV). (After Baldwin and Schouest, 1990, reprinted by permission Kluwer Academic.)



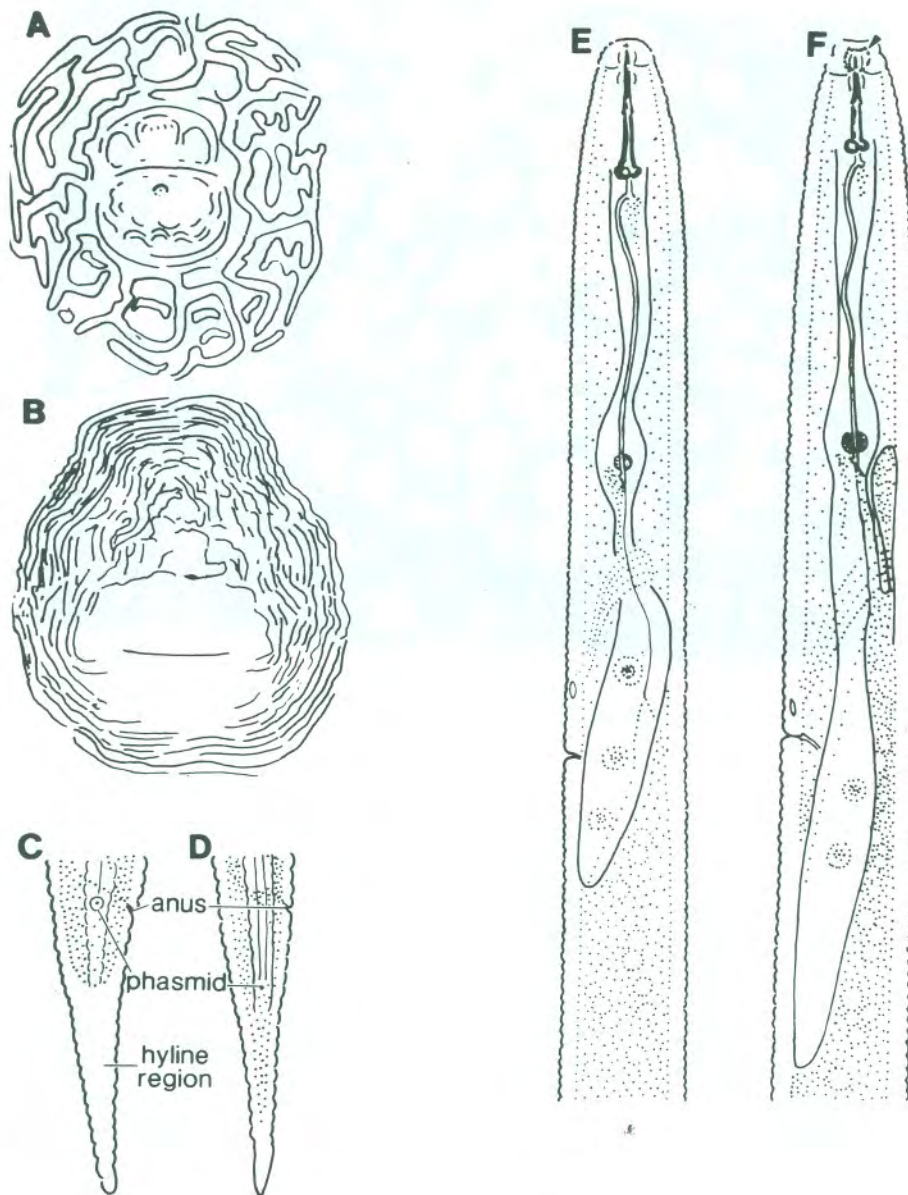


FIGURE 7 Morphological features distinguishing Heteroderinae from *Meloidogyne*. (A) Terminal region of female of Heteroderinae. (B) Terminal region of female of *Meloidogyne*. (C) Tail region of second-stage juvenile (J2) of Heteroderinae with lens-like phasmid and hyaline terminus. (D) Tail region of J2 of *Meloidogyne* with pore-like phasmid. (E) Anterior region of male of Heteroderinae. (F) Anterior region of male of *Meloidogyne* (arrowhead indicates position of amphidial cheek).



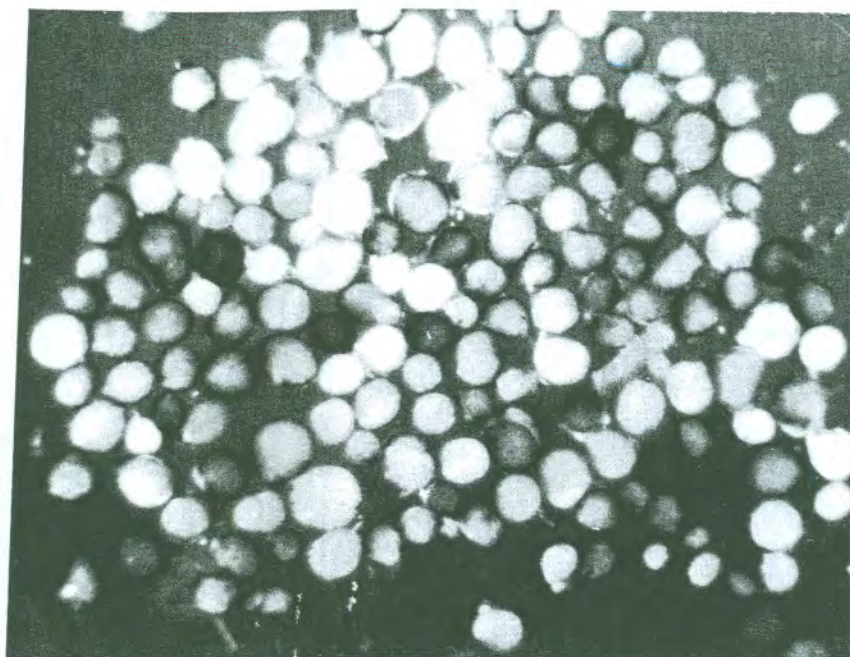


FIGURE 8 White females and pigmented cysts of *Punctodera chaltoensis*.

wall. By this definition genera with cysts include *Afenestrata*, *Heterodera*, *Cactodera*, *Globodera*, *Punctodera*, and *Dolichodera*; the majority of heteroderine genera lack cysts (Table 1). Genera with females which become cysts and genera with females that do not share similar features of shape, cuticle layering, surface patterns, and digestive, reproductive, and sensory systems.

All Heteroderinae females have a narrow anterior protuberance or "neck" and swollen body, but genera vary in details for shape (Fig. 6). *Verutus* is readily recognized by its reniform shape, whereas other heteroderines are more swollen and overall shape is particularly affected by the presence or absence of a terminal cone (Fig. 11). The cone apparently forms in response to differential elasticity of the body wall as the female enlarges, i.e., posteriorly the body wall is least elastic for girth expansion (Cordero, 1989). It is uncertain if reduced elasticity is a function of cuticle thickness, cuticle layering and the physical nature of layers, attachment points of vaginal muscles, or there parameters. Some genera lacking a cone, such as *Meloidodera*, do not have cysts; other genera with globose females and no cone, including *Globodera*, do form cysts. Many genera have distinct terminal cones so that the female is lemon-shaped as in non-cyst-forming *Atalodera* or cyst-forming *Heterodera*. The genus *Thecavermiculatus* shares many specialized characters with *Atalodera* but the cone is reduced, as is also the case in certain species of *Cactodera* and *Heterodera*. In some cases fine details of female/cyst shape or size can be characteristic of species and of some limited value for identification as noted for *Heterodera cardiolata* or *Cactodera estonica* (Golden, 1986). Although intraspecific variability is usually great, taxonomic reliability of shape and size of females/cysts can sometimes be improved by considering the largest individuals in the population (Hirschmann, 1956; Thorne, 1961).



TABLE 1 Genera of Heteroderinae and Numbers of Valid Species<sup>a</sup>

| Genera                         | Authority   | Number of species |
|--------------------------------|---|-------------------|
| <i>Heterodera</i> <sup>b</sup> | Schmidt, 1871                                     | 57                |
| <i>Afenestrata</i>             | Baldwin and Bell, 1985                            | 1                 |
| <i>Cactodera</i>               | Krall and Krall, 1978                             | 9                 |
| <i>Globodera</i> <sup>b</sup>  | Skarbilovich, 1959                                | 12                |
| <i>Punctodera</i> <sup>b</sup> | Mulvey and Stone, 1976                            | 3                 |
| <i>Dolichodera</i>             | Mulvey and Ebsary, 1980                           | 1                 |
| <i>Atalodera</i>               | Wouts and Sher, 1971                              | 4                 |
| <i>Thecavermiculatus</i>       | Robbins, 1978                                     | 4                 |
| <i>Camelodera</i>              | Krall, Shagalina, and Ivanova, 1988               | 1                 |
| <i>Bellodera</i>               | Wouts, 1985                                       | 1                 |
| <i>Sarisodera</i>              | Wouts and Sher, 1971                              | 1                 |
| <i>Rhizonema</i>               | Cid Del Prado Vera, Lownsbery, and Maggenti, 1983 | 1                 |
| <i>Hylonema</i>                | Luc, Taylor, and Cadet, 1978                      | 1                 |
| <i>Ekphymatodera</i>           | Baldwin, Bernard, and Mundo, 1989                 | 1                 |
| <i>Cryphodera</i>              | Colbran, 1966                                     | 4                 |
| <i>Meloidodera</i>             | Chitwood, Hannon, and Esser, 1956                 | 6                 |
| <i>Verutus</i>                 | Esser, 1981                                       | 3                 |

<sup>a</sup>Groupings generally correspond to tribes of Baldwin and Schouest (1990).

<sup>b</sup>Genera with economically most important species.

The body wall cuticle of Heteroderinae females is modified from the A and B layers present in vermiform Tylenchida to include a broad C layer; in some genera, including non-cyst-forming *Atalodera* and cyst-forming *Globodera*, an additional D layer occurs (Shepherd et al., 1972; Cliff and Baldwin, 1985) (Fig. 9). The presence or absence of the D layer among cyst nematodes was used to support separation of round and lemon-shaped cysts into distinct genera (Shepherd et al., 1972). However, *Heterodera*, previously reported to lack a D layer, was recently found to have a very thin D layer 4 weeks after the final molt (Cordero, 1989). Overall thickness of cuticle does not seem to relate to number of layers. For example, *Punctodera*, with a D layer, may have a very thin cuticle. Homology of layers in the female and layers in the cyst have not been established, nor is it known if particular cuticular layers or other parts of the body are especially responsible for the color that occurs in many dead females and cysts (Fig. 8). Changes in color are attributed to action of phenoloxidase on substrates in the cyst wall (Awan and Hominick, 1982; Ellenby, 1946a, 1955), but the precise process and nature of variation in color are unknown. Cyst color varies among species from light tan, as in *Heterodera zae*, to shades of brown and nearly black in other species (Golden, 1986). In some cases the sequence of color change as a female matures is distinctive, as in *G. rostochiensis* which forms a golden, followed by a brown cyst, versus *G. pallida* with no golden stage. Although color may be helpful in identification, it must be used cautiously because color variations may be associated with age, translucence, reflection, surface texture, and variable environmental influences on the cyst (Hesling, 1978; Golden, 1986).



The color of a young cyst may be masked by the presence of a subcrystalline layer, a layer external to the cuticle of some species (Fig. 10A,B). The material may occur on molted fourth-stage cuticles but is most conspicuous in adults and young cysts where it varies greatly in thickness from a uniform film to a thick layer apparently cracked into a pattern of blocks. The subcrystalline layer occurs in both cyst- and non-cyst-forming taxa, and its presence or absence and thickness, while variable, may be somewhat species-specific. Brown et al. (1971) proposed that the subcrystalline layer was partially composed of a fatty acid generated by a symbiotic fungus feeding on metabolic products of the nematode. However, subsequent investigations show that the subcrystalline layer persists in aseptic culture (Zunke, 1986; Cordero, 1989).

Overall cuticular surface patterns, and particularly those of the midbody region, occur in diverse forms among females and cysts of Heteroderinae. These particular patterns may characterize specific taxa (Fig. 10). These midbody patterns broadly include striated and zig-zag. However, particular patterns may be further specified as fine or coarse, ridged, reticulate, lacelike, or punctate. Striated patterns are common among some non-cyst-forming genera including *Meloidodera* and *Cryphodera*. Wouts (1985) questions homology of this pattern with the similar parallel ridges of *Bellodera*, and cyst-forming *Dolichodera*; questions of homology with the parallel ridges or broken wavy lines of some *Cactodera* must also be considered. Zig-zag patterns occur in noncyst genera such as *Atalodera* as well as most cyst nematodes including *Heterodera*. Zig-zag patterns range from coarse to fine. They also vary in details of anastomosing and reticulation, and they may be associated with punctations (Fig. 10G). Punctations especially characterize *Punctodera* where they occur as distinct rows beneath the zig-zag surface, but they also occur with varying reliability and clarity in many other genera (Golden, 1986). Previously punctations were interpreted as pores or pits (Franklin, 1939; Thorne, 1928), but they are more likely homologous with optically and electron dense deposits in the A layer of the cuticle. In some taxa these

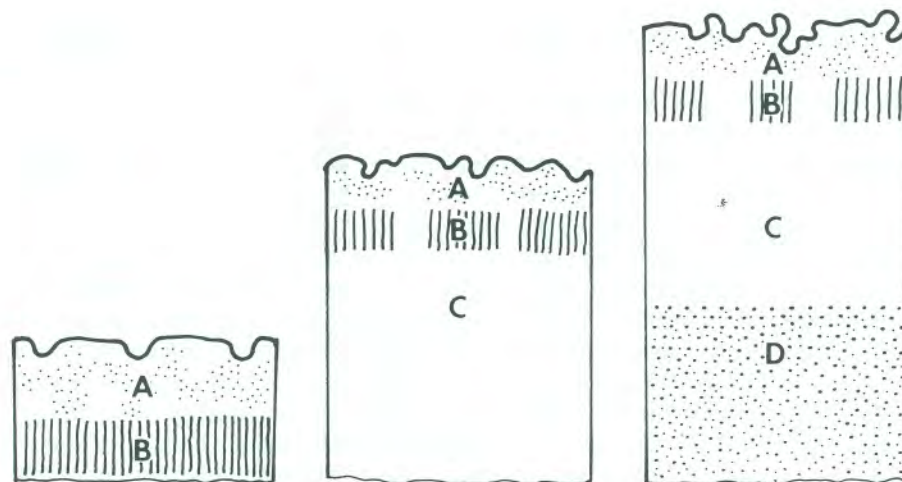


FIGURE 9 Diagrammatic cross-sections of female cuticles showing A and B layers alone as they occur in males and second-stage juveniles, as well as presence of layers C and C+D as they occur in adult females of Heteroderinae. (After Baldwin and Schouest, 1990; reprinted by permission Kluwer Academic.)



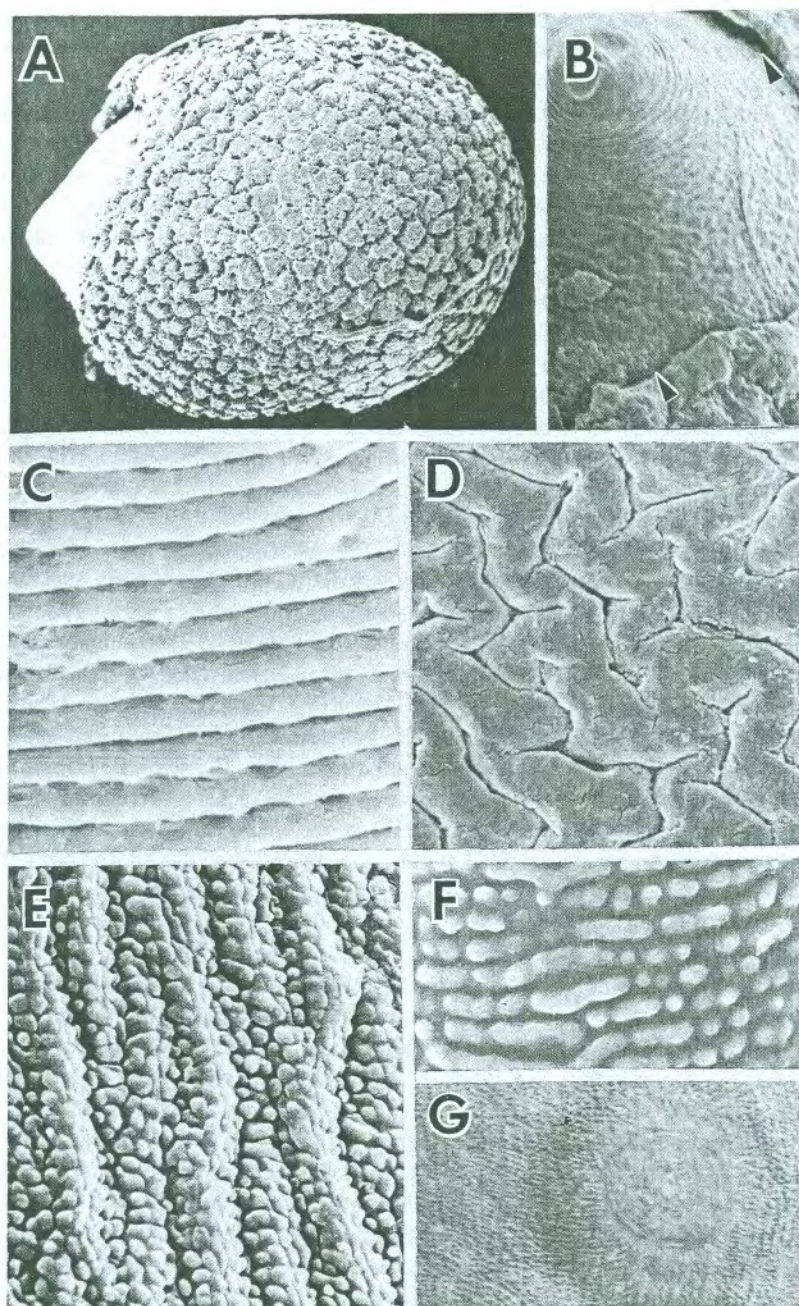


FIGURE 10 Surface patterns of females and cysts of Heteroderinae (SEM unless indicated otherwise). (A) Subcrystalline layer, lateral view of cyst of *Heterodera avenae*. (B) Enlargement of terminal region from A showing boundary of subcrystalline layer (arrowheads). (C) Striated cuticle, *Rhizonema sequoiae*. (D) Zig-zag cuticle, *Atalodera lonicerae*. (E) Tuberculate cuticle with longitudinal striae, *Ekphymatodera thomasoni*. (F) Cuticle of tuberculate neck region of *Globodera rostochiensis*, (G) subsurface cuticular punctations, *Punctodera chalconensis* (light microscopy).



deposits occur in periodic globules (= punctations?), whereas in others the material is diffuse (Cliff and Baldwin, 1985; Baldwin, unpublished) and may not be apparent with light microscopy (= no punctations?).

The derivation of the surface patterns of heteroderine cysts and females is not clear. Franklin (1939) and Wieser (1953) considered them to be derived from the cuticular annulations of second-stage juveniles. In *H. schachtii*, video-recorded development indicates that the striated pattern persists only a short time after infection; by early fourth stage the midbody has irregular longitudinal ridges. The zig-zag pattern first forms posteriorly in the late fourth stage and spreads to the midbody prior to the last molt (Cordero, 1989). There is not yet an explanation as to how the various patterns develop differently among genera and species.

Cuticular surface patterns of the midbody of females and cysts are helpful in species identification as first shown by Taylor (1957) but have become less useful with awareness of the large number of heteroderine species and discovery of intermediate patterns which make precise terminology and characterization more difficult to apply (Hesling, 1978). Midbody cuticular patterns vary within a population, from one region of the body to another, with age, and between females and cysts of a given species. Improved understanding of these variables throughout Heteroderinae may allow further standardization of conditions for comparing patterns and the use of finer details and more precise descriptive terminology for taxonomic characterization (Othman et al., 1988).

The surface pattern anteriorly is similar among heteroderine females and cysts with striations throughout the neck region, but some taxa, such as *Globodera*, are distinctive by abundant neck tubercles (Othman et al., 1988) (Fig. 10F). The en face region typically includes a squarish labial disc just anterior to a plate consisting of six fused lips (Fig. 13G), but in some genera, such as *Verutus*, the lateral lips are partially separate from the rest of the plate (Othman and Baldwin, 1985). The excretory pore of heteroderine females generally occurs near the base of the neck at the level of the medium bulb or further posteriorly; however, in *Bellodera* it occurs far anterior, near the level of the stylet knobs (Fig. 25C).

The surface pattern of the posterior region of females and cysts varies among heteroderines and is usually modified from that of the midbody. However, in *Meloidodera*, the striae are unchanged at the terminus, forming concentric rings around the anus and phasmid openings; posteriorly the position of lateral lines is indicated by interruptions in the striae, not unlike the lateral lines of some *Meloidogyne* females. In *Verutus* the striae are interrupted or continue around the anus (Othman and Baldwin, 1985; Baldwin et al., 1989) (Fig. 14A). In *Meloidodera* and *Verutus*, the pattern of striae is barely interrupted at the equatorial vulva. In other heteroderines the vulva is terminal in both cyst- and non-cyst-forming species the surrounding terminal pattern is coarser and more irregular than at midbody; there is little or no evidence of lateral lines and no evidence of phasmid openings (Fig. 14). The anus is relatively dorsal to the terminal vulva and distance between the two varies from 150  $\mu\text{m}$  in some cyst-forming nematodes to only a few micrometers in *Atalodera* (Fig. 14B), and finally *Sarisodera* where the anus occurs on the lip of the vagina. The intervening perineal area (*sensu* Green, 1971b) often has distinctive cuticular markings. For example, in *Globodera* the pattern may be mazelike or have parallel ridges, and the number of ridges between vulva and anus may vary with the species (Figs. 14E, 21D, E). In the immediate area of the vulva of most *Globodera* the vulva spans a basin or slight depression which has a crescent-shaped structure on both the dorsal and ventral rims. The crescents are covered with nonsensory cuticular protuberances which may be tightly packed, scattered, or, in some species, absent (Stone, 1986) (Fig. 14E, F). In *Heterodera*



cysts a region analogous to the rim of the basin may have wrinkles (rivulets) or other patterns distinctive among certain species (Golden, 1986) (Figs. 11, 14B–D).

In cyst-forming nematodes, excluding *Afenestrata*, the cuticle in the area surrounding the vulva is thin-walled consisting of loose mesh fibers (Cordero, 1989). The area eventually ruptures in the mature cyst. This ruptured area is the fenestra, and the size and shape of fenestrae is variable among genera and species (Figs. 11 and 12). Fenestrae occur in two basic patterns: with two openings (semifenestrae), one on each side of the vulva and surrounding tissue, or circumfenestrate with a single hole which deletes the vulva and surrounding tissue (Figs. 12C, 23A). Circumfenestrae encompass most or all of the basin, but exclude the crescents (Fig. 14E). If the semifenestrae are separated by a wide bridge enclosing a short vulva and surrounding tissue, and if the holes are each more than one-half a circle, the pattern is bifenestrate (Fig. 12B). If the bridge is narrow and the semifenestrae are flattened next to the bridge, the pattern is ambifenestrate (Stone, 1986) (Fig. 12A). In *Punctodera* the circumfenestrate is accompanied by a distinct anal fenestra (Fig. 12D). Circumfenestrae without anal fenestration are associated with round cyst nematodes including *Globodera* and *Dolichodera*, as well as in the cyst of *Cactodera* which has a small cone. Both bifenestrae and ambifenestrae are common in *Heterodera*, but bifenestrae are variable within species and may be difficult to apply in a diagnosis (Stone, 1986). In other cases the narrow bridge of some species such as *H. carotae* may break giving a false appearance of a circumfenestra and thereby confound diagnosis for the inexperienced (Golden, 1986).

Taxonomic characters associated with fenestrae include the distance from the anus to the nearest edge of fenestrae. Dividing this measurement by length of fenestrae gives Granek's ratio as defined by Hesling (1973), a helpful but variable tool for species diagnosis. Other commonly used characters include width and length of vulval slit and surrounding bridge.

Some surface patterns of the posterior region of heteroderine females and cysts are associated with the reproductive system. The vulva and associated lips lead to a dorsoventrally flattened vagina which connects to two long, coiled reproductive tracts (Fig. 1B–D). Each tract consists of an elongate uterus which connects to a short oviduct and spermatheca; the spermatheca connects to a long growth zone and relatively short germinal zone of the ovary (Triantaphyllou and Hirschmann, 1962). The cuticle-lined vagina is enclosed by a circular sheath of muscles near the uterus, the sphincter vagina (Fig. 11). Additional bundles of muscle fibers, the dilatores vagina, extend from the cuticle lining of the vagina to the body wall cuticle on the dorsal and ventral side of the vulva. In *H. schachtii* the dilatores vagina occur as six muscles on each side at four levels resulting in 48 muscles. In other heteroderine genera, particularly those that do not lay eggs, musculature is diminutive (Cordero, 1989). In many genera the cuticle thickens at the proximal end of the vagina in mature females and forms an underbridge (Fig. 11). The underbridge approaches the adjacent body wall cuticle, sometimes forking at the junction. The underbridge persists in the cyst and the thinner cuticle of the vagina may also persist in the cyst as a "sheaf" (Golden, 1986). The hypodermis of the posterior region of cyst-forming heteroderines includes regions of crystalline cuticular material which are deposited unevenly on the inner body wall cuticle as the female becomes senescent (Cordero, 1989). Large projections of the material extend into the body cavity and they become dark-colored, persisting in the cyst as bullae (Fig. 11) which are characteristic of many *Heterodera*, *Dolichodera*, and some *Punctodera* cysts. Bullae are particularly associated with species that have a pronounced underbridge, and they are predominant just internal from the underbridge. Their presence, size, and pattern may be useful for diagnosis. In *Cactodera* and some *Heterodera* small



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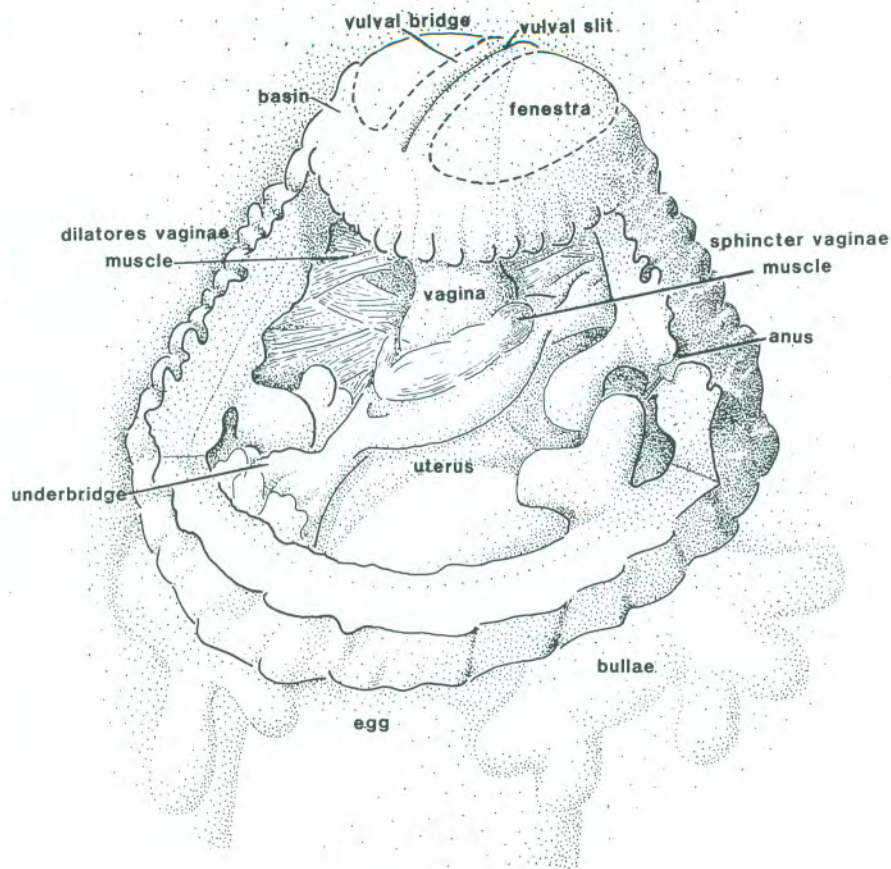


FIGURE 11 Illustration of terminal cone region of female of *Heterodera schachtii* with cutaway showing internal structures.

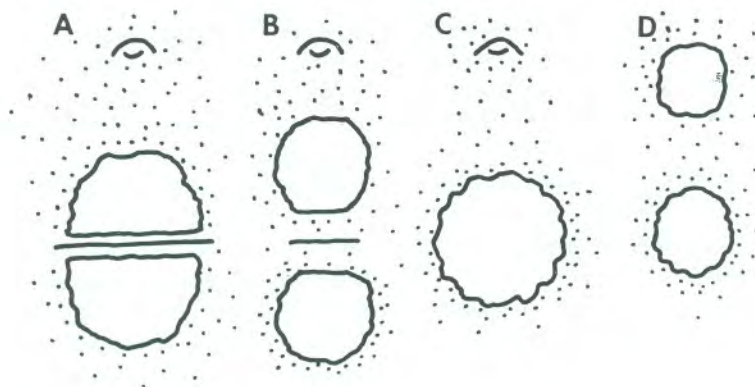


FIGURE 12 Fenestral patterns of terminal region of Heteroderinae. (A) Semifenestrate-am-bifenestrate vulval region; anal region not fenestrate. (B) Semifenestrate-bifenestrate vulval region, anal region not fenestrate. (C) Circumfenestrate vulval region anal region not fenestrate. (D) Circumfenestrate vulval region; separate anal fenestra.



pigmented structures, vulval denticles, are apparent near the apex of the vulval cone (Golden and Raski, 1977). Although they may resemble small bullae, Cordero (1989) demonstrated homology with remnants of vaginal muscles which persist in the cyst.

Poorly understood structure of the cyst include Mulvey's bridge, which may occur in some species at right angles to the underbridge. Some have speculated that Mulvey's bridge may be a hardened remnant of muscle (Mulvey, 1959), but recent studies suggest it is more likely of cuticular origin (Cordero, 1989). Cells specifically involved in secretion of the gelatinous matrix of eggs have not been identified although tissue surrounding the uterus is filled with rough endoplasmic reticulum and seems a likely source of exudate (Cordero, 1989). Absence or presence of matrix and the size of egg mass may vary among species, but it is not usually of diagnostic value.

The digestive system of heteroderine females consists of a stylet, esophagus, intestine, rectum, and anus apparently with little variation among species, except in the size and shape of the stylet and distance of the dorsal gland orifice to the stylet knobs. The anus is important in identification with respect to its distance from the vulva as well as its fenestration in cysts of *Punctodera*. Little is known about the fine structure of the digestive system of the female heteroderine, whereas males and juveniles have been thoroughly investigated (Baldwin, 1982; Baldwin and Hirschmann, 1976; Baldwin et al., 1977; Endo, 1984, 1987, 1988).

The sensory system of female heteroderines has not been adequately investigated. Apparently anterior sensory organs, including amphids and labial papillae, are well developed and active, whereas phasmids are only visible in females of *Verutus* and *Meloidodera* (Othman and Baldwin, 1985, 1986; Othman et al., 1986, 1988).

Males of heteroderines are vermiform, with a short, rounded tail lacking caudal alae (Fig. 13L, M). The body of males of most species is twisted as much as 90°, although in *Verutus*, males are not twisted. Males of most species develop from sedentary globose fourth-stage juveniles, although in *Meloidodera* they may develop from nonfeeding fourth-stage vermiform juveniles (Hirschmann and Triantaphyllou, 1973). The male length varies from 450 to 1700 µm. However, length may be affected by environmental considerations such as nutrition before the final molt; thus, intraspecific variation is so great that male length is generally not useful as a diagnostic character. In contrast to females, the cuticle of males consists solely of an A (exocuticle) and B (endocuticle) layer (Fig. 9).

Surface structures have been examined in males of many heteroderines with SEM (Baldwin, 1986; Othman and Baldwin, 1985, 1986; Othman et al., 1986, 1988). In each case the body is annulated. There are three or four lateral lines and the outer bands are usually areolated. The lateral lines originate 7–10 annules from the lip region. The basic surface pattern of the lip region of heteroderine males is hexaradiate consisting of a labial disc surrounded by six lips, four submedial and two lateral (Fig. 13D–F, J, K). Males of a number of genera have lip patterns with longitudinal blocks on the head region similar to those in many Hoplolaimidae; these are visible with light microscopy and can assist in diagnosis of species, including some *Meloidodera*, *Cryphodera*, *Atalodera*, and *Thecavermiculatus*. Similarly, narrow lips characterize some genera such as *Sarisodera* and *Rhizonema*, the fusion of the labial disc with the submedial lips is distinctive in *Heterodera* (Fig. 13D). Nevertheless, lip patterns of males tend to have more intraspecific variation than those of second-stage juveniles, and the diagnostic value of many aspects of male lip patterns is limited. Posteriorly, the tail length of males may be diagnostic, and a sheath (tubus) that extends from the cloaca and partially encloses retracted spicules may be distinctively large in some genera including *Sarisodera* and *Afenestrata*. The tail terminus may be smooth or



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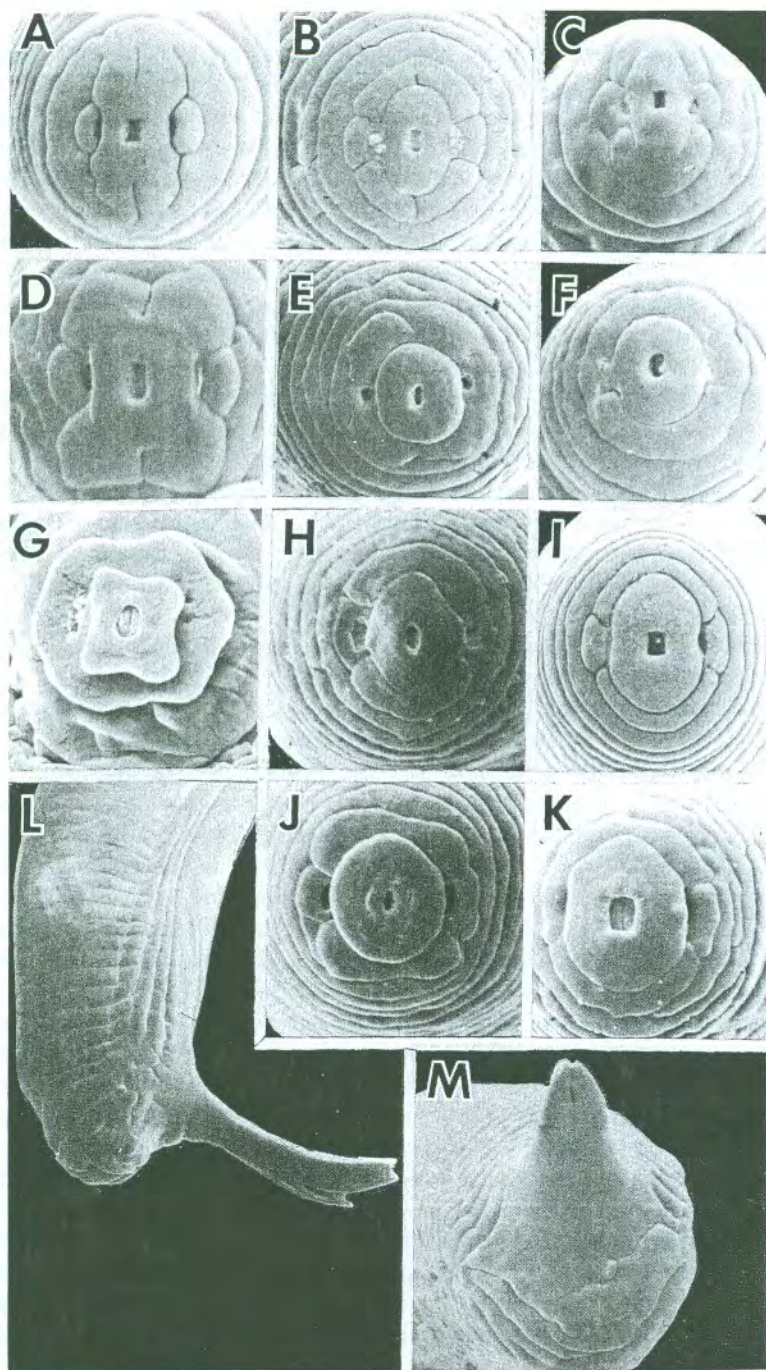


FIGURE 13 En face lip patterns and the terminal region of the male of Heteroderinae. (A) *Heterodera glycines*, second-stage juvenile (J2). (B) *Globodera rostochiensis*, J2. (C) *Punctodera chaltoensis*, J2. (D) *H. glycines*, male. (E) *G. rostochiensis*, male. (F) *P. chaltoensis*, male. (G) *H. trifolii*, female. (H) *Verutus californicum*, J2. (I) *Rhizonema sequoiae*, J2. (J) *V. californicum*, male. (K) *R. sequoiae*, male. (L) Terminal region of male of *H. schachtii* with bifid spicule tip. (M) End view of terminal region of *R. sequoiae* without bifid tip. (B, C, E, F after Othman et al., 1988; reprinted by permission, *Revue de Nematologie*; J after Baldwin et al., 1989, reprinted by permission *J. Nematol.*)



have complex ridges, or tubercles, but the patterns are highly variable, even within a given population (Fig. 13L, M).

The reproductive system of heteroderine males is composed of a pair of retractable copulatory spicules which protrude from a cloaca (Figs. 1, 13L, M). The cloaca leads to the vas deferens, which in turn connects with a single testes. The spicules have a broad proximal end, a cylindrical shaft, and a flattened pointed blade with incurved edges; the broad end is attached to two protractor muscles (Clark et al., 1973). The pair of blades interlock along part of their length to form a conduit for sperm transmission from the cloaca. The spicules are innervated and spicule neurons include those which terminate in a minute channel which opens near the tip. The tip may be rounded as in *Rhizonema* or *Globodera*. Conversely, it may be bifid as in *Heterodera*, *Cactodera*, and *Verutus* (Fig. 13L, M). Spicule length varies from 20 to 45  $\mu\text{m}$ , and reportedly it is 2.5–4% of male length (Geraert and DeGrisse, 1981); almost the entire range of length is expressed within some genera (e.g., *Heterodera* spp). The cuticle-lined tract in which spicules move is thickened dorsally, forming a gubernaculum.

The reproductive system of heteroderine males is linked to the digestive system through the common terminal duct, the cloaca. Although the stylet, dorsal esophageal gland orifice, esophagus, and intestine generally appear well developed and robust relative to infective juveniles, males apparently do not feed (Fig. 7E). This lack of feeding might be reflected, however, by diminutive esophageal musculature and dorsal gland (Baldwin et al., 1977; Baldwin, 1982). The excretory pore generally occurs at the level of the esophageal gland lobe.

The sensory system of heteroderine males includes well-developed amphids and six inner labial sensillae which open to the exterior and are probably chemoreceptive. In addition, four outer labial and four cephalic receptors terminate beneath the cuticle surface. Phasmids, while present in *Meloidodera*, are diminutive or absent in males of most heteroderines (Fig. 13L, M) (Carta and Baldwin, 1990a, b).

Second-stage juveniles of heteroderines are slender with a rounded anterior and tapering tail, with total body length varying from about 330 to 700  $\mu\text{m}$  (Figs. 1, 15A, D). Generally length is sufficiently stable within species to be a useful diagnostic character (Wouts and Weischer, 1977), although some rare populations include aberrant giant or dwarf juveniles (Mulvey, 1959, 1960a). As in males, the cuticle consists only of an A and B layer, although it is modified posteriorly to include a fibrous (collagenous?) hyaline region (Figs. 7C, 9, 15A, D). The length of this hyaline region varies among species and may be diagnostic.

Surface structures have been examined in second-stage juveniles of many heteroderines with SEM (Baldwin, 1986; Othman and Baldwin, 1985, 1986; Othman et al., 1986, 1988). The body is annulated and possesses lateral lines similar to that of males, except that they terminate relatively anteriorly on the tail, often only a few annules posterior to the phasmid opening (Fig. 7C). The basic surface pattern of the lip region of heteroderine juveniles is hexaradiate consisting of a labial disc surrounded by six lips, four submedial and two lateral (Fig. 13A–C, H, I). Posterior to the disc and lips, head annules vary in number among species and may be useful in some diagnoses. Contrary to some males, there are no longitudinal blocks. In addition to narrow submedial lips distinguishing *Sarisodera* or *Rhizonema* (Fig. 13I) and fusion of submedial lips with the labial disc characteristic of *Heterodera* (Fig. 13A), other features of lip patterns of juveniles are useful systematic characters. For example, *Punctodera* has submedial lips fused with head annules (Fig. 13C), and in *Atalodera*, *Thecavermiculatus*, and some cyst-forming genera, lateral lips are



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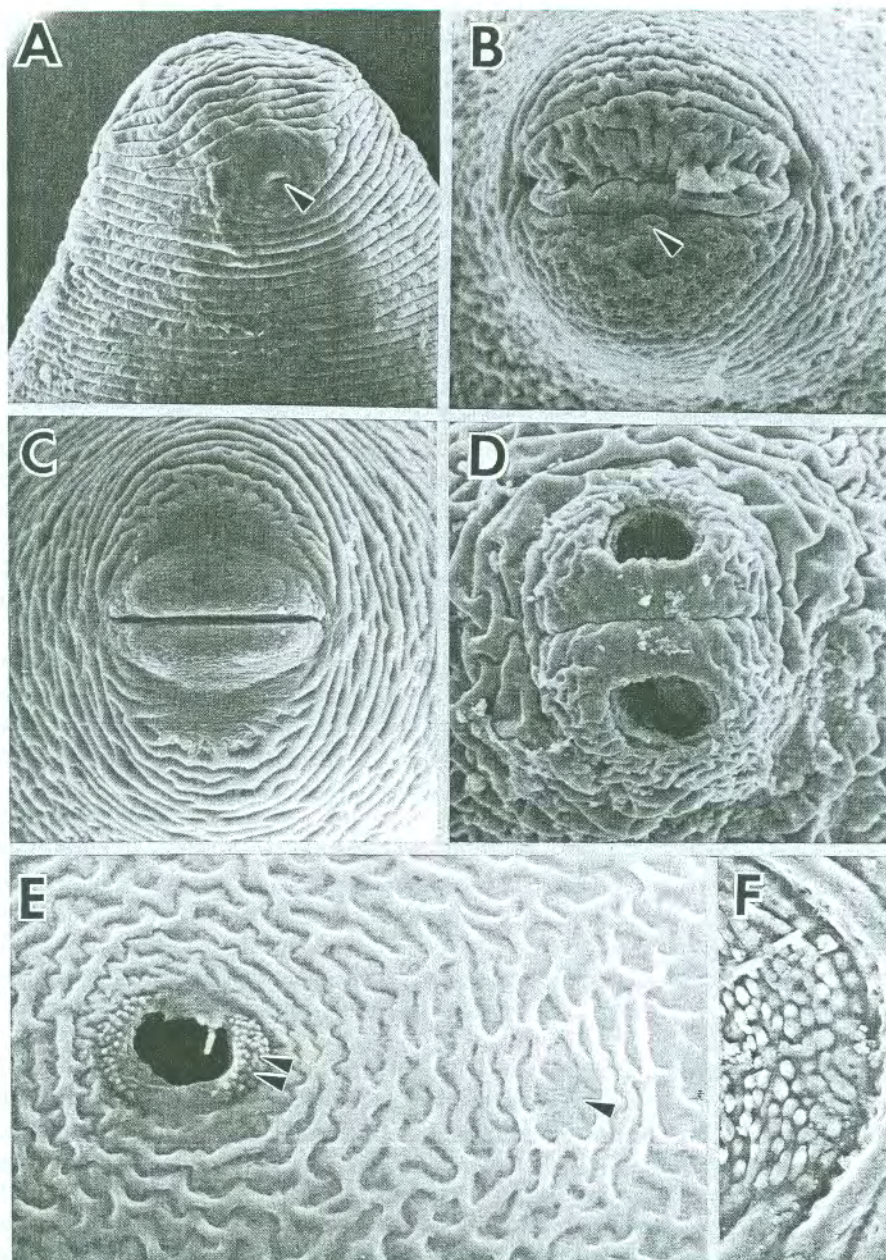


FIGURE 14 SEM of posterior region of Heteroderinae. (A) Female of *Verutus californicus* showing anus (arrowhead). (B) Female of *Atalodera lonicerae* showing vulval lips and anus (arrowhead). (C) Female of *Heterodera trifolii* showing vulval lips. (D) Cyst of *Heterodera fici* with semifenestra. (E) Cyst of *Globodera* sp. with circumfenestrae. Arrowhead indicates position of anus, double arrowheads indicate perineal tubercles on vulval crescent. (F) Enlargement of tubercles from E.



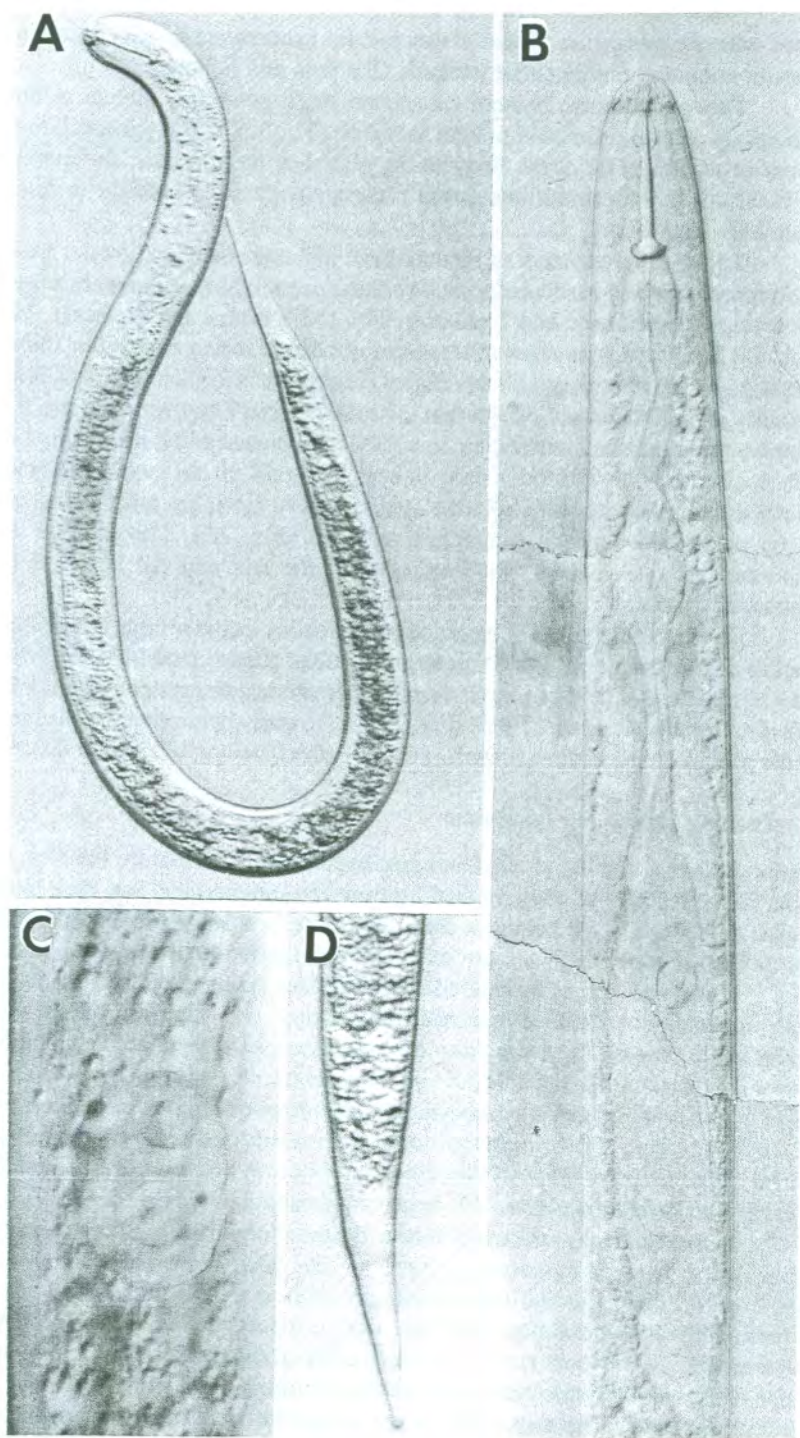


FIGURE 15 Morphology of second-stage juveniles (J2) of Heteroderinae. (A) Entire J2. (B) Anterior region showing stylet and ventral overlap of esophageal glands. (C) Genital premordium. (D) Hyaline region of tail.



fused with the labial disc. These distinctive lip patterns are relatively stable and useful in identification and phylogenetic analysis (Baldwin and Schouest, 1990).

The reproductive system of second-stage juveniles, including both males and females, is an oval primordium with four cells (Fig. 15C). The primordium occurs slightly posterior to the center of the body in the region of the intestine. In heteroderines with a terminal vulva, the primordium doesn't migrate posteriorly until the third stage and third molt (Fig. 1B).

The digestive system of second-stage juveniles includes a stylet whose length and knob morphology is particularly stable so that even minute differences may be diagnostic for species (Hirschmann and Triantaphyllou, 1979; Wouts and Weischer, 1977) (Figs. 15, 17A–C). The esophagus of juveniles resembles that of males, except that the musculature or dorsal gland are relatively well developed (Fig. 15B). The gland region fills the body width in nearly all heteroderines, except that in *Atalodera* and *Thecavermiculatus* it is particularly narrow, and it may be intermediate in width in *Hylonema* and *Verutus* (Figs. 15B, 25A, B). The position of the excretory pore is near the level of the esophageal gland lobe. The intestine, which may be highly vacuolated in starved juveniles, joins a muscular rectum and opens posteriorly through a cuticle-lined anus (Fig. 7C). The position of the anus is important because it marks the beginning of the tail, and tail length is often a useful diagnostic character.

The nervous system of heteroderine juveniles includes highly developed amphids as well as a full complement of 16 anterior sensillae (Endo, 1980). Posteriorly, the phasmid may terminate as a pore as in cyst-forming nematodes, or the opening may lead to a broad lenslike ampulla (Baldwin, 1985) (Fig. 7C, D). In many heteroderines, the internal structure of the phasmid may begin to deteriorate soon after hatching (Carta and Baldwin, 1990a, b).

#### 4. Feeding Habits and Parasitism

Heteroderinae are obligate sedentary parasites that feed as mature females, generally with most of their enlarged body protruding from the root surface, and their elongate anterior region embedded in the host root (Fig. 16). As second-stage juveniles, they induce highly specialized nurse cells which are sustained throughout the life of the parasite (Fig. 3).

Details of feeding by heteroderines has been documented throughout the life history with inverted interference contrast microscopy and high-resolution video-enhanced recording, by examining nematodes in vitro culture. After an infective juvenile settles in the region of the vascular cylinder, the stylet probes, and finally penetrates an adjacent cell. Ingestion of cell contents is associated with alternate stylet protrusion, intermittent pumping of the metacarpus, and synthesis in esophageal glands followed by release of contents of the dorsal gland ampulla through the stylet and into the host cell (Wyss and Zunke, 1986). During this initial contact the cell hypertrophies and a nurse cell begins to form.

Nurse cells may take many forms; the best known are multinucleate syncytia which are characteristic of cyst-forming genera (Fig. 3A). However, syncytia also occur in non-cyst-forming heteroderines including *Atalodera* and *Verutus*. Many non-cyst-forming genera, such as *Meloidodera* and *Sarisodera*, induce a single giant cell with one large nucleus (Fig. 3B). Nonheteroderines such as *Rotylenchulus* and *Meloidogyne* also induce nurse cells, but their similarity to those of heteroderines may be superficial. For example, the multinucleate nurse cells of *Meloidogyne* and *Rotylenchulus reniformis* are coenocytes because they originate by hypertrophy and karyokinesis without cytokinesis. This is in contrast to the heteroderine syncytium which forms from merging hypertrophied adjacent cells, apparently through enlargement of plasmodesmata openings between cells and putative dissolution of cell walls (Jones, 1981a, b; Mundo-Ocampo and Baldwin, 1983).





FIGURE 16 Females of *Heterodera schachtii* feeding on roots.

Nurse cells allow the parasite to sequester basic nutrients from adjacent plant tissues for nematode development and reproduction. The host, in response, continuously replaces the lost cell nutrients. The flow of nutrients from adjacent plant tissue to the nurse cell may be enhanced by increased numbers of plasmodesmata or by increased surface area associated with wall ingrowths, particularly in regions in contact with xylem (Fig. 3C, D). During prolonged feeding, both single uninucleate giant cells and syncytia increase in size, first expanding toward the root stele, and then extending several millimeters longitudinally. As the nurse cell increases in size, adjacent cells may be crushed and hyperplasia may occur in surrounding tissues. Nurse cells typically have a feeding tube and a plug or thickening of the cell wall around the point of stylet penetration. Their dense cytoplasm appears to be the result of loss of a central vacuole and replacement with numerous small vacuoles, as well as abundant organelles including mitochondria, plastids, and Golgi (Endo, 1987; Jones, 1981a, b). Whether the nurse cell has one or many nuclei, the nuclear and nucleolar volume is greatly increased, and multilobed (Fig. 3A, B). Conditions unfavorable for development of the nematode such as a resistant host may be associated with a "hypersensitive response," i.e., the nurse cell is not adequately established and is surrounded by localized lignification and necrotic brown tissue which, at least in potatoes, is autofluorescent (Robinson et al., 1988).

### B. Agricultural Importance

The worldwide agricultural impact of cyst nematodes is probably second only to root-knot nematodes. Cyst nematodes are set apart by the number of highly pathogenic species specialized on major agricultural commodities including grains, root crops, and most



legumes. Many of the most serious cyst nematode pests are spread worldwide, in part because eggs in cysts remain viable under conditions of dispersal that would be fatal to most nematodes. Protective cysts often confound management practices which would be effective against other nematodes; they may escape nematicides and only long rotations may be effective. Furthermore the value of many resistant varieties is sometimes limited by "resistance-breaking" pathotypes or races.

Although worldwide losses to cyst nematodes are considerable, they are difficult to quantify, in part because many costs are indirect. Losses are indirect through interactions with other biotic factors including pathogenic bacteria, fungi, and probably viruses. Miller (1986) citing the work of Evans and Brodie (1980) notes, for example, that losses to potato cyst nematode are particularly high in the presence of *Verticillium*. These interactions may be facilitated by wounds associated with penetration of juveniles as well as physiological changes of the host which result in increased susceptibility to secondary pathogens. Losses of soybean to *H. glycines* are increased by inhibition of root nodulation of nitrogen-fixing bacteria (Lehman et al., 1971). Similarly, nitrogen fixation on peas is inhibited by *H. goettingiana* (Fig. 19B, C). Losses to cyst nematodes may also be compounded by abiotic factors. In Mexico, *Punctodera chacoensis* may reduce yields on corn (*Zea mays*) by nearly 100%, but losses reportedly can often be offset by increased water and fertilizer. On the other hand, Mai (1977) notes that losses to potato cyst nematode may result in a harvest less than the seed pieces, even with heavy application of fertilizer. Symptoms similar to nutrient deficiencies are common, but their expression varies with the crop and depends on soil texture, nutrient makeup, and pH. Greater susceptibility to damage by heat and draught is widely reported as a result of heteroderine infection (Barker and Lucas, 1984; Steele, 1984), but expression of these symptoms is clearly affected by condition such as soil type. Cost of additional fertilizer and water must be considered in assessing damage by cyst nematodes. Other losses include expenses of management including nematicides. Other subtle losses are due to rotation with crops of lesser value or use of resistant varieties which sometimes require compromises in desirable qualities or yield. Since cultivars resistant to heteroderines typically have a hypersensitive reaction to infection, the plants may be adversely affected by invasion of juveniles and unsuccessful nurse cells. Quarantine against cyst nematodes adds to economic losses, with regulation of the potato cyst nematode in the USA being one of the most extensive and expensive (Mai, 1977; Miller, 1986). In some cases losses to cyst nematodes have been exacerbated through closed markets, with clean produce being rejected from an area wider than the actual region of infestation; in other cases markets may be closed to "harmless" species, subspecies, or races which are not readily distinguished from a related pathogen. Indirect losses to cyst nematodes measured in the expense of research programs, such as breeding for resistance, are nearly impossible to estimate but undoubtedly add greatly to the expense of coping with heteroderines.

Losses to cyst nematodes may be dramatic including deformed roots (e.g., carrots, potatoes), necrosis, and plant death. More often damage is subtle, with unevenly distributed nematodes apparent in a field as patches of stunted growth, vulnerable to water stress and wilt (Figs. 18–20, 22, 23). Stunted plants may be chlorotic, sometimes with browning of leaf margins or read veining. Often symptoms can be confused with other problems of crop production including nutrient deficiencies, soil compaction, or toxicity from agricultural chemicals (Moore, 1984). The means by which cyst nematodes induce poor growth is not fully understood. Often it is suggested that feeding interferes with water and nutrient absorption, perhaps through blocked vessels or mechanical damage related to the expansion of nurse cells. Conversely, Seinhorst (1986) notes that plant weights may be greatly reduced without visible signs of root damage; he suggests that the primary effect of cyst nematodes,

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even at small densities, is reduced growth by retarded development, and that secondary effects may be decreased water consumption, early senescence, and perhaps reduced potassium content. Seinhorst's view of retarded development may be consistent with observations of Norton (1984) that corn plants infected with *H. avenae* were only 2 feet tall in mid-August with no inflorescences, whereas unaffected plants were 6 feet tall with fully formed tassels. Similar observations are made on corn infected with *H. zea* (Koshy et al., 1970b) and *P. chalconensis* (Jeronimo, 1988).

Although the heteroderines include some of the most destructive pests of agriculture, investigation of their unusual characteristics may be a valuable source of insight into basic biology. The usual host-parasite relationship in which the nematode alters the development of host cells, after years of investigation, continues to confound understanding. However, new tools of specific labeling and monoclonal antibodies promise insight into these mechanisms and perhaps into processes of host differentiation in general (Hussey, 1988). Heteroderines have contributed to pioneering investigations of pheromones and other attractants of nematodes, although there are many opportunities for further investigation of communication between nematodes as well as host specialization. Heteroderines, with their remarkable persistence in a cyst, may prove to be good tools for investigation of diapause in general. Heteroderines may also contribute to our general understanding of evolution. They are well suited to phylogenetic investigation because they can often be obtained in large numbers, often can be grown under controlled conditions on tissue cultured hosts, and they have a range of characters which can be scrutinized from living cultures with respect to comparative development, fine structure, and molecular biology.

## II. TAXONOMY

### A. Genera

#### 1. Relationships

Insight into phylogenetic relationships of Heteroderinae is essential to a useful, stable taxonomic system which readily accommodates discoveries of new species. Yet phylogenetic relationships both of Heteroderinae to other Tylenchida and within Heteroderinae are controversial. Difficulties in determining phylogenetic relationships are due to the large number of genera and paucity of known reliable characters.

The taxonomic relationship of Heteroderinae to other Tylenchida historically has implied a unique common ancestor between cyst nematodes and root-knot nematodes. From 1909, these nematodes generally shared the same genus until Chitwood (1949) clearly described root-knot nematodes and recognized the genus *Meloidogyne* as separate from *Heterodera*. The relationship between the two genera was believed to be further strengthened by description of *Meloidodera* as an "intermediate noncyst forming link" between *Heterodera* and *Meloidogyne* (Chitwood et al., 1956). The proposed close relationship between *Heterodera* and *Meloidogyne* was believed to be supported not only by this intermediate, but by the shared characters of enlarged sedentary females and sexual dimorphism, males lacking caudal alae, and perhaps inducement of multinucleate nurse cells for feeding. Many systematic schemes, while recognizing a close relationship between heteroderines and meloidogynines, have also suggested close phylogenetic ties with other Tylenchida with globose females including *Tylenchulus*, *Rotylenchulus*, and *Nacobus*. In their reappraisal, Luc et al. (1988) underscore the historical view of a shared ancestor between heteroderines and root-knot nematodes, considering Heteroderidae as including



Heteroderinae (e.g., *Heterodera*: cyst nematodes, *Meloidodera*: noncyst nematodes) and Meloidogyninae (e.g., *Meloidogyne*: root-knot nematodes); they also include Nacobdoderinae, an unusual group of three rare species in *Nacobdodera*, *Meloinema*, and *Bursadiera*.

An alternate view of phylogenetic relationships is that the heteroderines and root-knot nematodes are "widely separated" (Wouts and Sher, 1971) and that their shared character is the enlarged female, and considered the shape of the male and loss of caudal alae as secondary adaptations to this shape. Therefore Wouts (1973a) proposed separate families, Heteroderidae (e.g., *Heterodera*, *Meloidodera*) and Meloidogynidae (*Meloidogyne*). Wouts (1973a) suggests that the Heteroderidae arose from vermiform, didelphic Hoplolaiminae with annulations, a short tail, large phasmids, and longitudinal lip striae. Ultrastructural evidence on host responses, the esophagus, cuticle, lip patterns, and other characters underscore the disparity between heteroderines and meloidogynines, and strengthens arguments of common ancestry between heteroderines and hoplolaimids.

Hypotheses of phylogenetic relationships within Heteroderinae based primarily on classical characters were proposed by Ferris (1979) and Wouts (1985). Baldwin and Schouest (1990) introduced a number of new characters and a more detailed analysis of classical characters for a parsimonious computer-generated phylogenetic analysis. Results supported three distinct groups of genera, designated as tribes within Heteroderinae: Sarisoderini, Ataloderini, and Heteroderini. Verutini, Cryphoderini, and Meloidoderini, while basically monogeneric, are also included to indicate equivalent sister group rank (Table 1). Each of these three groups of genera is supported as a line originating from a unique common ancestor; in addition, Ataloderini and Heteroderini are proposed as collectively having a unique common ancestor. New evidence to test hypotheses of relationships among heteroderines, meloidogynines, and hoplolaimids as well as within Heteroderinae will undoubtedly be forthcoming through ultrastructural, developmental, and molecular biological approaches.

Although Heteroderinae includes 17 genera, major agricultural pathogens primarily occur in three cyst-forming genera: *Heterodera*, *Globodera*, *Punctodera* (Table 1).

### *Heterodera*

*Heterodera* Schmidt, 1871

- syn. *Tylenchus* (*Heterodera*) Schmidt, 1871
- Heterodera* (*Heterodera*) Schmidt, 1871
- Heterobolbus* Raillet, 1896
- Bidera* Krall and Krall, 1981
- Ephippiodera* Shagalina and Krall, 1981

**Diagnosis:** Heteroderinae Filipjev and Schuurmans Stekhoven

**Females.** Cyst present. Body more or less lemon-shaped, with posterior cone. Cuticle surface with zig-zag pattern of ridges; D layer diminutive; absent in young females and in cone of mature females.\* Vulva terminal. Vulva area of cyst with two fenestrae (ambifenestrated or bifenestrated); no anal fenestration. Underbridge generally present; perineal tubercles absent. Bullae present or absent. Eggs retained in body; in some cases egg masses also present; egg surface smooth.

\* Based on previous reports (Shepherd et al., 1972), Luc et al. (1988) considered absence of a D layer a character of *Heterodera*. Recent investigations suggest a rudimentary D layer anterior to the cone in mature females (Cordero, 1989).



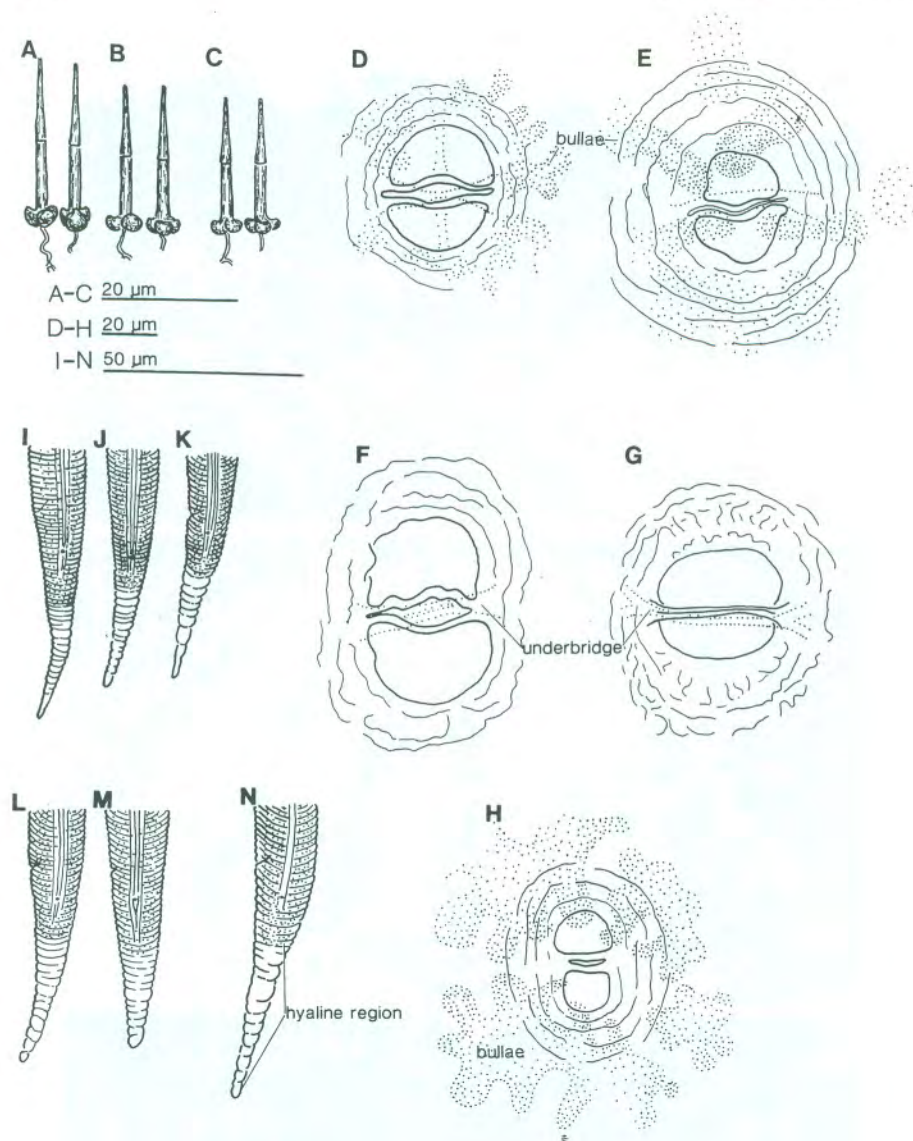


FIGURE 17 Characteristics for identification of some species of *Heterodera*. (A) *Heterodera trifolii*, second-stage juvenile (J2) stylet (left dorsal, right lateral view). (B) *Heterodera glycines*, J2 stylet. (C) *Heterodera zaeae*, J2 stylet. (D) *H. glycines*, terminal region of cyst; (E) *H. zaeae*, terminal region of cyst. (F) *Heterodera cruciferae*, terminal region of cyst. (G) *H. carotae*, terminal region of cyst. (H) *Heterodera avenae*, terminal region of cyst. (I) *H. trifolii*, J2 tail. (J) *H. glycines*, J2 tail. (K) *H. zaeae*, J2 tail. (L) *Heterodera goettingiana*, J2 tail. (M) *H. cruciferae*, J2 tail. (N) *H. avena*, J2 tail. (A, B, I, J redrawn after Hirschmann, 1956.)





FIGURE 18 Field damage by *Heterodera* spp. (A) *Heterodera schachtii* on cabbage. (Courtesy H. L. Rhoades.) (B) *H. schachtii* on red table beet. (C) *Heterodera glycines* on soybean. (A, courtesy H. L. Rhoades; B, courtesy J. L. Townshend; C, courtesy R. S. Hussey. )

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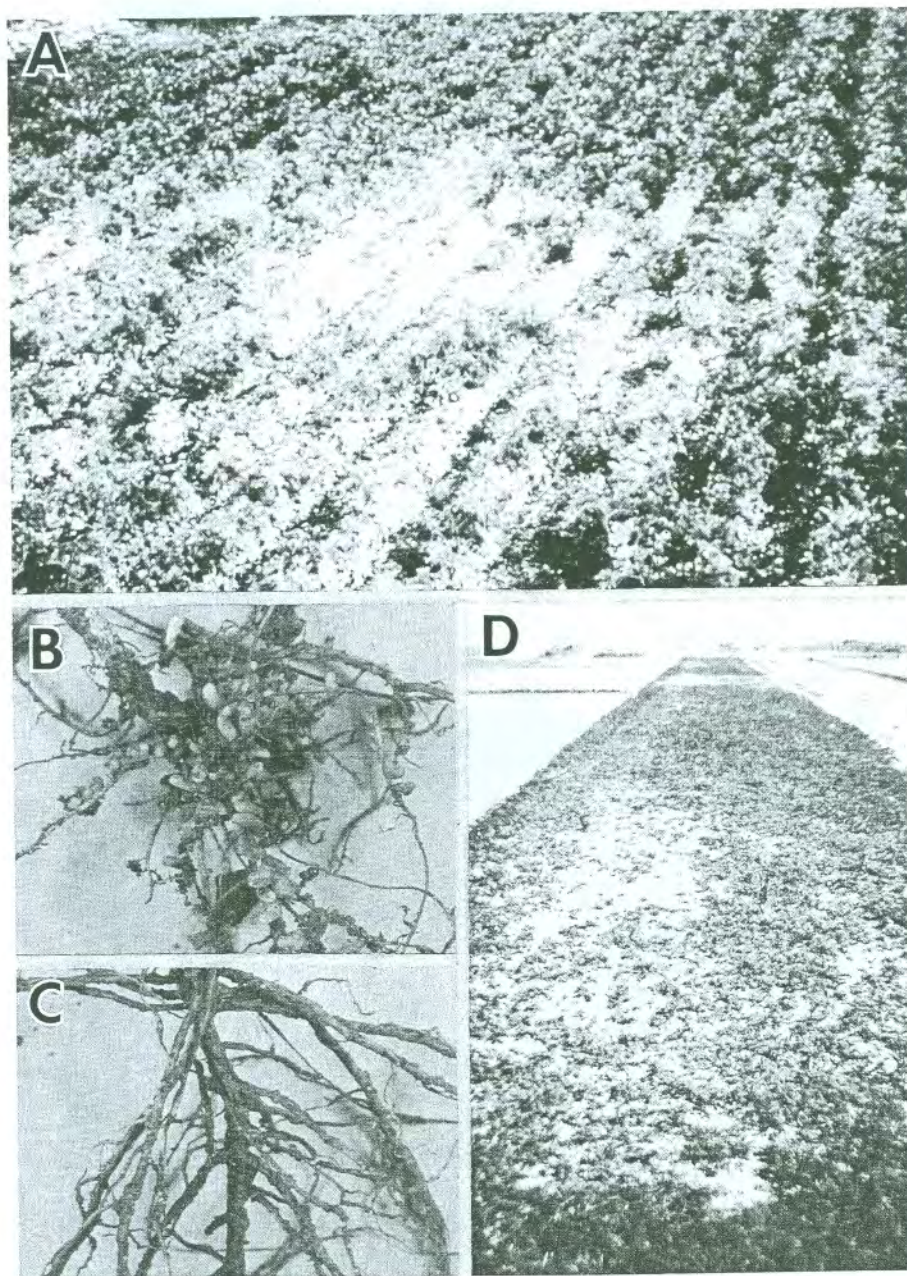


FIGURE 19 Field damage by *Heterodera* spp. (A) *Heterodera goettingiana* on peas. (B) Control lacking *H. goettingiana* and with extensive nodulation. (C) *H. goettingiana* inhibition of nitrogen-fixing nodulation on pea. (D) Damage by *Heterodera carotae* on carrot. (A–C courtesy C. Green; D, courtesy N. Greco.)





FIGURE 20 Field damage by *Heterodera avenae*. (A) Wheat crop (left) is severely chlorotic following attack by *H. avenae*. Rye (right) is tolerant, remaining green. (B) Field damage on oats. (A and B courtesy F. Green.)



*Males.* Body twisted. Lateral field with four (rarely three) lines. Spicules  $> 30 \mu\text{m}$  long, distal extremity with single or more often bifid distal tip.

*Second-stage juveniles.* Lateral field with four (rarely three) lines. Esophageal glands filling body cavity. Tail conical, pointed; hyaline part variable, generally half tail length. Phasmids opening porelike. En face pattern with fusion of submedial lips with labial disc.

*Nurse cell.* Syncytium generally with wall ingrowths.

*Species.* (Table 2)

*Identification.* Although *Heterodera* includes nearly 60 species, many of these are only found in limited regions or restricted hosts, so that routine identification of the economically most important species in a given region can be simplified. In addition, three groupings of related species are recognized within *Heterodera*, so that familiarity with characteristics of each species group can quickly narrow choices. Comparison and keys to all the species of *Heterodera* is beyond the scope of this chapter and nearly comprehensive keys are published elsewhere (e.g., Golden, 1986). Instead we have selected representatives of the *schachtii*, *goettingiana*, and *avenae* groups based on broad distribution, economic importance, and recent awareness and interest (Table 3; Fig. 17). The *schachtii* group has a long vulval slit ( $> 35 \mu\text{m}$ ), is ambifenestrate, and bullae and underbridge are well developed. The *goettingiana* group has a long vulva slit ( $> 30 \mu\text{m}$ ), underbridge is absent or very slender and weakly developed, ambifenestrate or bifenestrate, and bullae are absent. The *avenae* group has a short vulval slit ( $< 16 \mu\text{m}$  long), is bifenestrate, and bullae and underbridge may or may not be present (Mulvey, 1972). Morphometrics of many populations of a given species has made it possible to identify a few reliable characters as aids to preliminary identification (Table 3; Fig. 17). In addition, increasing recognition is being given to the value of second-stage juveniles for identification (Wouts and Weischer, 1977). Confirmation of identity requires more thorough examination of descriptions and comparison with closely related species of the three basic groups (Table 2).

*Heterodera schachtii* A. Schmidt 1871 (the sugar beet cyst nematode)

*Synonymns and history.* The sugar beet nematode, *H. schachtii*, devastated sugar beet production in Europe during the second half of the nineteenth century (Thorne, 1961). Previously, poor growth of sugar beets was associated with "exhausted soils" resulting from continuous planting without rotation, but in 1850 Schmidt observed that stunted beets were covered with fine hairs full of white bodies. He subsequently described the white bodies as a nematode pathogen and identified common cultural practices contributing to the dispersal of the nematode throughout production areas in Europe (Filipjev and Schuurmans Stekhoven, 1941; Thorne, 1961).

The sugar beet cyst nematode was taxonomically described from the host *Beta vulgaris* L. and from a locality near Aschersleben, East Germany by A. Schmidt (1871) and named *Heterodera schachtii* in honor of Schacht (Raski, 1950). shortly after its description, Orley placed *H. schachtii* in a different genus, *Tylenchus schachtii* (Schmidt, 1871) Orley, 1880. During a period of confusion concerning races of cyst nematode (see history of *G. rostochiensis* below), the sugar beet cyst nematode was designated *H. schachtii minor* by O. Schmidt (1930) to distinguish it from the oat cyst nematode. However, Franklin (1940) designated the "beet strain" as a separate species which regained the original name of *H. schachtii* A. Schmidt.

*Hosts.* Although *H. schachtii* is primarily associated with *B. vulgaris*, its host range extends to *Spinacea* (spinach), *Brassica* (cabbage, brussels sprouts, cauliflower, broccoli, turnip), *Raphanus* (radish), and a diversity of common weeds of the Brassicaceae



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Brassicaceae

TABLE 2 Species of *Heterodera*

*Schachtii* Group

- Heterodera schachtii* A. Schmidt, 1871  
syn. *Tylenchus schachtii* (A. Schmidt, 1871) Orley, 1880  
syn. *Heterodera schachtii minor* O. Schmidt, 1930  
*H. amygdali* Kirjanova and Ivanova, 1975  
*H. cajani* Koshy, 1967  
syn. *H. vigini* Edward and Misra, 1968  
*H. ciceri* Vovlas, Greco, and Di Vito, 1985  
*H. daverti* Wouts and Sturhan, 1979  
*H. elachista* Ohshima, 1974  
*H. fici* Kirjanova, 1954  
*H. galeopsidis* Goffart, 1936  
syn. *H. schachtii galeopsidis* Goffart, 1936  
*H. gambiensis* Merny and Netscher, 1976  
*H. glycines* Ichinohe, 1952  
*H. lespedezae* Golden and Cobb, 1963  
*H. leuceilyma* Di Edwardo and Perry, 1964  
*H. limonii* Cooper, 1955  
*H. medicaginis* Kirjanova in Kirjanova and Krall, 1971  
*H. oryzae* Luc and Berdon Brizuela, 1961  
*H. oryzicola* Rao and Jayaprakash, 1978  
*H. oxiana* Kirjanova, 1962  
*H. rosii* Duggan and Brennan, 1966  
*H. sacchari* Luc and Merny, 1963  
*H. salixophila* Kirjanova, 1969  
*H. sonchophila* Kirjanova, Krall, and Krall, 1976  
*H. sorghi* Jain, Sethi, Swarup, and Srivastava, 1982  
*H. tadshikistanica* Kirjanova and Ivanova, 1966  
*H. trifolii*, Goffart, 1932  
syn. *H. schachtii* var *trifolii* Goffart, 1932  
*H. paratrilolii* Kirjanova, 1961  
*H. rumicis* Poghossian, 1961  
*H. scleranthii* Kaktina, 1957  
*H. zae* Koshy, Swarup, and Sethi, 1971

*Goettingiana* Group

- H. bergeniae* Maqbool and Shahina, 1988  
*H. canadensis* Mulvey, 1979



TABLE 2 (Continued)

- H. cardiolata* Kirjanova and Ivanova, 1969  
*H. cruciferae* Franklin, 1945  
*H. cyperi* Golden, Rau, and Cobb, 1962  
*H. delvii* Jairajpuri, Khan, Setty, and Govindu, 1979  
*H. goettingiana* Liebscher, 1892  
*H. graminis* Stynes, 1971  
*H. graminophila* Golden and Birchfield, 1972  
*H. humuli* Filip'ev, 1934  
*H. longicolla* Golden and Dickerson, 1973  
*H. mediterranea* Volvas, Insera, and Stone, 1981  
*H. menthae* Kirjanova and Narbaev, 1977  
*H. methwoldensis* Cooper, 1955  
*H. mothi* Khan and Husain, 1965  
*H. pakistanensis* Maqbool and Shahina, 1986  
*H. phragmitidis* Kazachenko, 1986  
*H. plantaginis* Narbaev and Sidikov, 1987  
*H. polygoni* Cooper, 1955  
*H. graduni* Kirjanova, 1971  
*H. raskii* Basnet and Jayaprakash, 1984  
*H. urticae* Cooper, 1955  
*H. uzbekistanica* Narbaev, 1980

#### Avenae Group

- H. arenaria* Cooper, 1955  
 syn. *Bidera arenaria* (Cooper, 1955) Krall and Krall, 1978  
*H. avenae* Wollenweber, 1924  
 syn. *H. schachtii* var. *avenae* Wollenweber, 1924  
*H. Bidera avenae* (Wollenweber, 1924) Krall and Krall, 1978  
*H. schachtii major* O. Schmidt, 1930  
*H. major* O. Schmidt, 1930  
*H. ustinovi* Kirjanova, 1969; Krall and Krall, 1978  
*H. bifenestra* Cooper, 1955  
 syn. *H. Bidera bifenestra* (Cooper, 1955) Krall and Krall, 1978  
*H. longicaudata* Seidel, 1972  
*H. Bidera longicaudata* (Seidel, 1972) Krall and Krall, 1978  
*H. filipjevi* (Madzhidov, 1981) Stone, 1985  
 syn. *Bidera filipjevi* Madzhidov, 1981  
*H. hordecalis* Andersson, 1975  
 syn. *Bidera hordecalis* (Andersson, 1975) Krall and Krall, 1978.



TABLE 2 (Continued)

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|   |
|---|
| <i>H. iri</i> Mathews, 1971   |
| syn. <i>Bidera iri</i> (Mathews, 1971) Krall and Krall, 1978                              |
| <i>H. latipons</i> Franklin, 1969   |
| syn. <i>Bidera latipons</i> (Franklin, 1969) Krall and Krall 1978                         |
| <i>Ephippiodera latipons</i> (Franklin, 1969) Shagalina and Krall, 1981                   |
| <i>H. mani</i> Mathews, 1971  |
| syn. <i>Bidera mani</i> (Mathews, 1971) Krall and Krall, 1978                             |
| <i>H. turcomanica</i> Kirjanova and Shagalina, 1965                                       |
| syn. <i>Bidera turcomanica</i> (Kirjanova and Shagalina, 1965) Krall and Krall, 1978      |
| <i>Ephippiodera turcomanica</i> (Kirjanova and Shagalina, 1965) Shagalina and Krall, 1981 |

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Source: Adapted from Luc et al., (1988).

(Cruciferae) and Chenopodiaceae families. Although Solanaceae are generally not hosts, some *H. schachtii* isolates have been reported to develop on tomato. Discrepancies occur among the large number of host range tests (Filipjev and Schuurmans Stekhoven, 1941; Franklin, 1972; Griffin, 1982; Raski, 1952; Steele, 1965; Winslow, 1954), which could reflect differences among isolates including physiological races (Miller, 1983). Other discrepancies may occur because juveniles penetrate the roots of some plants which are unable to sustain feeding, development, and reproduction; such plants might be included in host lists but their inclusion could be misleading. Although *H. schachtii* has a broad host range, damage to the sugar beet production is generally of greatest importance (Graney and Miller, 1982). Franklin (1972) suggested that damage to other brassicas occurs rarely and is associated with very high initial inoculum but in the USA, Canada, and Poland a number of brassicas are severely affected including table beets (Brzeski, 1969; Miller, 1986) (Fig. 18A, B). Griffin and Waite (1982) suggest that *H. schachtii* is a potential threat to tomato production, particularly when it occurs in combination with root-knot nematodes. However, in California, tomatoes in rotation with sugar beets for many years are not affected by *H. schachtii*, regardless of whether or not root-knot nematodes are present (Thomason, pers. commun.).

**Distribution.** *Heterodera schachtii* favors temperate regions but apparently tolerates a broad range of climates; it is widespread in Europe, the United States, and Canada. Thorne (1961) believed that some populations of *H. schachtii* were introduced to the USA on sugar beets, but considered other populations to be indigenous to weed hosts in the southwestern deserts of the USA including those of Utah and California. *Heterodera schachtii* also occurs in parts of the Middle East and USSR, western and southern Africa, Australia, Chile, and Mexico. It is readily dispersed with soil and plant parts, an important consideration in control (see below).

**Biology.** Lemon-shaped cysts remain dormant in the soil from one host season to the next with only a percentage hatching and emerging each year. Consequently, large populations accumulate with continuous planting of sugar beet. Fully developed eggs containing second-stage juveniles hatch in response to the stimulus of root exudates and emerge from the cyst. Hatching is favored at 25°C and can be stimulated by host and nonhost root exudates and may even occur in the absence of exudates. Second-stage



TABLE 3 Compendium for Identification Among Select Heteroderidae of Particular Economic Significance (Fig. 17).

| <i>Schachtii</i> Group: Bullae and underbridge well developed; vulval slit > 35 μm, ambifenestrate                                |                                     |                             |                            |                                  |          |
|---|-------------------------------------|-----------------------------|----------------------------|----------------------------------|----------|
| Species   | Bullae                              | J2 stylet length (μm)       | J2 tail length (μm)        | J2 stylet knobs shape            | Hosts    |
| <i>H. schachtii</i>   | Scattered                           | 25–27                       | 48–55                      | Anchor                           | Wide     |
| <i>H. glycines</i>  | Scattered                           | 22–25                       | 40–49                      | Subventral rounded               | Wide     |
| <i>H. trifolii</i>  | Scattered                           | > 27                        | > 55                       | Anchor                           | Wide     |
| <i>H. zeae</i>  | Four distinct “fingers”             | < 22                        | 40–49                      | Concave on top                   | Graminae |
| <i>Goettingiana</i> Group: No bullae, underbridge poorly developed or absent; vulval slit > 30 μm; ambifenestrate or bifenestrate |                                     |                             |                            |                                  |          |
| Species   | Underbridge                         | Egg mass                    | J2 hyline part tail μm     | Hosts                            |          |
| <i>H. goettingiana</i>  | Slender but present                 | Small                       | > 34                       | Legumes                          |          |
| <i>H. crucifera</i>   | Slender but present                 | Small                       | < 26                       | Crucifers (especially Brassicae) |          |
| <i>H. carotae</i>   | Very thin; rarely persists in cysts | Large, often size of female | 26–32                      | Carrots                          |          |
| <i>Avenae</i> group: Bullae and underbridge present or absent; short vulval slit (< 16 μm), bifenestrate                          |                                     |                             |                            |                                  |          |
| Species   | Bullae                              | Underbridge                 | J2 lateral field           | Width vulval bridge (μm)         |          |
| <i>H. avenae</i>  | Well-developed                      | present                     | Four lines outer two faint | Wide; 18–39                      |          |

juveniles have greatest motility in soil at 15°C in soil that is less than saturated. They penetrate the epidermal host root tissue behind secondary root tips and become sedentary in the vicinity of the vascular tissue where they induce formation of syncytial nurse cells. Rate of development is optimal at 18–28°C, with adults occurring about 18 days after penetration and brown cysts developing in about 38 days (Franklin, 1972; Griffin, 1988; Raski, 1950). The white females protrude from host roots and attract males for copulation and fertilization. Gravid females secrete a gelatinous matrix into which they may deposit more than 100 eggs (Raski, 1950); but as many as 600 eggs may persist in the female body and young cyst (Raski, 1950; Thorne, 1961). Early in the season when hosts are vigorous, some eggs may hatch almost immediately and multiple generations occur in a single growing season. But late in the season, as plant roots deteriorate, cysts full of eggs are released into the soil until conditions are suitable for hatch and infection.



**Control.** The first line of defense against *H. schachtii* is to exercise extreme caution to prevent its spread to noninfested areas. The previous practice of moving tare soil from factories back into fields resulted in spread in many growing areas in the USA (Thomason, pers. commun.). Similarly, cysts may be spread by canal water (Faulkner and Bolander, 1966) and farm machinery. They may also be dispersed by survival in the digestive tract of cattle grazing postharvest sugar beet residue (Kontaxis et al., 1971).

Attempts to develop commercially acceptable cultivars of sugar beet with resistance to *H. schachtii* have not yet been successful, so that most practices aimed at management of this pest include rotations with nonhosts. Rotation with grains or leguminous crops is effective, particularly if sugar beets are limited to one year in five, but this approach is costly. Chemical control is difficult because eggs and juveniles in the cyst may be somewhat protected; it is also expensive and may be environmentally hazardous. Nevertheless, nematocides, including aldicarb and 1, 3-dichloropropene, have been important in reducing yield loss where long rotations are not practical (Miller, 1986). Müller (1986) considers trap crops risky, but suggests that rotation combining green manure with resistant crucifers may effectively reduce populations. Since natural antagonists of the sugar beet cyst nematode are abundant, biological control may eventually prove useful in managing these nematodes.

*Heterodera trifolii* Goffart, 1932 (the clover cyst nematode)

**Synonyms and history.** White clover (*Trifolium repens* L.) is frequently unthrifty and wilted during warm weather in Europe and the causal agent was recognized as clover cyst nematode. The nematode was first described as *H. schachtii* var. *trifolii* Goffart, 1932 but no type material was designated. A cyst-infected piece of clover root from Goffart's collection could have provided type specimens but the tissue was lost during an attempt at remounting. Therefore, a cyst with eggs from a new collection on *T. repens* near Rendsburg, Schleswig-Holstein, Germany, believed to approximate the type locality, was designated a neotype (Wouts and Sturhan, 1978) [It is noteworthy, however, that Mulvey and Golden (1983) and Mulvey and Anderson (1974) indicate the type host as *Trifolium pratense*.] Goffart's original collection, like the neotype, apparently came from a population without males; in this respect *H. trifolii*, a mitotic parthenogenetic species, is distinct from *H. diverti*, a cyst nematode of clover which has abundant males and is cross-fertilizing (Wouts and Sturhan, 1978). In the years following the original description of *H. trifolii*, its distinctiveness from *H. glycines* with respect to morphology and host range was not clear until Hirschmann's (1956) detailed comparisons clearly defined the two species. The monosexual species *Heterodera lespedezae* (described above in relation to *H. glycines*) and *H. galeopsidis* are regarded as closely related to *H. trifolii*, and it is suggested that these and certain other species may be polyploid forms ( $2n = \text{about } 27$ ) that have evolved from diploid amphimictic relatives of the *H. schachtii* group ( $n = 9$ ) (Fig. 5). As such they may best be represented as subspecies within a species complex (Triantaphyllou and Hirschmann, 1978; Maas et al., 1982; Sikora and Maas, 1986). Other species have been proposed as distinct from *H. trifolii* but are included as junior synonyms by Luc et al. (1988); these are *H. paratrilfolii* Kirjanova and Ivanova, 1966; *H. rumicis* Poghossian, 1961; and *H. scleranthii* Kaktina, 1957.

**Host range.** *Heterodera trifolii* has a broad host range within the pea family *Fabaceae* (Leguminosae) including *Trifolium* (clover), *Medicago* (alfalfa), *Lespedeza*, *Glycine* (soybean, some cultivars), *Pisum* (pea), and *Phaseolus* (greenbean). It also attacks many nonlegumes representing diverse families; genera including *Dianthus* (carnation), *Vinca* (vetch), *Lotus*, *Melilotus*, *Spinacea* (spinach), *Polygonum*, *Rumex*, and *Chenopodium* (Thorne, 1961; Norton and Isely, 1976; Mulvey and Anderson, 1974). Individual



populations vary in host range (Maas et al., 1982), an important consideration in pest management strategies. In addition, the broad host range of *H. trifolii* indicates the importance of considering reservoirs of the pathogen in control.

**Distribution.** *Heterodera trifolii* is present throughout Europe as well as the USSR; it has also been reported in the Mediterranean region including Israel and Libya. It is present in Australia, New Zealand, and India. *Heterodera trifolii* may be the most widely dispersed cyst nematode in North America, reported primarily in pastures and turf with white clover in 30 of the United States including Hawaii, and throughout southern Canada (Mulvey and Anderson, 1974; Mulvey and Golden, 1983). Although the nematode may be indigenous to both North America and the Old World, some speculate that the nematode was introduced to North America. Indeed, some suggest that cysts could be dispersed long distance by bird migrations (Sikora and Maas, 1986) as has also been reported for *H. glycines* (Epps, 1971).

**Biology.** Young females lay eggs in a gelatinous matrix but as the female matures eggs are retained and persist in the cyst (Mulvey, 1959). Hatching of second-juveniles from eggs in the cyst takes place over a period of years whenever moisture requirements are favorable and requirements for breaking diapause are met. Hatch occurs over a temperature range of 4–31°C, but optimum temperature is 17.2°C (Oostenbrink, 1967). Hatch may also be favored by the presence of certain host leachates, but not all hosts seem to affect hatch (Winslow, 1955). Following the penetration of the root tips and establishment of a feeding site near the stele (Mankau and Lindford, 1960), the rate of development is primarily affected by soil temperature. At an optimum of about 25°C the life cycle is completed in 17 days (Norton, 1967; Mankau and Linford, 1960), but at cooler temperatures of 10–20°C egg laying does not occur until about 1 month after host penetration (Mulvey, 1959). Several generations may take place within a season, so that populations may increase rapidly (Mulvey, 1959; Yeates and Risk, 1976).

In many cases clover is only damaged by very high numbers of *H. trifolii* and damage is most apparent in mature plants that have been cut (Sikora and Maas, 1986; Seinhorst and Sen, 1966). With large numbers of infective juveniles, clover, and even nonhosts, may first be damaged by penetration because multiple invasions may kill a root tip (Sikora and Maas, 1986). Hosts are also damaged by diversion of nutrients from the plant, interaction with other pathogens (Sikora and Maas, 1986; Ennik et al., 1964; Yeates, 1973), and in some cases inhibition of nitrogen fixation (Yeates et al., 1977). High population levels may reduce water uptake, as reflected by wilting in warm weather (Thorne, 1961).

**Control.** Control of *H. trifolii* by rotation or use of alternative crops is confounded by the broad host range and susceptibility, which may vary among nematode populations and races (Sikora and Maas, 1986). Although resistance may also be difficult to maintain against such a heterogeneous pathogen, some lines of white clover are reportedly resistant; resistance is inherited by more than one gene (Dijkstra, 1971; Kuiper, 1960). Chemical control of *H. trifolii* is feasible for ornamentals such as carnation, and solarization, as discussed for *H. carotae*, may also be effective (Sikora and Maas, 1986).

#### *Heterodera glycines* Ichinohe, 1952 (the soybean cyst nematode)

**Synonyms and history.** Cyst nematodes may have been known to occur on soybeans in north central Japan since the late 1800s, although Ichinohe (1961) notes that a report by Hori (1915) was apparently the first to bring widespread attention to the soybean cyst nematode and its causal role in "yellow dwarf" disease. Subsequent reports in Japan by Ito (1921), Tanaka (1921), and Fujita and Miura (1934) compared morphology and host range of the soybean cyst nematodes with sugar beet cyst nematodes; they concluded that cysts of



soybean were probably a race of *H. schachtii*. It was also reported that the distribution of this soybean race extended to Korea and Manchuria (Yokoo, 1936; Nakata and Asuyana, 1938). During this period, cyst nematodes, including the soybean cyst nematode, were generally considered races of *H. schachtii*, but in 1940 Franklin's comparative morphological descriptions led to many cyst "races" being elevated to species. It was taxonomically consistent that the morphological distinctions of the soybean cyst nematode and its economic importance led Ichinohe (1952) to elevate the putative soybean race to a new species, *H. glycines*, with the type host soybean (*Glycine max*) and the type locality of Obihiro-shi, Hokkaido, Japan. About the same time the soybean nematode was detected and found to be widely distributed in three counties of North Carolina (Winstead et al., 1955; Thorne, 1961). Although the distribution and host range of *H. glycines* and *H. trifolii*, the clover cyst nematode, overlap, Hirschmann (1956) clarified morphological differences between them. *Heterodera glycines* is now known throughout most of eastern USA, and also occurs in Taiwan, Colombia, and the Middle East (Moore, 1984). It has considerable intraspecific variability with respect to its capacity to infect different hosts and cultivars (Golden et al., 1970; Inagaki, 1979; Ross, 1962; Triantaphyllou, 1975b) and there are reports of morphological distinctions among isolates (Faghihi et al., 1986b; Golden and Epps, 1965; Koliopanos and Triantaphyllou, 1971; Miller and Duke, 1967; Riggs et al., 1982). Some isolates, previously believed to be *H. glycines* which heavily attacked Kobe lespedeza (*Lespedeza striata*) in North Carolina, were subsequently recognized as morphologically distinct from both *H. glycines* and *H. trifolii*, and were described as a new species, *H. lespedezae* (Bhatti et al., 1972; Golden and Cobb, 1963). This species may occur in the same locality with *H. glycines*, and some isolates may even attack soybean (Fagbenle et al., 1986), so that the two species are often confused.

**Hosts.** *Heterodera glycines* is of major economic importance on soybeans (Fig. 18C). It has a broad host range, especially among legumes, including *Phaseolus* (e.g., greenbeans), *Lespedeza*, *Vicia* (vetch), *Trifolium* (clover), and *Pisum* (pea), but it also attacks a number of nonlegumes including ornamentals, such as *Geranium*, and *Papaver* (poppy) as well as many weeds (Moore, 1984). The host range, and particularly weed hosts, is an important consideration, particularly for management strategies involving sanitation, quarantine regulation, and crop rotation. Host range on soybean cultivars varies with putative "races," some cultivars being resistant to certain races and susceptible to others (Golden et al., 1970). However, races of *H. glycines* are quantitative and determined by gene frequencies, which may shift by selection within a given population (Triantaphyllou, 1975b). Thus, host range tests often are not reliable for characterizing races (Riggs et al., 1988). Yet new races are being described to accommodate the great range of variation (Golden et al., 1970; Riggs et al., 1981; Riggs and Schmitt, 1988). Although isolates may be distinct with respect to morphology, serology, isozymes, or 2-D protein patterns, these have not been linked to host variants (Faghihi et al., 1986b; Ferris et al., 1986; Koliopanos and Triantaphyllou, 1971; Radice et al., 1988; Riggs et al., 1982). However, the potential of restriction fragment length polymorphisms for identifying races of soybean cyst nematode is being explored (Kalinski and Huettel, 1988).

**Distribution.** *Heterodera glycines* may have originated in the orient including Japan, Korea, China (e.g., Manchuria), where soybeans are historically an important crop. It has been suggested that *H. glycines* was introduced to the United States on bulbs from Japan and that it subsequently spread to 26 central and southeastern states (Riggs et al., 1988; Wrather et al., 1984). An alternative hypothesis is that populations of the soybean cyst nematode have been endemic on a variety of weed hosts, and only become apparent as soybean culture became widespread in the United States. The origin and genealogy of



populations of *H. glycines* might prove to be traceable through ongoing investigations of molecular biology of geographic isolates (Ferris et al., 1985, 1986; Radice et al., 1988; Sandall and Powers, 1988). Some reports suggest that cysts may be ingested and dispersed by birds (Epps, 1971) or mammals (Smart, 1964), and undoubtedly man has dispersed nematodes through moving water or soil, as well as soil peds on seed, vehicles, and agricultural products (Wrather et al., 1984). Soybean cyst nematode is now reported in Taiwan, Egypt, Colombia, Indonesia, and parts of Canada and the Soviet Union.

**Biology.** A female of *H. glycines* produces a gelatinous matrix in which one or more males is likely to be attracted. Once fertilized the diploid amphimictic female produces 200–600 viable eggs (Moore, 1984). Some eggs are exuded into the gelatinous matrix and may hatch quickly, so that several generations may occur in a single growing season. Other eggs, perhaps the majority, are retained in the cyst after death of the female and continue to hatch at a slow rate, so that 50–90% are released within a year and some eggs may survive in the cysts up to 8 years under favorable cool, moist conditions (Moore, 1984). Esser and Langdon (1967) report that cysts held at  $-40^{\circ}\text{C}$  for 7 months still contain viable eggs. However, at  $36^{\circ}\text{C}$ , development in the egg is halted at the four-cell stage and eggs die (Alston and Schmitt, 1988). Hatching is greatest at 26 and  $22^{\circ}\text{C}$  (day and night) and is also enhanced by pod-producing rather than vegetative soybeans (Hill and Schmitt, 1989). Root diffusates are believed to play a role in hatching of second-stage juveniles (Tsatsum and Sakurai, 1966). Diffusates may also be involved in attraction and penetration of juveniles to host roots. Second-stage juveniles generally penetrate host roots near the tip. They become sedentary and establish a syncytial feeding site. Time required for the nematode to complete molts to adults is usually from 21 to 24 days at ideal soil temperatures of  $21\text{--}24^{\circ}\text{C}$ . Cooler soil temperatures increase length of the cycle but outside a range of  $10\text{--}34^{\circ}\text{C}$  development is not completed (Moore, 1984; Slack et al., 1972; Wrather et al., 1984).

Susceptible reactions to *H. glycines* can result in yield losses in individual fields exceeding 70% with overall losses of soybean to this nematode in the southern USA estimated at 2–4% (Wrather et al., 1984). Symptoms include stunting, yellowing, browning of leaf margins, and loss of leaves with reduced flower and seed production. Lateral roots may be increased in number and there may be fewer *Rhizobium* nodules for nitrogen fixation. The most severe losses are associated with sandy soils (Koenning et al., 1988; Todd and Pearson, 1988).

**Control.** Since the soybean cyst nematode can greatly limit production of soybeans, past management strategies must be considered. A primary defense has been to attempt to limit spread to noninfested areas by sanitation, including cleaning of contaminated farm vehicles and bean seed, and enforcing quarantine regulations. Since many agricultural crops are nonhosts of *H. glycines*, crop rotation is an effective approach to management. In warm climates persistence of cysts with viable eggs may be relatively short, many eggs hatch, and juveniles may senesce in the soil prior to planting. In such cases rotations of 1 year may be effective. However, in cooler climates where eggs are likely dormant through winter, nearly synchronous hatching may occur near the time of planting; thus rotations as long as 3 years may be needed (Moore, 1984). One year in a nonhost may reduce populations by 75%, and 2 years by 92% (Moore, 1984). Rotation programs must be specific to the region and must consider possible weed hosts. Moreover, rotations may include, in addition to a nonhost, both a resistant and a susceptible soybean cultivar (Riggs, 1977) to reduce pressure toward shifts in gene frequencies to resistance-breaking races (Moore, 1984).

A number of soybean cultivars with resistance to *H. glycines* are available, but their resistance is generally specific to particular putative races as determined by soybean differential tests (Moore, 1984; Riggs et al., 1988). In some cases resistant genes are linked



to undesirable characteristics (e.g., black seed coat in Peking), and suitable resistant cultivars are not necessarily available in lines adapted to all the geographic areas in which soybeans are grown (Wrather et al., 1984). Resistant varieties must be managed carefully to avoid shifts in gene frequencies of the nematode and thus buildup of new races which may occur during 2–4 years of continuous cropping. Although Moore (1984) suggests that a combination of resistant cultivars and rotation is likely to be more economical than use of nematicides, both fumigant and nonfumigant nematicides may be effective in reducing populations of soybean cyst nematode. Nematicides, however, are environmentally and economically costly and, due to protection of eggs in the cyst and a preliminary increase in root feeding sites, they only reduce initial populations (Wrather et al., 1984). There is some evidence that nematicides are more effective when planting is late, as activity of infective juveniles in the soil may be greatest (Hussey and Boerma, 1983).

Several fungi have been recognized as parasites of eggs of *H. glycines*, and natural predators may act in conjunction with other management practices to reduce nematode populations. Fields in continuous cropping with susceptible cultivars may have a decline in populations of soybean cyst nematodes due to increase in natural antagonists (Hartwig, 1981). However, these biological control factors generally are understood insufficiently to manipulate them as part of management strategies.

*Heterodera zae* Koshy, Swarup, and Sethi, 1971 (the corn cyst nematode)

**Synonyms and history.** While collecting the oat cyst nematode, *H. avenae*, in Rajasthan, India during 1969, a sample mixed with an unknown second species was discovered on *Zea mays* L. and taxonomically described as *Heterodera zae* (Koshy et al., 1970). Additional samples of *H. zae* were discovered in Egypt and Pakistan, and in 1981 it was reported in Maryland (Sardanelli et al., 1981). Shortly thereafter, Golden and Mulvey (1983) redescribed *H. zae*, with greater morphological and SEM detail. They also compared populations from India and the USA.

**Hosts.** The corn cyst nematode was first recognized as distinct from *H. avenae* by its reproduction on maize and barley but not on a number of other grains susceptible to *H. avenae* (Bhargava and Yadav, 1978; Koshy et al., 1970). Ringer et al. (1987) carried out extensive host range tests on cyst populations from Maryland. All 22 cultivars of *Zea mays* tested, as well as *Zea mexicana* (teosinte), were susceptible. Other economic hosts include some cultivars of barley (*Hordeum vulgare*), oat (*Avena sativa*), rice (*Oryza sativa*), sorghum (*Sorghum bicolor*, with poor nematode reproduction), sugar cane (*Saccharum* sp.), and wheat (*Triticum aestivum*). Several grass weed hosts have been identified in India and the USA (Ringer et al., 1987; Srivastava and Swarup, 1975; Verma and Yadav, 1978). Populations from India and the USA apparently differ some in their host ranges, although these have not yet been compared under identical conditions. *Heterodera zae* has been associated with a number of dicots including legumes, solanaceous plants, cucurbits, crucifers, and many ornamentals, but reproduction has not been detected on any dicot (Krusberg, pers. commun.). Curiously, populations from Pakistan are reported to be widespread on citrus, pear, and garlic (Maqbool, 1981), but these also may be field associations and reproduction on these hosts has not been established.

**Distribution.** *Heterodera zae* is widespread in India but also occurs in Pakistan, the Nile Valley, Egypt, and Maryland (Krusberg and Sardanelli, 1982; Sardanelli et al., 1981). In Maryland it is found primarily in heavy silty-clay soils and population densities are usually sparse with 1–10 cysts/250 cm<sup>3</sup> soil (Krusberg, pers. commun.). Although the corn cyst nematode could be indigenous to all of these areas, its apparently narrow distribution in the western hemisphere suggests recent introduction.



**Biology.** The life cycle of *H. zae* is completed in about 22 days (Lauritis et al., 1983; Verma and Yadav, 1975) if temperatures are optimally warm (about 30°C). Second-stage juveniles hatch readily and penetrate both the main root and lateral roots of the host, and a syncytium is initiated. Postembryogenesis is typical for the genus (Shahina and Maqbool, 1989). The final molt to mature females with a gelatinous egg mass is completed in about 10 days, but eggs are not laid into the mass until about 14 days after penetration (Lauritis et al., 1983). Males, which are rare, apparently are not required for reproduction (Hutzell, 1984). Under condition in Maryland, cysts with infective juveniles apparently only persist in fallow soil for about 2 years (Krusberg and Sardanelli, 1989). The corn cyst nematode is considered an economic pest in India, but pathogenicity to corn in the field has not been demonstrated in Maryland (Ringer et al., 1987). The nematode is however, a potential threat to corn production in the USA. However, its spread and pathogenicity could be restricted by high-temperature requirements (>30°C) which are more likely to be sustained in soils of the Southeast than in the corn belt of the USA. Preliminary microplot tests in Maryland suggest that high densities of the nematode reduce yields of corn in sandy soils, particularly where other stresses such as low soil fertility occur (Krusberg, pers. commun.)

**Control.** Since May 1984, a quarantine has been imposed on the areas of Maryland infested with *H. zae* but only a few tests have been carried out on its pathogenicity and strategies for management. Preliminary trials show that several fumigants reduce soil population density, but without an increase in corn yield (Krusberg, pers. commun.). Crop rotation may be confounded by the wide host range including a number of weed hosts. Sources of resistance in *Zea mays* are unknown.

*Heterodera goettingiana* Liebscher, 1892 (the pea cyst nematode)

**Synonyms and history.** Liebscher (1890) was the first to attribute yellowish stunted pea plants (*Pisum sativum* L.) at the agriculture institute in Göttingen, Germany to a cyst nematode which he at first considered a strain of *H. schachtii*. His investigations of this nematode indicated morphological and biological distinctions, which let him to consider the pea cyst nematode as a new species, *H. goettingiana* (Di Vito and Greco, 1986). Liebscher's recognition of a distinct species was remarkable in 1892, considering that most other cyst nematodes were viewed as strains of *H. schachtii* for another 50 years, and little was known about biology and pathogenicity of *H. goettingiana* until the mid-1900s (Franklin, 1951; Goffart, 1941).

**Host range.** Winslow (1954) and Jones (1950b) indicate several hosts of *H. goettingiana* in the Fabaceae (Leguminosae), including peas (*Pisum sativum* L.), broadbean (*Vicia faba*), vetch (*Vicia* spp.), soybean (*Glycine max*), lentils (*Lens sculenta*), and weed hosts including *Pisum*, *Vicia*, and perhaps *Lathyrus*. Conflicting reports suggest that populations may differ in their response to ornamental sweet pea or grosspea (*Lathyrus odoratus*) (Di Vito et al., 1980; Jones, 1950b; Stone and Course, 1986; Thorne, 1961; Winslow, 1954). Di Vito et al. (1980) found that many legumes susceptible to other cyst species are resistant to *H. goettingiana*, including various clovers (*Trifolium* spp.), lupine (*Lupinus* sp.), and chickpea (*Cicer arietinum*). In the case of chickpea, tissues are invaded but become necrotic and only males develop (Varo Alcala et al., 1970). Attempts to find resistance in garden peas have failed (Oostenbrink, 1951; Stone and Course, 1986). Di Vito and Greco (1986) report a few families and cysts on the nonleguminose plant *Asperula arvensis* L. Symptoms are typically of cysts nematodes, including patches of stunted and chlorotic plants in the field (Fig. 19A).



**Distribution.** Shortly after *H. goettingiana* was found in Germany, it was reported in Great Britain (1912) and France (1917) (Di Vito and Greco, 1986). Although it occurs throughout the world, it is most widespread in Europe including Germany (Goffart, 1941), the Netherlands (Oostenbrink, 1951), Great Britain (Jones, 1965), and Belgium (D'Herde, 1966). It occurs in the USSR and in the Mediterranean region including Spain, Portugal, Italy, Sicily, Malta, Israel, and Algeria. It has been reported in the USA (Thorne, 1961), but it is not widespread, and Stone and Course (1986) suggest that U.S. populations are chance introductions. Undoubtedly *H. goettingiana*, like other cyst nematodes, is spread locally by water and farm vehicles, but possible natural means of long-distance dispersal are unknown.

**Biology.** The life history of *H. goettingiana*, from egg through four molts, adult and cyst, is illustrated by Macara (1963) and thoroughly discussed by Stone and Course (1986) and Di Vito and Greco (1986). Cysts with eggs are highly persistent and in cooler climates may remain viable in the absence of a host for 12 years (Brown, 1958; Di Vito and Greco, 1986). Development takes 3–15 weeks depending on soil temperature and moisture as well as host species. Thus, only one or two generations are completed during the growing season for peas in England, but three generations may occur in southern Italy (Di Vito and Greco, 1986). Under ideal conditions, including cool soil (10–13°C), females mate and produce a gelatinous matrix which may have more than 100 eggs; however, under adverse conditions eggs are not usually exuded but are retained within the cyst (Greco et al., 1986). Development is inhibited below 4.4°C or above 25°C, even where soil moisture is adequate (Beane and Perry, 1984; Di Vito and Greco, 1986; Jones, 1975). Unfavorable conditions, including poor hosts, favor development of males (Guevara-Benite et al., 1970; Jones, 1965).

Hatching is greatest at about 15°C. Although age of host was not considered in early tests of response to root exudates, more recent investigations indicate that exudates are required for a high percentage of hatch and that exudates from older hosts (e.g., 16-week-old broadbeans) are apparently most effective in stimulating hatch (Beane and Perry, 1983; Shepherd, 1963). Infective juveniles penetrate host roots and induce a syncytium (Volvas and Inserra, 1978), causing stunting and yellowing which is most evident at the flowering stage. In peas, *Rhizobium* nodulation and nitrogen fixation is inhibited (Fig. 19B, C), seed production is greatly reduced, and nematode-infected plants are vulnerable to root invasion and death by soil fungi.

**Control.** The pea cyst nematode may be highly persistent in some soils; nevertheless, the host range is relatively narrow and 3 to 6 year rotations with nonhosts generally reduce populations to levels that are not damaging. However, possible weed hosts must be carefully controlled in such rotations (Di Vito and Greco, 1986). In some warm regions, such as those with Mediterranean climates (where irrigation can be provided), late varieties of peas can be used which tolerate soil conditions that are too warm for rapid development of the pea cyst nematode (Greco et al., 1986b). Cultivars are not yet available with resistance to *H. goettingiana*, although some species of *Pisum* may show some promise as sources of resistance (Di Vito and Perrino, 1978; Di Vito and Greco, 1986). Chemical control of the pea cyst nematode is confounded by its slow rate of hatch; nevertheless a number of nematicides are shown to be useful in management programs (Di Vito and Greco, 1986; Stone and Course, 1986).

*Heterodera cruciferae*. Franklin, 1945 (the Brassica or cabbage cyst nematode)

**Synonyms and history.** Franklin recognized that what were commonly considered biological strains of *H. schachtii* until 1940 were four morphologically distinct species



which are now recognized as *H. schachtii*, *G. rostochiensis*, *H. goettingiana*, and *H. avenae*. However, even within the newly defined *H. schachtii*, she recognized a distinct strain in specimens from a plot of old cabbage plants. The nematodes did not infect sugar beet and cysts were smaller than those of *H. schachtii*. She described the cyst nematode of cabbage as *Heterodera cruciferae* from the type host, *Brassica oleracea*; and type locality at St. Albans, England (Franklin, 1945). Although there were some initial criticism that the characters diagnosing *H. cruciferae* were difficult to use in identification and may not be reliable (Miles, 1951), the species became clearly established with subsequent morphological investigations (Stone and Rowe, 1976).

*Hosts.* *Heterodera cruciferae* has a narrower host range than *H. schachtii* but apparently attacks all species of *Brassica* including common agricultural crops of cabbage, brussels sprouts, cauliflower, broccoli, turnips, and radish (Franklin, 1945, 1951; Jones, 1950b). Cruciferae (Brassicaceae) other than *Brassica* may be less susceptible to the nematode, and a few crucifers including *Aethionema*, *Hesperis*, and *Matthiola* are not hosts at all (Winslow, 1954). Some members of Labiatae, the mint family, may be hosts, and certain species could be important as weed reservoirs (Stone and Rowe, 1976).

*Distribution.* *Heterodera cruciferae* is widespread in England, where it was first described, but it also occurs throughout Europe including Ireland, Netherlands, Belgium, Germany, Switzerland, France, Portugal, Turkey, Yugoslavia, Bulgaria, Hungary, Poland, and the USSR. In the United States, *H. cruciferae* is only known to occur in California where Raski (1952) described it as widespread and well established; it is not known if the nematode is indigenous to California or if it was introduced from Europe. Curiously, in California it is rarely if ever found separate from *H. schachtii*. *Heterodera cruciferae* was described from South Australia where it is speculated that contaminated wooden barrels or crates from Europe were responsible for its introduction (Stirling and Wicks, 1975).

*Biology.* Unlike most temperate heteroderines, *H. cruciferae* parasitizes cool-weather or winter-grown crops, so that the number of generations completed in a season depends on the growing period; in northwestern Europe this is one generation on transplanted summer cauliflowers and cabbage, but as many as three generations on late cultivars of brussels sprouts, spring cauliflower, and spring cabbage (Stone and Rowe, 1976). Juveniles of *H. cruciferae* are stimulated to hatch from eggs of cysts in the presence of diffusates from *Brassica* spp., but not by diffusates of other hosts (Shepherd, 1965; Winslow, 1953). Second-stage juveniles explore and probe the root tip (Doncaster and Seymour, 1973) and at temperatures above 4°C they invade roots and establish a syncytial feeding site typical of cyst nematodes. Mackintosh (1960) speculates that secondary roots compensate for some potential damage of the nematode to the host, and agreed with Franklin (1951) that some crop failures attributed to *H. cruciferae* actually may be due to secondary fungal invaders. Lear et al. (1966) found that the nematode may interact synergistically with the fungus causing club root disease. Severe crop damage in Europe seems to be primarily on transplanted seedlings; conversely, in California and southern Australia damage may be more widespread and severe (Lear, 1971; Stirling and Wicks, 1975; Stone and Rowe, 1976).

*Control.* The limited host range of *H. cruciferae* makes it subject to excellent management by crop rotation. Several fumigants are effective in reducing initial populations (Lear et al., 1965a, b, 1966; Stirling and Wicks, 1975; Stone and Rowe, 1976).

*Heterodera carotae* Jones, 1950 (the carrot cyst nematode)

*Synonyms and history.* Prior to knowledge of the carrot cyst nematode "carrot sickness" had been attributed to pathogenic fungi. In 1931, when virtually all cyst



nematodes were considered strains of *H. schachtii*, Triffitt (1931) reported females on carrots (*Daucus carota*) in England which were atypical of *H. schachtii* because they were small with a strikingly large egg sac (Greco, 1986). By 1944, when Jones discovered the carrot cyst nematode, many "strains" of *H. schachtii sensu lato* were being described as morphologically distinct species. Perhaps this context invited closer morphological inspection of the carrot cyst nematode which was then described as *H. carotae* on the type host, *Daucus carota* L., from the Isle of Ely, England (Jones, 1950).

**Hosts.** The host range of *H. carotae* is restricted to *Daucus* including *D. carota* ssp. *sativus*, *D. carota* ssp. *sarota*, *D. pulcherrimus* (Jones 1950a; Mathews, 1975; Winslow, 1954), and the wild Umbelliferae, *Torilis* spp. Vallotton, 1980). However, the life cycle reportedly is only completed on *Daucus carota* L. and *Torilis leptophylla* L. (Mugniery and Bossis, 1988). The weed host *Torilis* is significant as an important source of infection of cultivated carrot (Greco, 1986). Infected fields of carrots show poor stands, with chlorotic plants and poor yields (Fig. 19D).

**Distribution.** *Heterodera carotae* occurs throughout the carrot-growing areas of Europe and has been reported from England, Ireland, Netherlands, Scotland, France, Italy, Switzerland, Germany, Sweden, Poland, Sweden, Czechoslovakia, Hungary (Mathews, 1975; Greco, 1986). It has also been reported from the USSR, Cyprus, and India (Greco, 1986), and from Michigan (Graney, 1985). *Heterodera carotae* may be dispersed locally on farm vehicles, but export of cysts adhering to tap roots or seeds could also account for more distant spread (Greco, 1986).

**Biology.** Temperature requirements for hatch and development of *H. carotae* are highly specific and frequently conditions are only suitable for one life cycle per season. However, with a long growing season, repeated crops, and cool temperatures, as many as four cycles may occur (Greco, 1986; Jones, 1950a; Mugniery and Bossis, 1988; Stelter, 1969). The source of repeated infections is eggs (typically about 160) exuded into the large egg sac. Second-stage juveniles hatch quickly from these eggs if root exudates from young carrots are present, if soil moisture is favorable, and if soil temperature is 15–20°C. Hatching occurs as low as 5°C but is repressed at 25°C (Greco et al., 1982, 1986; Winslow, 1955). In addition to eggs in the egg mass, many eggs are protected in the cyst. Eggs from cysts less than 2 months old rarely hatch, but second-stage juveniles hatch from mature cysts when conditions of soil temperature and moisture are suitable (Aubert, 1986; Greco, 1981, 1986). Curiously, eggs in the cyst are apparently unaffected by host leachates (Greco, 1986). Second-stage juveniles invade the tips of host feeder roots at 5–30°C but do not develop below 10°C; they establish a typical syncytial feeding site and at 20°C adult females and fertilization occurs at 26 days (Greco, 1986; Volvas, 1978). Heavily infected plants are stunted and the tops become yellowish red and necrotic; tap roots are small and unmarketable and lateral roots may proliferate (Greco, 1986).

**Control.** Management strategies for *H. carotae* including rotation might seem promising because of the narrow host range of this species. However, eggs protected in cysts are persistent, and rotations of 4–5 years are apparently required for adequate reduction of inoculum (Bossis, 1986; Bossis and Mugniery, 1988; Greco, 1986; Vallotton, 1983). Although no resistant varieties are known, early cultivars appear less susceptible than late ones (Greco, 1986), perhaps because they escape field conditions ideal for hatch and development of the nematode. Greco (1986) suggests that because *H. carotae* is also inactive at high soil temperatures, yield losses could be reduced in warm countries by planting in the late summer. Various nematicides are economically feasible on early crops (Bossis, 1986; Greco, 1986; Greco et al., 1986b; Mathews, 1975). Because of the sensitivity of *H. carotae* to high temperatures, solarization of soil in summer with polyethylene sheets



or mulch may result in temperatures that are lethal to eggs if populations are low and soil temperatures can be elevated at an adequate depth. Solarization may create additional beneficial conditions, such as increased antagonists to the nematode (Greco, 1986; Greco et al., 1985).

*Heterodera avenae* Wollenweber, 1924 (oat cyst nematode)

**Synonyms and History.** *Heterodera schachtii* was reported as attacking cereals in Germany by Kühn in 1874 and in the years following there were several references to the "oat strain" of *H. schachtii* (Franklin, 1957; Hansen, 1904; Rostrup, 1896). Moortensen et al. (1908) designated *H. schachtii* var. *avenae* but only recorded the occurrence of the nematode, and no morphological description was included. Wollenweber in 1924 used the name *H. schachtii* var. *avenae* for a population from oats (*Avena sativa* L.) in Aschersleben, Germany; he gave a more complete description including diagnostic characters on the cyst, which, combined with knowledge of the host, could be used for identification (Thorne, 1961). Schmidt (1930) also observed morphological differences between the oat and beet strain of cyst nematode, and particularly noted that the second-stage juveniles were longer in *H. avenae*; he adopted the name *H. schachtii* ssp. *major*. However, Filipjev (1934) elevated the older variety name to species *Heterodera avenae*, which after some controversy (Franklin, 1957) has been adapted as consistent with the international zoological rules of priority. Although original type material was not designated, a neotype from Aschersleben has been proposed (Franklin et al., 1959).

*Heterodera avenae*, together with other bifenestrate cyst nematodes having a short vulva, were placed in a genus *Bidera* Krall and Krall (1978), but Mulvey and Golden (1983) synonymized *Bidera* with *Heterodera*. Although Wouts (1985) retained *Bidera*, it was rejected by Stone (1986) and Luc et al. (1988). Other synonyms of *H. avenae* include *H. ustinovi* Kirjanova, 1969 and *Bidera ustinovi* (Kirjanova, 1969) Krall and Krall, 1978.

**Hosts.** Hosts of *H. avenae* are primarily restricted to Poaceae (Gramineae) including economically important cereals, oats (*Avena*), wheat (*Triticum*), barley (*Hordeum*), and rye (*Secale*). Other hosts are noncereal grasses including *Agropyrum*, *Agrostis*, *Alopecurus*, *Brachypodium*, *Bromus*, *Cynosurus*, *Echinochloa*, *Festuca*, *Koeleria*, *Lolium*, *Phalaris*, *Phleum*, *Poa*, *Polypogon*, *Setaria*, *Sorghum*, *Vulpia*, *Zerna*, and *Zea* (Andersen, 1961; Bovien, 1953; Filipjev and Schuurmans Stekhoven, 1941; Stoyanov, 1982; Thorne, 1961; Williams and Siddiqi, 1972). Many grasses, such as *Zea* (corn), are poor hosts (Johnson and Fushtey, 1966), but even a low rate of reproduction must be considered in rotations. In Canada corn is severely injured by an intolerant reaction to invading juveniles which do not complete development (Miller, 1986). There are reports of *H. avenae* occurring worldwide in a variety of habitats, *Pisum*, *Sonchus*, and *Trifolium*, but they are limited to certain restricted areas or could be results of contamination of samples (Thorne, 1961), or cyst species other than *H. avenae*. *Heterodera avenae* consists of as many as 20 pathotypes (Andersen and Andersen, 1982, 1986; Brown, 1982a, b; Stone and Hill, 1982; Stone and Williams, 1974), and populations are also biochemically diverse (Dalmasso et al., 1982). In addition, several species are morphologically similar to *H. avenae*. Thus some populations of *H. avenae* may vary in host range from others, and closely related species may also differ in host range (e.g., *H. mani* Mathews, 1971 and *H. hordecalis* Anderson, 1975).

**Distribution.** *Heterodera avenae* is widespread throughout a variety of climates including northwestern Europe, the Mediterranean region (Italy, Spain, Greece, Israel, North Africa), North America (particularly Canada but also California and Michigan), India, New Zealand, Australia, and perhaps Japan (Grandison, 1982; Graney, 1985; Hackney, 1981; Williams and Siddiqi, 1972). Nevertheless, the species seems to be diverse



so that populations from a given region may be particularly adapted to the environmental conditions of that region, and may also differ in pathogenicity on host species and cultivars. This diversity and occurrence in nonagricultural habitats (e.g., in California) could reflect wide dispersal aside from the activities of man. McLeod (1968) notes that *H. avenae*, like other cyst nematodes, spreads through soil very slowly unless distribution is promoted by rainfall runoff, wind, and activities of man. Wide distribution in dry southern Australia may be attributed to transport of cysts during turbulent dust storms (Brown, 1984; Meagher, 1982a). Some regions of southern Australia may lack the nematode primarily because heavy soils do not favor its development (Brown, 1984).

**Biology.** Although *H. avenae* occurs worldwide in a variety of habitats, it completes only one or two generations per year, depending on the population (Valdeolivas and Romero, 1985). Whether or not hatching of second-stage juveniles from eggs within cysts is stimulated by root exudates is controversial, and even roots of poor hosts may be attractive for penetration (Andersen and Andersen, 1986; Johnson and Fushtey, 1966). The hatching rate from a cyst may vary from 40 to 90%. Eggs can survive within cysts for years, particularly under cool, dry conditions (Meagher, 1982a). Infective juveniles enter behind the root cap and move intracellularly to the growth zone, establishing the feeding site near the endodermis or pericycle. Sedentary females mature from 6 to 9 weeks after penetration, whereas males leave the roots in about 3 weeks. Although a gelatinous material is secreted through the vulva of white females of *H. avenae*, eggs are not laid through the small vulval slit but rather escape through the fenestrae of the cyst, usually at the beginning of the subsequent growing season. In field conditions, populations develop to higher numbers of individuals after moist and cool periods. Although temperature requirements appear to be complex, cool temperatures (2–10°C) are optimal for egg hatching, whereas dry conditions during growth of the host seem to favor development of the parasite (Williams and Siddiqi, 1972). Populations of different areas vary in response to moisture contents of soil. Indian and Australian populations are better adapted to arid conditions, whereas European populations seem to be less resistant to dry conditions (Williams and Siddiqi, 1972). Populations may also vary in response to soil type. Reproduction is typically favored in sandy and calciferous soils, but there are exceptions (Filipjev and Schuurmans Stekhoven, 1941; Williams and Siddiqi, 1972).

Cereals infected with *H. avenae* generally are stunted (Fig. 20). Leaves yellow and may even be tinged with purple. Root systems are reduced in size and highly branched with a proliferation of short, thick side roots. Seminal root growth is especially impaired in intolerant cultivars (Volkmar, 1989). Stunted, chlorotic plants may appear in patches within a field of otherwise healthy plants (Fig. 20) (McLeod, 1968; Williams and Siddiqi, 1972), and some symptoms may be enhanced by interaction with secondary pathogens (e.g., *Rhizoctonia solani*; Brown, 1984) as well as physiological stresses.

**Control.** Damage of *H. avenae* is most severe when hosts such as wheat or barley are grown continuously, but populations can be greatly reduced by 3-year rotations with noncrops such as legumes, where such rotations are economically feasible. In Australia, rotation with legumes has the added benefit of improving nitrogen-depleted soils which are common in the southern wheat belt (Brown, 1982a, 1984). In addition to rotation, in some regions crops can be planted sufficiently early to establish a good root system prior to heavy rainfall. Heavy rain maximized hatch and population densities of infective juveniles (Brown, 1984; Meagher, 1982b). Although resistant varieties are useful for control of *H. avenae* on barley or oats, their value may be limited by specificity to certain pathotypes, possible effectiveness only under certain environmental conditions, and limited availability of resistant varieties (Andersen and Andersen, 1982, 1986; Brown, 1982b, 1984; Hansen,



1986). Yet resistance in oats and barley generally is not linked to undesirable horticultural characteristics, and resistant cultivars tolerate invasion and hypersensitive reaction to the nematode with little adverse reaction. Resistance in wheat is limited, although some lines are available in durum wheat. Brown (1984) indicates that resistance in other types of wheat is linked to low yield potential and therefore is not likely to be accepted by growers.

As with many cyst nematodes, resistant quiescent juveniles in cysts may be difficult to control by fumigation, although reports indicate a striking response to preplant fumigants such as ethylene dibromide (EDB) on the sandy soils of southern Australia (Brown, 1984; Gurner, 1982). Generally, however, fumigation may only be economically worthwhile for certain high-value crops, in small areas where infestation is very heavy, or in small isolated introductions where there may be hope of eradication (McLeod, 1968). There is some promise that biological control agents, particularly certain fungi, may prove useful for suppressing populations of *H. avenae* (Andersson, 1982; Kerry, 1975; Kerry and Crump, 1977). Recently, chitin was reported to be as effective as EDB or aldicarb in increasing wheat yield and controlling the nematode (Spiegel et al., 1989). Restriction of spread, regulation by quarantine, and sanitation (e.g., care not to move contaminated soil on farm equipment) play an important role in limiting infection by *H. avenae*.

### **Globodera**

*Globodera* Skarbilovich, 1959

syn. *Heterodera* (*Globodera*) Skarbilovich, 1959

*Diagnosis.* Heteroderinae Filipjev and Schuurmans Stekhoven

*Females.* Cyst present. Body spheroidal, without terminal cone. Cuticle surface with zig-zag pattern of ridges; distinct D layer present. Vulva terminal; perineal tubercles on crescents near vulva. Anus and vulva both in a vulval basin. Underbridge and bullae rarely present; circumfenestrae develops around vulva in cyst; no fenestration around anus. All eggs retained in body (no egg mass); egg surface smooth.

*Males.* Body twisted. Lateral field with four lines. Spicules >30  $\mu$ m, distally pointed.

*Second-stage juveniles.* Lateral field with four lines. Esophageal glands filling width of body cavity. Tail conical, pointed, with terminal region half hyaline. Phasmid openings porelike. En face pattern typically with six separate lips; variants with fusion of adjacent submedial lips.

*Nurse cell.* Syncytium, generally with wall ingrowths.

*Species.* (Table 4)

*Identification.* *Globodera* includes less than a dozen species, many of which are considered unimportant because their distribution is narrow or they are not known on economic hosts. Nevertheless the genus is especially significant because of the worldwide economic impact of two species, *G. rostochiensis* and *G. pallida*, the potato cyst nematodes. Identification between the two species is essential to some management strategies such as use of resistant cultivars. A species complex, the tobacco cyst nematodes, *G. tabacum* (*G. tabacum tabacum*; *G. tabacum solanacearum*, *G. tabacum virginiae*) *sensu* Stone, 1983, while globally less important than potato cyst nematodes, is included in this review. Subspecies *G. t. tabacum* is damaging on tobacco in Connecticut and Massachusetts. *Globodera t. solanacearum* damages tobacco and *G. t. virginiae* occurs on solanaceous weeds (and at least experimentally on tobacco) in the southern USA. *Globodera* is widespread on weed hosts in Mexico and Central America and these are putatively *G. t. virginiae*. It is not clear if additional subspecies of *G. tabacum* occur in Mexico, or if species



TABLE 4 Species of *Globodera*


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|---|
| <i>Globodera</i> Skarbilovich, 1959                                     |
| syn. <i>Heterodera</i> ( <i>Globodera</i> ) Skarbilovich, 1959          |
| <i>Globodera rostochiensis</i> (Wollenweber, 1923) Behrens, 1975        |
| syn. <i>Heterodera schachtii rostochiensis</i> Wollenweber 1923         |
| <i>H. schachtii solani</i> Zimmermann, 1927                             |
| <i>G. achilleae</i> (Golden and Klindic', 1973) Behrens, 1975           |
| syn. <i>Heterodera achilleae</i> Golden and Klindic', 1973              |
| <i>G. artemisiae</i> (Eroshenko and Kazachenko, 1972) Behrens, 1975     |
| syn. <i>H. artemisiae</i> Eroshenko and Kazachenko, 1972                |
| <i>G. hypolysi</i> Ogawa, Ohshima, and Ichinohe, 1983                   |
| <i>G. leptonepia</i> (Cobb and Taylor, 1953) Behrens, 1975              |
| syn. <i>H. leptonepia</i> Cobb and Taylor, 1953                         |
| <i>G. millefolii</i> (Kirjanova and Krall, 1965) Behrens, 1975          |
| syn. <i>H. millefolii</i> Kirjanova and Krall, 1965                     |
| <i>G. mirabilis</i> (Kirjanova, 1971) Mulvey and Stone, 1976            |
| syn. <i>H. mirabilis</i> Kirjanova, 1971                                |
| <i>G. pallida</i> (Stone, 1973) Behrens, 1975                           |
| syn. <i>H. pallida</i> Stone, 1973                                      |
| <i>G. pseudorostochiensis</i> (Kirjanova, 1963) Mulvey and Stone, 1976  |
| <i>H. pseudorostochiensis</i> Kirjanova, 1963                           |
| <i>G. tabacum tabacum</i> (Lownsbery and Lownsbery, 1954) Behrens, 1975 |
| syn. <i>H. tabacum</i> Lownsbery and Lownsbery, 1954                    |
| <i>G. tabacum solanacearum</i> (Miller and Gray, 1972) Behrens, 1975    |
| syn. <i>H. solanacearum</i> (Miller and Gray, 1972)                     |
| <i>G. solanacearum</i> (Miller and Gray, 1972)                          |
| <i>G. tabacum virginiae</i> (Miller and Gray, 1968) Behrens, 1975       |
| syn. <i>H. virginiae</i> (Miller and Gray, 1968)                        |
| <i>G. virginiae</i> (Miller and Gray, 1968)                             |
| <i>G. zelandica</i> Wouts, 1984   |

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Source: Adapted from Luc et al., (1988).

not included in the *G. tabacum* complex are present. Indeed some isolates from weed hosts in Mexico which do not infect potato are morphologically similar or even identical to *G. pallida*, a similarity that undoubtedly confounds management strategies for the potato cyst nematodes (Miller, pers. commun.). Taxonomic relationships which reflect phylogeny among some groups of *Globodera* and particularly those of the *G. tabacum* complex are elusive. One hypothesis is that a continuum of morphological variants occurs within some members of the genus because interspecific and intrasubspecific hybridization occurs not only under experimental conditions (e.g., Miller, 1983) but in nature. Such fertile hybrids may give rise to isolates with recombination of morphological characters. Because of the current taxonomic dilemmas concerning *Globodera*, we consider identification of subspecies of the *G. tabacum* beyond the scope of this review, and instead emphasize



TABLE 5 Compendium for Identification Among Select *Globoderas* (Fig.21)

| Species                   | J2 stylet knob shape  | No. cuticular ridges between vulva-anus | Granek's ratio of cysts            | Host  |
|---------------------------|---|---|------------------------------------|---|
| <i>G. rostochiensis</i>   | Rounded: dorsal may slope posteriad                             | 16-31 ridges (about 22) <sup>a</sup>    | 1.3-9.5 (4.5) <sup>a</sup>         | No tobacco potato                           |
| <i>G. pallida</i>         | Pointed anteriorly; anterior surface of dorsal slightly concave | 8-20 ridges (about 12) <sup>a</sup>     | 1.2-3.5 (2.3) <sup>a</sup>         | No tobacco potato <sup>c</sup>              |
| <i>G. tabacum</i> complex | Pointed to rounded anteriorly; dorsal slightly concave          | 10-14 ridges                            | 1-4.2 (2.8 or less) <sup>a,b</sup> | Tobacco <sup>d</sup> no potato <sup>c</sup> |
|                           | J2 stylet length (μm)   | Female stylet length (μm)               |                                    |   |
| <i>G. rostochiensis</i>   | (21-23)<br>21.8-22 <sup>a</sup>                                 | (21-25)<br>23 <sup>a</sup>              |                                    |   |
| <i>G. pallida</i>         | (21-26)<br>22.8-24 <sup>a</sup>                                 | (23-29)<br>27 <sup>a</sup>              |                                    |   |
| <i>G. tabacum</i>         | (19-28)<br>22.8-24 <sup>a</sup>                                 | (18-30)<br>25 <sup>a</sup>              |                                    |   |

<sup>a</sup>Measurement which are most typical (Golden, pers. commun.).<sup>b</sup>Generally less than 2.1 in *G. t. tabacum*.<sup>c</sup>See text for reports of exceptions.<sup>d</sup>*G. t. virginiae* only occurs on tobacco experimentally. Also many Mexican populations do not reproduce on tobacco or potato (Miller, pers. commun.).

morphological characters reported to be useful in distinguishing the combined subspecies of *G. tabacum* with *G. pallida* and *G. rostochiensis* (Table 5). Identification of the *G. tabacum* complex is often aided by the slightly more pointed anterior surface of stylet knobs and concave surface of the dorsal knob on second-stage juveniles relative to *G. rostochiensis* in which the knobs are more rounded and the dorsal knob slopes posteriorly (Fig. 21A-C). Miller and Gray (1968, 1972) illustrate a concave posterior-sloping dorsal knob in females of *G. t. virginiae* and *G. t. solanacearum*. These knobs apparently differ from the more rounded knobs in females of *G. rostochiensis*. However, J2 and female stylet knobs of the *G. tabacum* complex are apparently not different from populations of *G. pallida*. The pattern between the vulva and anus of the *G. tabacum* complex may form a zig-zag maze rather than more or less parallel ridges of *G. rostochiensis* Miller and Gray, 1968, 1972), but the pattern in *G. tabacum* may overlap with the highly variable patterns of *G. pallida*. Granek's ratio, the distance from the anus to the nearest edge of the vulva



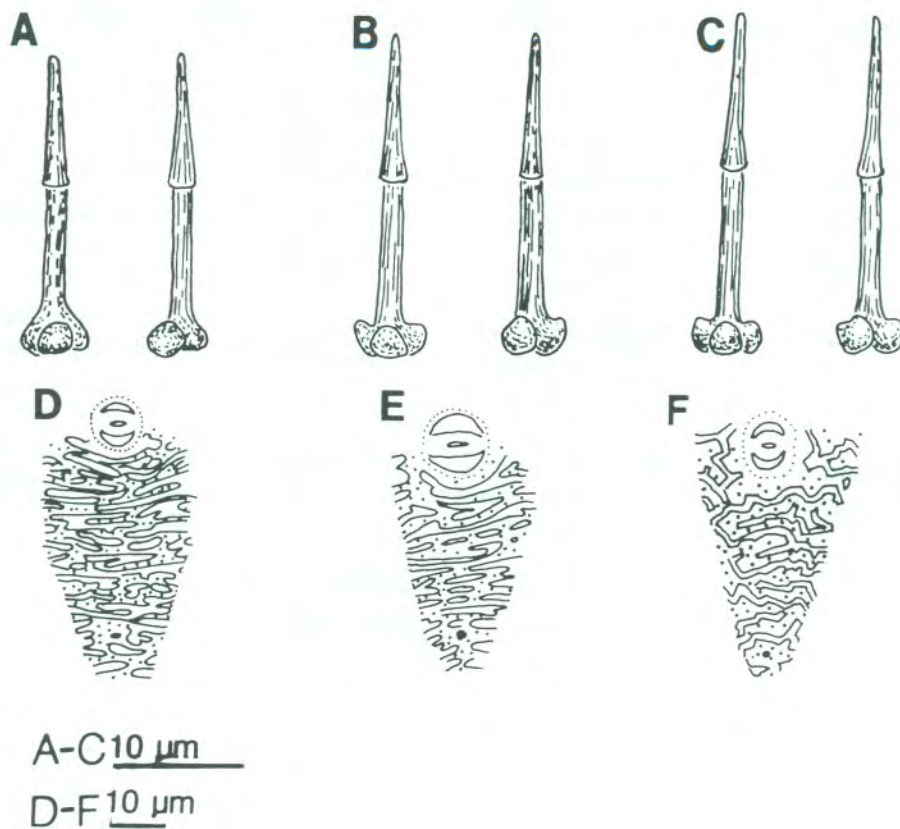


FIGURE 21 Characteristics for identification of some species of *Globodera*. (A) *Globodera rostochiensis*, stylet of second-stage juvenile (J2) (left dorsal and lateral view). *Globodera pallida*, stylet of J2. (C) *Globodera tabacum tabacum*, stylet of J2. (D) *G. rostochiensis*, anal-vulval region of female. (E) *G. pallida*, anal-vulval region of female; (F) *G. tabacum*, anal-vulval region of female. (A, B, D, E, redrawn after Stone, 1973.)

opening divided by the diameter of the vulva (Granek, 1955) or length of the fenestra (Hesling, 1973), may be useful. Granek's ratio in the *G. tabacum* complex may overlap with *G. pallida*, particularly in subspecies *G. t. virginiae*, but in other subspecies it is distinctive in that the mean of a number of individuals in a population is generally less than 2.1 (Fig. 21D-F). Because of the morphological distinctiveness of the *G. tabacum* complex is subtle, and variation among subspecies and populations is great, a bioassay including certain potato cultivars susceptible to other cyst nematodes may prove to be the most reliable approach to identification by the inexperienced. Subspecies of *G. tabacum* rarely reproduce on potato, and *G. rostochiensis* and *G. pallida* rarely reproduce on tobacco. Nevertheless, there are several reports of isolates that behave to the contrary (Lownsbery and Lownsbery, 1954; Miller and Gray, 1968, 1972). Stone (1972) reports infection by subspecies of *G. tabacum* on *S. tuberosum* "Arran Banner." However, subsequent tests did not support Stone's initial findings except in rare cases where a few females were found on a test plant (Miller, pers. commun.; Miller et al., 1974; Stone and Miller, 1974). Some isolates of *G. rostochiensis*



from Venezuela readily reproduce on tobacco (Meredith, 1976), and under experimental condition a few females of *G. pallida* have been reported on tobacco (Parrot and Miller, 1977).

Stone (1972; 1973) gives the most complete differential diagnoses of *G. rostochiensis* and *G. pallida*. He suggests that females of *G. pallida* are internally cream-colored whereas *G. rostochiensis* is golden. *Globodera rostochiensis* and *G. pallida* generally differ in the number of ridges between the vulva and anus, with nearly twice as many ridges occurring in *G. rostochiensis* (Table 5). In *G. rostochiensis*, the stylet knobs of the second-stage juveniles are rounded but the dorsal knob may slope posteriorly, whereas in *G. pallida* it is elongated along the longitudinal axis of the nematode and the knobs are pointed anteriorly (Fig. 21A, B). When a number of individuals of a population are carefully measured, the mean length of the female stylet of *G. rostochiensis* typically is longer than that of *G. pallida* (27 vs. 23  $\mu\text{m}$ ; Stone, 1972, 1973). Many diagnostically useful morphometrics for *G. rostochiensis* and *G. pallida* have relatively stable means, but often include a few unusual individuals which extend the range (Table 5). Golden (pers. commun.) considers Granek's ratio particularly valuable for separating the two species; although unusual variants occur, the mean of a number of individuals of a population is generally near 4.5 for *G. rostochiensis* and 2.3 for *G. pallida* (Table 5).

Stone suggests the SEM lip patterns are useful for distinguishing between *H. pallida* from other cyst nematodes but this was not substantiated by Othman et al. (1988), whose investigation indicated considerable variation within species. Promising nonmorphological methods for identification include hybridization of unknown with known DNA fragments to separate populations of *G. rostochiensis* from *G. pallida* (Burrows and Perry, 1988; Marshall and Crawford, 1987). Further investigations are needed to identify fragments that are species-specific and to expand the investigations to additional species.

Identification of *G. rostochiensis*, *G. pallida*, and the *G. tabacum* complex, having the greatest practical application, is considered here. A key by Golden (1986) includes additional species of the genus.

*Globodera rostochiensis* (Wollenweber, 1923) Behrens, 1975

*Globodera pallida* (Stone, 1973) Behrens, 1975 (potato cyst nematodes)

**Synonyms and history.** Kühn was the first to report potato as a host of *H. schachtii* in 1881 when this species encompassed all cyst nematodes. Perhaps potato cyst nematodes were not widespread at the time, since through the 1800s other authors considered solanaceous plants as not susceptible to *H. schachtii sensu lato* (Franklin, 1951). In the early 1900s the cyst nematode of potato became more widely known throughout Europe and many concluded that at least one form of *H. schachtii* was specialized on this host, causing "soil sickness of potatoes" (Spears, 1968). Wollenweber (1923) recognized morphological differences between the potato cyst nematodes and cyst nematodes of sugar beet and proposed the separate species, *Heterodera rostochiensis*. Others continued to consider potato cysts as subspecific within *H. schachtii* until 1940 when Franklin published a more complete morphological description and diagnosis of *H. rostochiensis*. Interest in the potato cyst nematode intensified as its wide distribution was recognized including discovery in 1941 of infested fields in Long Island (USA). Description of additional species of cyst nematodes prompted Golden and Ellington (1972) to redescribe *H. rostochiensis* to allow more precise comparison with related species; about the same time Stone (1972) recognized a second species of potato cyst nematode, *H. pallida*. These several "related" species were primarily set apart by the absence of a terminal cone resulting in round cysts. The group was first represented taxonomically by a subgenus, *Globodera* Skarbilovich. Subsequently,



Mulvey and Stone (1976) confirmed Behrens (1975) in elevating the round cyst nematodes, including *H. rostochiensis* and *H. pallida*, to generic rank resulting in *Globodera rostochiensis* and *Globodera pallida*.

**Hosts.** The potato cyst nematodes parasitize about 90 species of the large genus *Solanum*. Many hosts are wild species of South America (Southey, 1965) including close relatives of potato, *S. tuberosum*, with varying levels of resistance, *S. tuberosum andigena*, *S. vernei*, and *S. sucrense* (Spears, 1968). However, other weed hosts such as *S. sarachoides*, *S. dulcamara*, and *Datura stramonium* in Europe may exacerbate persistence of this nematode in certain agricultural areas (Goodey et al., 1965, Stone, 1973). Although the potato cyst nematodes are not typically found on tobacco, we have noted exceptions (see "Identification"; Meredith, 1976; Parrott and Miller, 1977). *Solanum tuberosum* is by far the most important agricultural host of potato cyst nematodes; other agricultural hosts are *S. melongena* (eggplant) and *Lycopersicon esculentum* (tomato) (Stone, 1973).

**Distribution.** For many years the potato cyst nematode was believed to be restricted in distribution to Europe and was thought to have originated there as a mutation from other cyst species (De Segura, 1952). However, discovery in the 1950s of the nematode on a ship from Peru led to surveys in South America and recognition that potato cyst nematode occurred on native plants in the Andean region of Peru and adjacent countries. The nematode was likely a pest of pre-Inca potato agriculture, with *G. pallida* still present on *Solanum acaule* in terraces uncultivated since ancient times (Jatala and Garzon, 1987). Today, a widely accepted hypothesis is that the potato cyst nematodes, like their potato host, originated in the mountains of South America and that they may have been introduced to Europe, with the potato, in the 1600s. Lack of awareness of these nematodes for more than 200 years is interpreted as evidence of a slow buildup of the nematodes in Europe (Spears, 1968). In addition, old potato cultivars may have been relatively tolerant to cyst nematodes, compared to the selected lines introduced following the Irish potato famine in the mid-1800s (Spears, 1968). From Europe, it is believed that the potato cyst nematodes were spread, primarily on seed pieces, throughout the potato-growing regions of the world including more than 50 countries (Evans and Stone, 1977; Mai, 1977). It is noteworthy, however, that the genus *Globodera* is widespread and that it includes apparently indigenous nonagricultural forms in Europe, Asia, America, and perhaps New Zealand. The range of the potato cyst nematodes on weed hosts prior to movement by commerce is unknown and commerce may not entirely account for its modern distribution (Ferris, 1979). Seinhorst (1986) suggests that containment or restricted spread in some regions, such as warmer climates and the USA, probably cannot be wholly attributed to successful quarantine, but rather adverse conditions in areas of introduction. Similarly, *G. rostochiensis* in northern Mexico probably has not moved into Texas on vehicles and become established in the potato-growing region of Texas, perhaps because of the high soil temperature (Miller, pers. commun.). In many regions *G. rostochiensis* and *G. pallida* occur together, but often temperature seems to restrict distribution of one or the other species. In cooler areas such as north of 15.6 S, *G. pallida* occurs exclusively, whereas the range of *G. rostochiensis* extends into regions with slightly warmer climates than are tolerated by *G. pallida* (Evans et al., 1975; Evans and Stone, 1977; Mai, 1977).

**Biology.** The life history of potato cyst nematodes follows the general pattern of other cyst-forming heteroderines. However, details of hatching, establishing feeding, mating, and cyst formation include adaptations peculiar to these nematodes, with some distinctions even between *G. rostochiensis* and *G. pallida*.

Tanned cysts, often with about 500 eggs, are especially persistent in soil; eggs within cysts may survive 28 years where soil type and temperature are ideal (Grainger,



1964), but even under ideal conditions the percentage of hatch decreases steadily over time. Hatching of freshly developed eggs apparently can occur in water, but for eggs in diapause, hatching is stimulated by host root diffusates which effect a change in the permeability of lipoprotein membranes of the eggshell. These diffusates allow leakage of solutes and increase in O<sub>2</sub> uptake (Atkinson and Ballantyne, 1977a, b) and hydration of juveniles (Ellenby and Perry, 1976; Perry et al., 1982; Clark and Perry, 1985; Perry and Feil, 1986). Hydration of juveniles is also associated with secretory granule accumulation in subventral glands in preparation for feeding after hatching (Perry et al., 1989). These changes may be accompanied by greater activity of juveniles within the egg including stylet thrusting (Doncaster and Shepherd, 1967). Root diffusates from both susceptible and resistant cultivars elicit similar effects (Mägi, 1971), but the effectiveness of diffusates depends on temperature; and some substances, such as exudates of the fungus, *Rhizoctonia solani*, inhibit hatching of one or sometimes both nematode species. *Globodera pallida* and *G. rostochiensis* differ in their response to various hatching agents and their concentrations (Clark and Hennessy, 1987). Furthermore, *G. pallida* hatches less freely and is less persistent at high temperatures than *G. rostochiensis* (Clarke and Perry, 1977; Robinson et al., 1987). The importance of root diffusates to hatching and completion of the life cycle of the potato cyst nematode has generated speculation on possible control measures that would interfere with the role of diffusates. Indeed, Perry and Beane (1988) demonstrated that activated charcoal in greenhouse pots temporarily limits hatching by interfering with diffusates. Hatched second-stage juveniles are attracted to penetrate the host just behind the root tip or lateral root. They move through the root and feed on the pericycle, cortex or endodermis, and become sedentary, inducing formation of a large syncytial transfer cell at the feeding site. (Spears, 1968). In resistant reactions, the host response typically involves localized necrosis and thickening of the syncytial walls, perhaps in response to accumulation of lignin which might act as a barrier to the flow of nutrients (Rice et al., 1986; Robinson et al., 1988).

Development from hatching to adult requires 38–45 days (Spears, 1968) and females mate within 50 days of root invasion (Evans, 1970). As the sedentary female enlarges, the tail end bursts through the root, becoming exposed for mating. Whereas females of *Globodera* produce little if any gelatinous matrix, they nevertheless exude a pheromone which attracts males for copulation (Green et al., 1970; Green and Greet, 1972; Greet et al., 1968). Males are motile and develop from sedentary saccate juvenile stages; some suggest that males are more abundant under environmental conditions which may be stressful to the population (Trudgill et al., 1967). Males do not feed and Evans (1970) reports they live up to 10 days inseminating up to 10 females, and each may be inseminated by more than one male. A degree of mating compatibility is conserved between *G. rostochiensis*, *G. pallida*, and many cyst nematodes, so that under laboratory condition males of one species may inseminate females of another, and in many cases hybrids are produced (Miller, 1983). We have noted that the possible occurrence of such hybrids in nature may account for the high variability in morphology and host specificity within some species and groups of species (Miller, pers. commun.). The potato cyst nematode is amphimitic with the basic  $n = 9$  chromosomes although some variants in chromosome numbers have been reported (Triantaphyllou, 1975a).

Eggs are retained within the body of the potato cyst female and the second-stage juvenile develops within the egg. Upon death, the body of the female becomes a cyst, changing in color from white to brown, also passing through a golden or orange phase in *G. rostochiensis* (Spears, 1968). Juveniles may hatch so that more than one generation is



completed per year on a crop if temperatures remain favorable or, in the absence of favorable conditions including a suitable host, they may persist within the cyst for years.

At low levels potato cyst nematodes do little damage, but after years of repeated potato culture, these cyst nematodes may increase in number to a point of limiting production, and we have noted that in some extreme cases the yield may be less than the seed pieces planted (Mai, 1977). Field symptoms of heavy infestations are similar among cyst-forming nematodes; first they induce poor growth in spots, followed by increase in size and number of the spots. Damage to the root system is typically associated with wilting of plants and stunting (Spears, 1968). Tomato plants yield symptoms similar to potatoes except that roots may have slight swelling resembling root-knot nematode nodules (Spears, 1968).

We have noted that potato cyst nematodes are heterogeneous, consisting of two morphologically and physiologically distinct species, *G. rostochiensis* and *G. pallida*. With the introduction of resistant potato cultivars, however, a greater diversity was recognized in response to these cultivars, leading to identification of a number of pathotypes and various schemes for their nomenclature (Canto and de Scurrah, 1977; Kort et al., 1977). Seinhorst (1986) notes that five pathotypes of *G. rostochiensis* and three of *G. pallida* are recognized but that the diversity of these nematodes is probably greater than our ability to distinguish the pathotypes; one limitation is that host differential tests typically indicate "susceptibility" or "resistance" of an isolate but do not easily accommodate intermediate responses. Diversity of pathotypes beyond the present nomenclature is also underscored at the level of molecular biology (Bakkar and Gommers, 1986; Fox and Atkinson, 1985a, b).

**Control.** It has been noted (see "Hosts") that closely related wild forms of potato—*S. tuberosum andigena*, *S. vernei*, *S. sucrense*—provide sources of resistance to potato cyst nematode which have been incorporated into agricultural cultivars. Although resistant cultivars stimulate hatching, roots respond to infection by necrosis and hypersensitive reaction. In resistant cultivars, juveniles often fail to mature to females, whereas production of males apparently is unrestrained (Seinhorst, 1986). Resistance is based on dominant gene, but females that are homozygously recessive for the virulence gene are capable of reproduction on resistant plants (Jones et al., 1981; Seinhorst, 1986). The effectiveness of resistant cultivars is confounded by pathotypes which overcome resistance, and more such pathotypes may be selected by repeated use of resistant cultivars (Seinhorst, 1986). Resistant cultivars are primarily useful as a means to maintain an already low population density of the potato cyst nematode below damaging levels, when the cultivars meet other commercial requirements. However, resistant cultivars are not available for every purpose, and those resistant to a range of pathotypes are in short supply (Seinhorst, 1986).

Crop rotation might be a promising method of control for a nematode with a narrow host range such as potato cyst nematode, except that the infective state is so persistent in the absence of a host. In most of Europe, where populations decrease only about 35%/year in the absence of a host, a 5-7 year rotation is needed to minimize damage, but in warmer climates, such as the Mediterranean area, decline is apparently faster and shorter rotations may be effective (Grainger, 1964; Seinhorst, 1986; Spear, 1968). Volunteer plants and weed hosts may interfere with effective rotations.

Trap crops, if implemented with caution and careful timing, are a promising method of reducing populations (Balandras, 1986; Carlsson and Videgard, 1971). Sprouted small tubers (with only a small reserve of nutrients) of a susceptible late cultivar are planted and invaded by juveniles. The plants are carefully sampled so that they can be destroyed just before the females produce eggs. Optimally this method can result in a 75% decrease in



populations and combined with chemical treatment of soil reduction of 90% has been achieved (Mugniery and Balandras, 1984).

Chemical control has the disadvantages of environmental hazard and high cost, but is often effective in managing the potato cyst nematode, particularly when integrated with other strategies. Whitehead (1986) notes that withdrawal of DBCP and EDB from general use may be discouraging investment in discovery and registration of new nematicides, yet nematicides are likely to be needed for potato production in the foreseeable future.

In some cases, as in the Netherlands, chemical treatment of the soil may be required by the government to keep nematode infestations at a low level nationally and thus to protect the international trade of seed potatoes (Seinhorst, 1986). Import of potatoes is widely regulated by quarantine laws as a first line of defense in managing potato cyst nematodes. In the USA the potato cyst nematode has successfully been limited to a small area, but under different regulatory conditions containment has been more difficult. For example, in Mexico the potato cyst nematode seems to be a relatively new introduction and spread within the mountainous regions of the country is rapid. Quarantine is confounded by a number of undescribed wild *Globodera* forms on weed hosts, which are morphologically similar to *G. rostochiensis* and *G. pallida*, but which do not reproduce on potato.

The potential for biological control of potato cyst nematodes has been considered by only a few investigators (Roessner, 1986). The Andes, being the putative origin of potatoes and *G. rostochiensis* and *G. pallida*, is deemed a possible source of natural enemies to the nematode, and several associated fungi were found in Peru (Jones and Rodriguez Kabana, 1985). Although antagonists of practical importance for management have not been found (Roessner, 1986), biological control may nevertheless be feasible in the future (Whitehead, 1986).

*Globodera tabacum* (Lownsbery and Lownsbery, 1954) Behrens, 1975 *sensu* Stone, 1983 (tobacco cyst nematode complex) including *G. tabacum tabacum* (Lownsbery and Lownsbery, 1954); *G. tabacum virginiae* (Miller and Gray, 1968); *G. tabacum solanacearum* (Miller and Gray, 1972)

*Synonyms and history.* The round cyst nematodes; previously known only as potato cyst nematodes, have long been recognized as heterogeneous in morphology and host range, so it was not surprising when a population with round cysts was found in Connecticut parasitizing shade tobacco. Reproduction on tobacco was contrary to previous host range tests of the potato cyst nematodes in Europe (Lownsbery and Lownsbery, 1954). In addition, the new population of cyst nematode did not develop on cultivars of potato tested (Lownsbery, 1953; Mai, 1952). Closer examination of the population indicated morphological differences from *G. rostochiensis* including patterns between the vulva and anus, and led to the description of the new species *Heterodera tabacum* Lownsbery and Lownsbery, 1954. A second cyst nematode which parasitizes tobacco, but which was recovered from horsenettle (*Solanum carolinense* L.), a weed in Virginia, was described as distinct from *H. tabacum* Miller and Gray, 1968, in part on the basis of the shape of female stylet knobs, as well as a higher value of Granek's ratio, and differential host response on certain species of *Nicotiana* (Miller and Gray, 1968). A nematode similar to *H. virginiae* had also been described in Mexico, but never published as a new species (Campos Vela, 1967); in subsequent investigations this was considered conspecific with *H. virginiae* (Golden and Ellington, 1972). Yet many populations, including that described by Campos Vela, do not reproduce on tobacco (Miller, pers. commun.). Furthermore, some populations of the Mexican cyst nematode are morphologically indistinguishable from *G. pallida*, although they do not reproduce on potato. A few years prior to the description of *H.*



*virginiae*, Osborne and Holmes recovered a cyst nematode parasitizing flue-cured tobacco and hosenettle on a farm in Virginia, but the nematode was not described as a new species and for several years was referred to as the "Osborne cyst." Miller and Gray (1972) noted that this nematode differed from *H. tabacum* and *H. virginiae* in its response to *Nicotiana* hosts and that morphological differences from *H. tabacum* and *H. virginiae* included the pattern of the vulva anal region and Granek's ratio. Shortly thereafter, the round cyst nematodes were increasingly recognized as distinctive from other cysts; these differences were first reflected by placement in a separate subgenus *Globodera* Skarbilovich, 1959, and later a separate genus *Globodera* including *G. tabacum*, *G. virginiae*, and *G. solanacearum* (Behrens, 1975; Mulvey and Stone, 1976).

Morphological characters are highly conserved among many species of *Globodera*. Stone (1983) believed that only *G. rostochiensis*, *G. pallida*, and *G. tabacum* could be consistently recognized morphologically. Furthermore, he suggested that *G. virginiae*, *G. solanacearum*, and *G. tabacum*, while apparently allopatric, were difficult to separate. This view was supported by multivariate analyses. Furthermore, Stone reported that the latter three species hybridize with viable offspring more readily than other species (i.e., *G. rostochiensis* and *G. pallida*; see also Miller, 1983). Stone considered that only *G. tabacum* was significant on agricultural hosts, and it was his opinion that this species alone needed to be recognized for practical taxonomy. Based on these views, he proposed that *G. tabacum*, *G. solanacearum*, and *G. virginiae* be given a new rank of subspecies within *G. tabacum* (Stone, 1983). Unfortunately, Stone did not propose a diagnosis for the new inclusive *G. tabacum*.

**Distribution.** *Globodera t. tabacum* is apparently restricted in distribution to Connecticut and Massachusetts, whereas *G. t. solanacearum* is only known to occur in Virginia and North Carolina (Barker and Lucas, 1984). *Globodera t. virginiae* also occurs in Virginia but is reported to be conspecific with populations of cyst nematodes which occur throughout Mexico and Central America.

**Hosts.** The three subspecies of the *G. tabacum* complex are primarily limited to host range to *Nicotiana* and *Solanum*, although host range tests including other plant genera are limited. All three subspecies of the *G. tabacum* complex reproduce on *Nicotiana tabacum* L. However, *N. tabacum* is a poor host for *G. t. virginiae* (Nusbaum, 1969; Barker and Lucas, 1984) and not observed to be a host under field conditions (Miller, pers. commun.). Differential responses separate the subspecies of *G. tabacum* on other *Nicotiana* species (Miller and Gray, 1972). Isolates of the potato cyst nematodes have been reported not to reproduce on *N. tabacum*. Conversely, *G. t. tabacum* was originally believed not to reproduce on potato, *Solanum tuberosum* (specifically *S. tuberosum* "Katahdin"; Miller and Gray, 1972) but subsequent reports indicate formation of some cysts on at least one potato cultivar, *S. tuberosum* "Arran Banner" (Stone, 1972). Lownsbery and Lownsbery (1954) reported *S. nigrum* as a host of *G. t. tabacum* but a nonhost of *G. rostochiensis*. Roberts and Stone (1981) tested eight isolates including the three subspecies of the *G. tabacum* complex on 19 other species of *Solanum*. Although isolates varied in their host range, the variation weakly confirmed subspecies, particularly when the data were corrected for a mislabeled population (Roberts; Miller, pers. commun.). About five host species were not susceptible to most nematode isolates. Nusbaum (1969) reported that *G. t. solanacearum* reproduces on tobacco, tomato, and eggplant but not on potato. Clearly, isolates of all three subspecies of *G. tabacum* are highly variable in response to many host isolates and cultivars, leading further support to the physiological heterogeneity of this group. *Globodera t. solanacearum* is particularly destructive on many cultivars of flue-cured tobacco (Fig. 22).



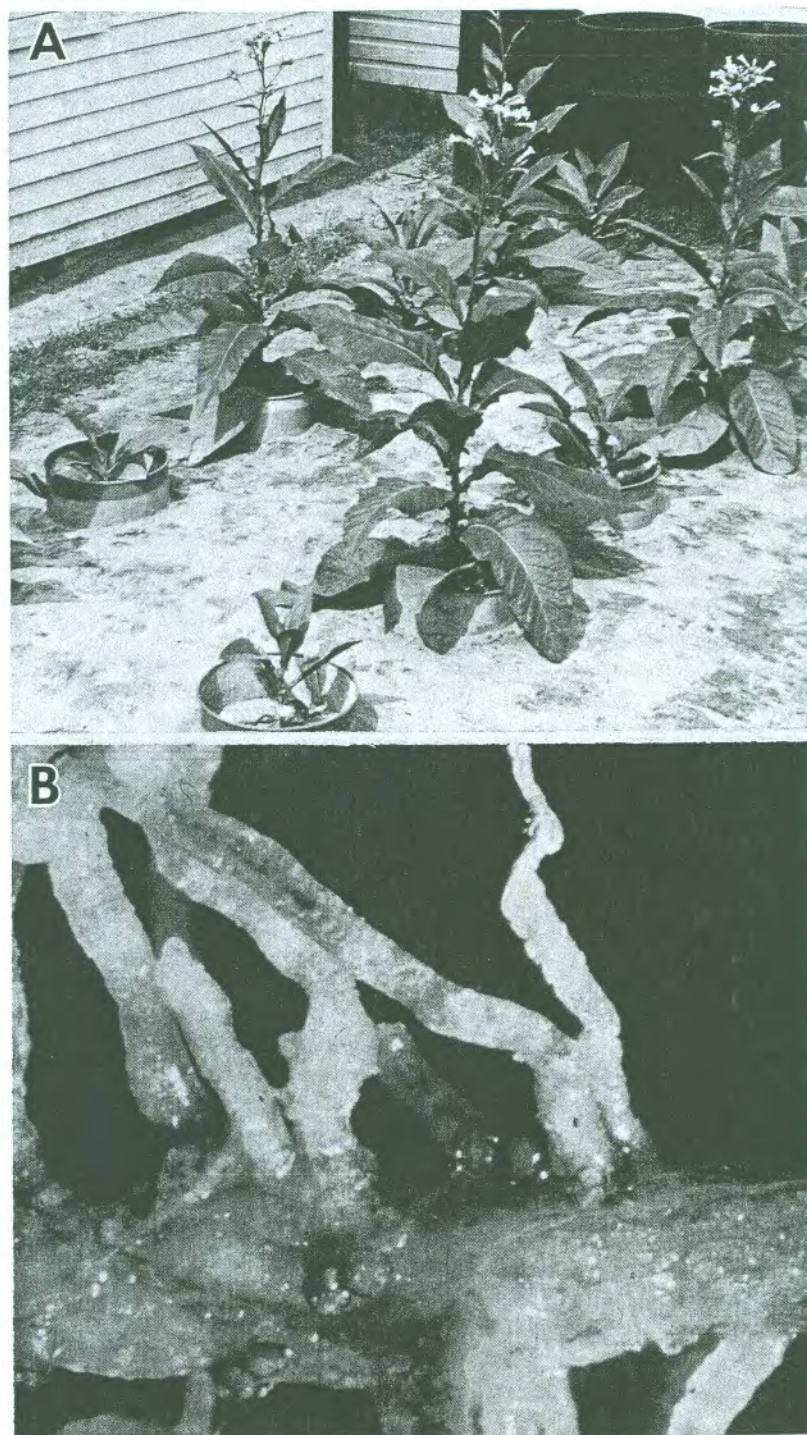


FIGURE 22 *Globodera tabacum solanacearum* of flue-cured tobacco. (A) Stunted infected plants adjacent to large noninoculated controls. (B) Cysts on roots (A, B courtesy L. I. Miller.)



**Biology.** Knowledge of the biology of the *G. tabacum* complex is primarily limited to reports in original descriptions and a few brief reviews (e.g., Barker and Lucas, 1984). Mature females of the *G. tabacum* complex retain eggs in the cyst, which may survive for years in the absence of a suitable host. Host exudates are believed to play a role in hatch followed by infection of seedlings. Females are fertilized and about 20 days is required for *G. t. tabacum* to produce eggs under field conditions, so that in the USA it may have four to five generations on a single tobacco crop (Barker and Lucas, 1984). Conversely, *G. t. solanacearum* is reported to require 32–82 days to complete a generation depending on conditions (34 days at 24–29°C; Adams et al., 1982; Miller and Gray, 1972), so that as few as two generations may be completed per year; *G. t. virginiae* apparently has similar generation time and temperature requirements (Miller and Gray, 1968).

Subspecies of *G. tabacum* may cause poor growth of tobacco and losses may exceed 50% (Barker and Lucas, 1984). *Globodera t. virginiae*, while reproducing poorly on tobacco, may cause considerable stunting on K-16 burley tobacco because of intolerance to invasion of infective juveniles (Barker and Lucas, 1984; Miller, pers. commun.).

**Control.** Tobacco cultivars with some resistance to the *G. tabacum* complex are available, and resistance in other *Nicotiana* species holds some promise for developing additional suitable lines (Baalawy and Fox, 1971; Barker and Lucas, 1984; LaMondia, 1988; Miller et al., 1972). Currently available lines are not tolerant of invasion and may be damaged by penetration of high nematode populations; nevertheless these lines may be effective in combination with nematicides (Johnson et al., 1989). Use of resistant cultivars may also be confounded by pathogenic variation of the nematode and the potential selection for pathogenicity (Elliott et al., 1986). The relatively narrow host range of these cyst nematodes also suggests that effective rotation programs could be developed as part of management programs (Barker and Lucas, 1984), although the relatively low economic value of rotation crops has discouraged their use (Johnson et al., 1989). Several nematicides give effective control, although in some cases their value could be limited by resistance of eggs retained within cysts (Miller, 1969, 1970; Barker and Lucas, 1984).

### **Cactodera**

*Cactodera* Krall and Krall, 1978  
syn. *Heterodera* Schmidt, 1959

**Diagnosis:** Heteroderinae Filipjev and Schuurmans Stekhoven

**Females.** Cyst present. Spheroidal to lemon-shaped with small posterior cone. Cuticle surface with irregular transverse ridges; distinct D layer present (except in *C. betulae*). Vulva terminal. In cysts, circumfenestrae develop around vulval region; no anal fenestration. Underbridge, perineal papillae and bullae absent, but denticles may be present. All eggs retained in body (no egg mass); egg surface smooth or tuberculate.

**Males.** Body twisted. Lateral field with four lines. Spicules >30 µm, bifid distal tip.

**Second-stage juveniles.** Lateral field with four lines. Esophageal glands filling body cavity. Tail pointed with terminal half hyaline. Phasmid openings porelike. En face pattern commonly with six separate lips; sometimes fusion of adjacent submedial lips, without fusion of labial disc and submedial lips (except *C. betulae*).

**Nurse cell.** Syncytium, generally with wall ingrowths.

**Species.** (Table 6)

**Identification.** *Cactodera* includes nine species, although the status of *C. betulae* and *C. chaubattia* in the genus is controversial (Baldwin and Schouest, 1990; Stone, 1986; Luc et al., 1988). *Cactodera* is distinctive from other heteroderines with the combination of



TABLE 6 Species of *Cactodera*


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| <i>Cactodera cacti</i> (Filipjev and Schuurmans Stekhoven, 1941) Krall and Krall, 1978<br>syn. <i>Heterodera cacti</i> Filipjev and Schuurmans Stekhoven, 1941   |
| <i>C. acnidae</i> (Schuster and Brezina, 1979) Wouts, 1985<br>syn. <i>H. acnidae</i> Schuster and Brezina, 1979  |
| <i>C. amaranthi</i> (Stoyanov, 1972) Krall and Krall, 1978<br>syn. <i>H. amaranthi</i> Stoyanov, 1972  |
| <i>C. aquatica</i> (Kirjanova, 1971) Krall and Krall, 1978<br>syn. <i>H. aquatica</i> Kirjanova, 1971  |
| <i>C. betulae</i> (Hirschmann and Riggs, 1969) Krall and Krall, 1978<br>syn. <i>H. betulae</i> Hirschmann and Riggs, 1969  |
| <i>C. chaubattia</i> (Gupta and Edward, 1973) Stone, 1986<br>syn. <i>G. chaubattia</i> (Gupta and Edward, 1973) Wouts, 1924<br><i>H. chaubattia</i> Gupta and Edward, 1973<br><i>H. mali</i> Kirjanova and Borisenko, 1975<br><i>G. mali</i> (Kirjanova and Borisenko, 1975) Behrens, 1975 |
| <i>C. estonica</i> (Kirjanova and Krall, 1963) Krall and Krall, 1978<br>syn. <i>H. estonica</i> Kirjanova and Krall, 1963  |
| <i>C. eremica</i> Baldwin and Bell, 1985   |
| <i>C. thornei</i> (Golden and Raski, 1977) Krall and Krall, 1978<br>syn. <i>H. thornei</i> Golden and Raski, 1977  |
| <i>C. weissii</i> (Steiner, 1949) Krall and Krall, 1978<br>syn. <i>H. weissii</i> Steiner, 1949  |

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a cyst and vulval cone with a circumfenestral (Fig. 23A). The pattern on the cuticle of females and cysts is often ambiguous with some zig-zag patterns in the cones becoming more parallel and horizontal at midbody, forming striations. Cuticular striations are unusual in cyst nematodes, occurring only in *Cactodera* and *Dolichodera*. Bullae are absent in *Cactodera* but vulval denticles, which are residual vaginal muscles (described as small, toothlike structures) within the vulval cone, are characteristically distinct in the genus. Golden and Raski (1977) and Cordero (1989) suggest that these denticles occur in other cyst nematodes, sometimes in combination with bullae (see "Morphology" above). Species of *Cactodera* are distinctive and generally easily identified by second-stage juveniles on the basis of length of the stylet, tail, and hyaline tail terminus. The shape of cysts and presence or absence of tubercles on eggs is also useful for species identification. Although the name may suggest that *Cactodera* is limited to cacti as a host, other hosts include *Euphorbia*, *Montia*, *Polygonum*, *Atriplex*, and certain grasses. Although affinity with *Cactodera* is uncertain, *C. betulae* attacks *Betulae* and a range of unrelated hosts (Golden and Raski, 1977), and *C. chaubattia* is reported from soil around *Malus* (Gupta and Edward, 1973). Golden (1986) provides a key including most species of *Cactodera*.



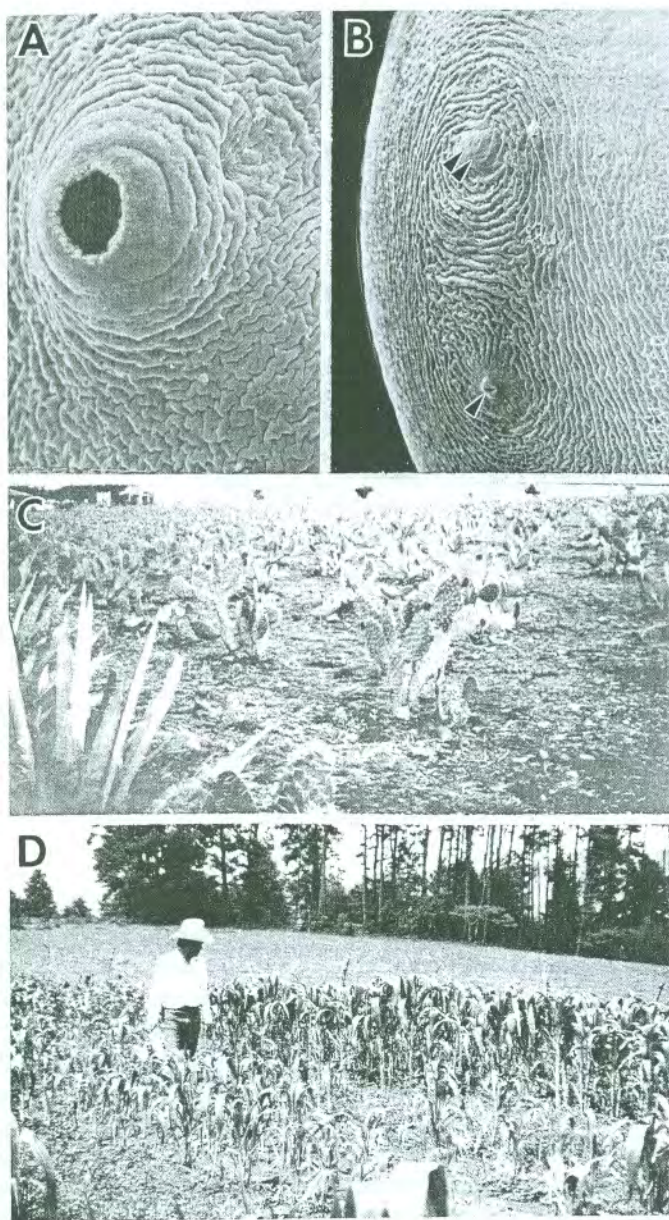


FIGURE 23 *Cactodera* and *Punctodera*. (A) Terminal region of female of *Cactodera cacti* showing cone (SEM). (B) Terminal region of female of *Punctodera chalcoensis*, lacking cone (SEM). Arrowhead indicates vulva; double arrow, anus. (C) Commercially grown cactus in Mexico, commonly infected with *C. cacti*. (D) Field plots in Mexico showing rows of stunted corn infected with *P. chalcoensis*, adjacent to taller controls in soil treated with Nematicure® and Furadan®.



*Cactodera cacti* (Filipjev and Schuurmans Stekhoven, 1941) Krall and Krall, 1978 (the cactus cyst nematode)

**Synonyms and history.** The cactus cyst nematode was first described as *H. schachtii* on cacti ([*Phyllocactus* (= *Epiphyllum*), *Cereus* (= *Heliocerus*)] in the Netherlands by Adam (1932) but Filipjev and Schuurmans Stekhoven (1941) redescribed the nematode as *Heterodera cacti*. Goffart (1936) believed the species to be closely related to *H. schachtii* because root exudates of sugar beet, a nonhost, nevertheless "activated" juveniles. Krall and Krall (1978) created the new genus *Cactodera* to include *C. cacti* and several additional species. The cactus cyst nematode may have originated on cacti in the New World but it has become widely distributed on ornamentals throughout the world.

**Hosts.** The cactus cyst nematode is apparently nearly restricted in host range to succulents of Cactaceae and Euphorbiaceae. As the widespread distribution of this nematode became apparent in the late 1950s a number of reports indicated a wide range of host species within the two families (Kumar, 1964; Southey, 1957; Shmal'ko, 1959). Since then records in the USA indicate a host range of 76 species of Cactaceae and two Euphorbiaceae (Langdon and Esser, 1969). Little is known of the pathogenicity of *C. cacti* on ornamental plants, although it is likely that they reduce plant vigor and interact with root-rotting organisms. They also affect the salability of cacti, since infected plants are often subjected to quarantine regulations targeting cyst nematodes in general.

**Distribution.** The cactus cyst nematode is probably native of Mexico (Krall and Krall, 1978) and perhaps Central and South America where it occurs widely in native habitats. Although it may be best adapted to arid subtropics, it has been widely dispersed on ornamentals and in cooler climates is commonly found in greenhouses. For example, Shmal'ko (1959) reports the cactus cyst nematode in the botanical garden of the Academy of Sciences in the USSR and indicates that the nematode was introduced on a large collection of succulent plants from foreign countries in 1946–1948. In the western hemisphere it is reported from Canada, Mexico, Colombia, Argentina, and Brazil, and in the USA from Florida, Colorado, Georgia, Minnesota, and New York. *Cactodera cacti* occurs in Europe in the Netherlands, England, France, Germany, Sweden, Switzerland, Austria, Belgium, Yugoslavia, Hungary, Czechoslovakia, and Italy. It is present in other Mediterranean regions of Malta, Algeria, and Israel and extends to the USSR, India, Japan, Korea, and Vietnam (Johnson, 1968; Mulvey and Golden, 1983; Krall and Krall, 1978).

**Biology.** Although the life history of *C. cacti* is generally similar to that of other cyst nematodes, it has not been investigated in detail. Under greenhouse conditions a generation takes 29–34 days (Shmal'ko, 1959), and in monoxenic cultures at 22°C a generation takes about 30 days (Cordero, 1989). In the Sonoran deserts of Mexico, it is not known if the nematode persists during unfavorable periods of cold or draught as a cyst, although Krall and Krall (1978) speculate that only one generation a year may occur under field conditions. Conversely, roots of long-lived succulents may provide adequate protection to sustain the nematodes throughout the year and the cyst may function primarily for dispersal among widely spaced hosts. Eggs are not deposited in a gelatinous matrix as for many other Heteroderinae; they are fully retained in the female body until death (Cordero, 1989).

The cactus cyst nematode occurs on cacti grown for food as well as on ornamentals (Fig. 23C). Shmal'ko (1959) reports that a number of species of infected ornamental cacti were stunted, had reduced turgor, and were subject to decay by secondary invaders. Langdon and Esser (1969) note that infected commercial plantings of *Schlumbergera* Lem (= *Zygocactus*) were wilted with an abnormal reddish color. In Mexico, cacti (*Opuntia* sp.) are extensively cultivated in large land holdings in several states for food, including fruit and cladodes (Fig. 23C). We recently detected *C. cacti* in commercial plantings in the states



of Zacatecas and Durango where cactus is one of the most important crops. Although pathogenicity of the nematode on agricultural *Opuntia* has not been established, it is likely that the nematode contributes to secondary root-rotting fungi and bacteria common in cacti. Similarly, pathogenicity and interactions are likely in commercial plantations of *Amaranth*, a high-protein seed crop of increasing agricultural importance, which is infected with *Cactodera amaranthi*, a species closely related to *C. cacti* and widespread throughout Mexico. In most of the world *C. cacti* is limited to ornamental plants and economic losses may relate to quarantine regulations and markets which reject plants infected with cyst nematodes.

**Control.** Quarantine regulations against cyst nematodes in general may be effective in containing *C. cacti*. Sanitation is undoubtedly important in control of cactus cyst nematodes, with care not to transport infected plants and soil. Since infection is limited to roots and the collar of the host, clean plants can generally be propagated from seed or vegetative parts in sterilized soil or other clean planting material. Where available, systemic nematicides may provide adequate control in ornamentals, and many fumigant nematicides are likely to be effective for controlling soil stages. Granular nematicides have been used with little success (Schneider, 1961; Shmal'ko, 1959).

### *Punctodera*

*Punctodera* Mulvey and Stone (1976)

syn. *Heterodera* Skarbilovich, 1947

**Diagnosis:** Heteroderinae Filipjev and Schuurmans Stekhoven

**Females.** Cyst present. Spheroidal, ovoid, or pear-shaped, without posterior cone. Cuticle surface with reticulate pattern, pronounced subsurface pattern of parallel rows of punctations. Punctations most pronounced on cyst. D layer present. Vulva terminal. In cyst, circumfenestrae develops around vulval region, separate fenestrae around anal region. Underbridge and perineal tubercles absent. Bullae present or absent. Eggs retained in body (no egg mass); egg surface smooth.

**Males.** Body twisted. Lateral field with four lines. Spicules >30  $\mu$ m, distally with single point.

**Second-stage juveniles.** Stylet 30  $\mu$ m. Lateral field with four lines. Esophageal glands filling body cavity. Tail conical with long hyaline terminal portion. Phasmid openings porelike. En face pattern with adjacent submedial lips fused with each other and partially with labial disc.

**Nurse cell.** Syncytium.

**Species.** (Table 7)

**Identification.** Cyst nematodes which are now considered *Punctodera* have been recognized for 60 years, primarily on the basis of a cyst without a cone but with both a vulval circumfenestra and an anal fenestra (Figs. 12D, 23B). Subsurface punctations, while

TABLE 7 Species of *Punctodera*

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| <i>P. punctata</i> (Thorne, 1928) Mulvey and Stone, 1976 |
| syn. <i>Heterodera punctata</i> Thorne, 1928             |
| <i>P. chaltoensis</i> Stone, Sosa Moss and Mulvey, 1976  |
| <i>P. matadorensis</i> Mulvey and Stone, 1976            |



indicated by the genus name, also occur in other heteroderines, although their intensity and occurrence in parallel rows is striking in *Punctodera* (Fig. 10G). *Punctodera punctata* is distributed worldwide on turf, wheat, and weed grasses and *P. matadorensis* is apparently limited to weed grasses at the type locality in Canada. Only with discovery of a third species, *Punctodera chalcoensis* in Mexico, has the economic menace of the genus and the importance of accurate species identification been understood. *Punctodera chalcoensis* and *P. matadorensis* can be separated from *P. punctata* by the spherical to subspherical shape of the females and cysts in the former vs. more elongate, pear-shaped females and cysts in the latter. Cysts of *P. chalcoensis* differ from those of *P. matadorensis* by small, scattered bullae or no bullae vs. massive and consistently present bullae in *P. matadorensis*. *Punctodera chalcoensis* also differs slightly by the shape of the stylet knobs of the second-stage juveniles, which are flat to slightly concave anteriorly in *P. chalcoensis* vs. strongly concave and anchor-shaped in *P. matadorensis*, and rounded in *P. punctata*. The esophagus of second-stage juveniles of *P. chalcoensis* and *P. punctata* occupies about 30% of the body length whereas in *P. matadorensis* it includes about 50% of the body length. Original diagnoses suggested that juveniles of *P. matadorensis* are larger than those of *P. punctata* but reexamination of types and additional populations indicate that these measurements are not reliable and that the size of juveniles overlaps the two species (Franklin, 1938; Horne, 1966; Mundo-Ocampo and Baldwin, unpublished; Wouts, 1985). Since *P. chalcoensis* is the only species known to reproduce on *Zea mays*, a bioassay may be useful in identification.

*Punctodera chalcoensis* Stone, Sosa-Moss, and Mulvey, 1976 (the Mexican corn cyst nematode)

**Synonyms and history.** The Mexican corn cyst nematode was first observed by Vazquez (1976) in corn (*Zea mays* L.) fields in Huamantla, Tlaxcala, Mexico in the late 1950s, and was considered *H. punctata* (= *P. punctata*; Becerra and Sosa Moss, 1978). In the early 1960s a cyst nematode was observed attacking corn in the Valley of Mexico at Chalco and subsequently in the states of Puebla and Tlaxcala which was also identified as *H. punctata* (Sosa-Moss and Gonzalez, 1973; Vazquez, 1976). Sosa-Moss (1965) believed that the Chalco population of the Mexican corn cyst nematode, unlike *H. punctata*, was limited to corn as a host. In 1976, a new genus, *Punctodera*, was proposed to accommodate *P. punctata* and a new species from Canada, *P. matadorensis* (Mulvey and Stone, 1976). Meanwhile, morphological differences were noted when comparing the Mexican corn cyst nematode with *H. punctata* populations from other countries (Sosa-Moss, 1965; Villanueva, 1974) and with *P. matadorensis* (Stone et al., 1976). These observations led to description of the Mexican corn cyst nematode as a distinct species, *P. chalcoensis*, with the type locality in Chalco, Mexico and *Zea mays* as the type host (Stone et al., 1976).

**Hosts.** Although *P. chalcoensis* has been tested on a variety of potential hosts including many Poaceae (Gramineae), reproduction only occurs on cultivated maize (*Zea mays* L.) and a wild type of maize, "teozinte" (*Zea mexicana* [Schrö.] Kuntz); Stone et al., 1976). Tests of five nematode populations on 13 corn hybrids (commonly grown in the USA), eight cultivars (from Mexico), six breeding lines (from CIMMYT in Mexico) did not indicate any resistant *Zea* (unpublished). Although there are informal reports of *P. chalcoensis* on weed hosts including *Bidens*, *Tithonia*, and *Wedelia*, our tests (unpublished) failed to demonstrate nematode reproduction.

**Distribution.** *Punctodera chalcoensis* is only reported from Mexico, where it is believed to be indigenous based on its narrow host range on *Zea*, a genus which is historically Mexican (Stone et al., 1976). Earlier reports of wide distribution in Mexico

Differentiation  
of the 3 spp.  
Morphological



often have not been recognized because identifications confused *P. chalcoensis* with *P. punctata*. However, recent surveys indicate broad distribution at elevations between 1500 and 2800 m throughout major corn-growing areas of Central Mexico from the Pacific Ocean to the Gulf of Mexico. These states include Mexico, Tlaxcala, Puebla, Veracruz, Michoacan, and Jalisco (Mundo et al., 1987; Santacruz, 1982; Vazquez, 1976). The temperate conditions which favor development of this nematode and its pathogenicity on corn, an important crop worldwide, may indicate potential for this nematode to become a widespread economic threat.

**Biology.** Becerra and Sosa Moss (1978) and Munoz (1983) concluded that the life cycle of *P. chalcoensis* spans the growing season of corn, so that only one generation occurs per year and that the cysts must remain in the soil during winter to initiate the next cycle. However, Jeronimo (1988) carried out a particularly thorough study and reported a typical heteroderine life cycle of about 30 days. Apparently fresh eggs may hatch readily, but once diapause is established within cysts, only a low percentage of hatch occurs each season. Villanueva (1974) reported that root exudates of most plants induce egg hatching of the Mexican populations, but that exudates from corn roots resulted in a significantly greater degree of hatching.

The environmental requirements of *P. chalcoensis* are unknown although the distribution at high elevations in Mexico, and its absence in corn fields in warmer subtropical regions suggests that it does not tolerate continuous warm, humid conditions.

*Punctodera chalcoensis* is highly damaging on corn in Mexico, causing severe yellowing, stunting, and even death of young seedlings (Fig. 23D). Sosa-Moss and Gonzalez (1973) observed that plants without supplementary fertilization showed more damage and less tolerance to the nematode. However, low inoculum levels (10 cysts/kg soil) induced a physiological effect that increased tolerance to further nematode attack. Greenhouse tests conducted by Hernandez (1965) suggest that improved varieties of corn were more tolerant to different levels of inoculum of the corn cyst nematode than local varieties.

**Control.** Too little is known of the biology of *P. chalcoensis* to develop precise control procedures. Whereas some corn cultivars may be tolerant of the cyst nematode, none are known to be resistant or to reduce population levels. Many farmers in Mexico recognize that continuous planting to corn results in reduced productivity and fallow 1 out of 3 years is a common practice which might reduce cyst populations. Although subsistence farmers have few acceptable crops for rotation with corn, large farms may be able to reduce populations by rotation with other grains such as wheat or barley. The persistence of the Mexican corn cyst nematode in the absence of a suitable host is not known. In some cases chemical control may be feasible and good control has been achieved with Furadan and Nematicure (Jeronimo, 1988). Becerra and Sosa Moss (1978) noted that early sowing prior to cool rains may allow the seedlings to get a foothold in advance of nematode hatch and thus result in less damage. Damage is minimized by good cultural practices including adequate fertilization and water.

Since *P. chalcoensis* is not likely to be dispersed with seed or harvested corn, containment is more feasible than for cyst nematodes of root crops and root propagules. Nevertheless, sanitation with respect to farm vehicles, water, and transport of contaminated soil is an important aspect of containment.



### Genera of Lesser Economic Importance

*Heterodera*, *Cactodera*, *Globodera*, and *Punctodera* are the most widely recognized Heteroderinae, with more than 70% of the known species of the subfamily. These four genera are cyst forming and include nearly all species of economic importance. With the exception of *Afenestrata* and *Dolichodera*, the remaining 13 genera of the subfamily do not form cysts. (Table 1). The importance of these 13 genera, while not directly apparent as *Heterodera* or *Globodera*, cannot be overlooked. Some lesser known, non-cyst-forming genera, including species of *Meloidodera* and *Thecavermiculatus*, have potential to attack agricultural crops. The history of agriculture suggests that indigenous nematodes may adapt from weed hosts to become important agricultural pests as new crops are introduced and agriculture extends to previously uncultivated areas. Furthermore, nematodes of restricted distribution and little economic importance may become a threat when introduced to new habitats. Some heteroderine genera restricted to natural ecosystems may have a significant impact on habitats such as forests, e.g., species of *Rhizonema*, *Sarisodera*, *Hylonema*, *Cryphodera*, and *Meloidodera* attack trees. In light of the physiological effects of more thoroughly studied heteroderines, it is plausible that these less familiar parasites of trees increase vulnerability of their hosts to stresses such as pollution, drought, and other pathogens.

Knowledge of all genera of Heteroderinae is essential to understanding evolution of the subfamily as a basis for stable, predictive taxonomy. Lesser known genera from natural habitats are particularly important to such investigations, in part because their biogeography, being little affected by man, often can be attributed to plate tectonics, which is useful for testing hypotheses of phylogeny (Ferris, 1979). Evaluation of processes such as diapause, cyst formation, and induction of nurse cells by heteroderines may contribute to understanding basic biological phenomena. However, these processes can best be understood in the context of evolution and variation within the subfamily as a whole. For example, insight into cyst formation may be gained through considering a transformation series including heteroderines that do not form cysts, as well as intermediates. Similarly, the process of induction of nurse cells may best be understood by considering not only syncytia of *Heterodera* and *Globodera*, but ancestral genera which do not induce syncytia, as well as genera which induce diminutive syncytia. Lesser known heteroderines are considered in four groups of genera to facilitate comparison. The groups do not fully represent taxonomic categories, but are largely based on the phylogenetic analysis of Baldwin and Schouest (1990): (a) cyst-forming genera include *Afenestrata* and *Dolichodera*; (b) ataloderines are *Atalodera*, *Thecavermiculatus*, and *Camelodera*; (c) sarisoderines are *Sarisodera*, *Rhizonema*, *Bellodera*, *Hylonema*, and *Ekphymatodera*;<sup>\*</sup> (d) ancestral species include *Verutus*, *Meloidodera*, and *Cryphodera*.

#### Cyst-forming

*Afenestrata* Baldwin and Bell, 1985

syn. *Afrodera* Wouts, 1985

*Dolichodera* Mulvey and Ebsary, 1980

*Afenestrata africana* and *D. fulvialis* are the only species of these cyst-forming genera; neither is reported outside their localities, respectively, in Ivory Coast and Quebec, Canada, and both are probably parasites of grasses. *Afenestrata* is similar to *Heterodera*, the cyst having a pronounced cone and zig-zag cuticular pattern, but it is distinguished from other cyst nematodes in that it lacks fenestration (Fig. 24C, D). *Dolichodera* is similar to *Globodera*, the cyst lacking a cone and having circumfenestrae (Fig. 24A, B). Unlike

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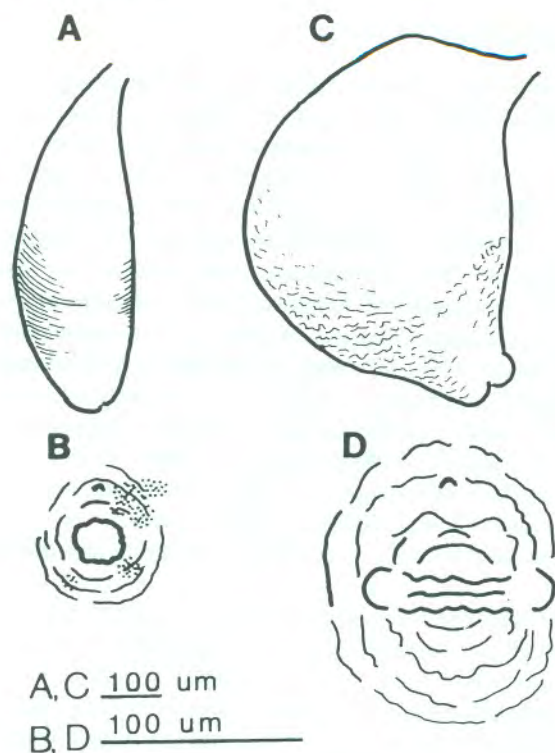


FIGURE 24 Characteristics for identification of *Dolichodera* and *Afenestrata*. (A) *Dolichodera fluvialis* cyst. (B) *D. fluvialis* cyst, terminal region showing circumfenestrae. (C) *Afenestrata africana* cyst. (D) *A. africana*, terminal region lacks fenestrae. (A and B redrawn after Mulvey and Ebsary, 1980.)

*Globodera*, the female body wall cuticle of *Dolichodera* is thin with fine striations. *Dolichodera* is unusual among heteroderines in that it was recovered from bottom sediment of a river; it is likely that the cysts were washed from plants on the shore. Luc et al. (1988) review the history and synonyms of *Afenestrata* and *Dolichodera* and include a complete diagnosis.

#### Ataloderines

*Atalodera* Wouts and Sher, 1971

syn. *Sherodera* Wouts, 1974

*Thecavermiculatus* Robbins, 1978

*Camelodera* Krall, Sagalina, and Ivanova, 1988

Non-cyst-forming *Atalodera* and *Thecavermiculatus* are similar in that they both have second-stage juveniles with very narrow esophageal glands (Fig. 25A, B), unlike other heteroderines. Contrary to most other non-cyst-forming heteroderines, the nurse cell induced by *Atalodera* and *Thecavermiculatus* is a syncytium. The syncytium is unlike that of most cyst-forming heteroderines, however, because it lacks wall ingrowths (Mundo and Baldwin, 1983). Females of *Atalodera* have a pronounced posterior cone whereas those of *Thecavermiculatus* have a greatly reduced cone (Fig. 25D, E; 26A). *Atalodera* includes four



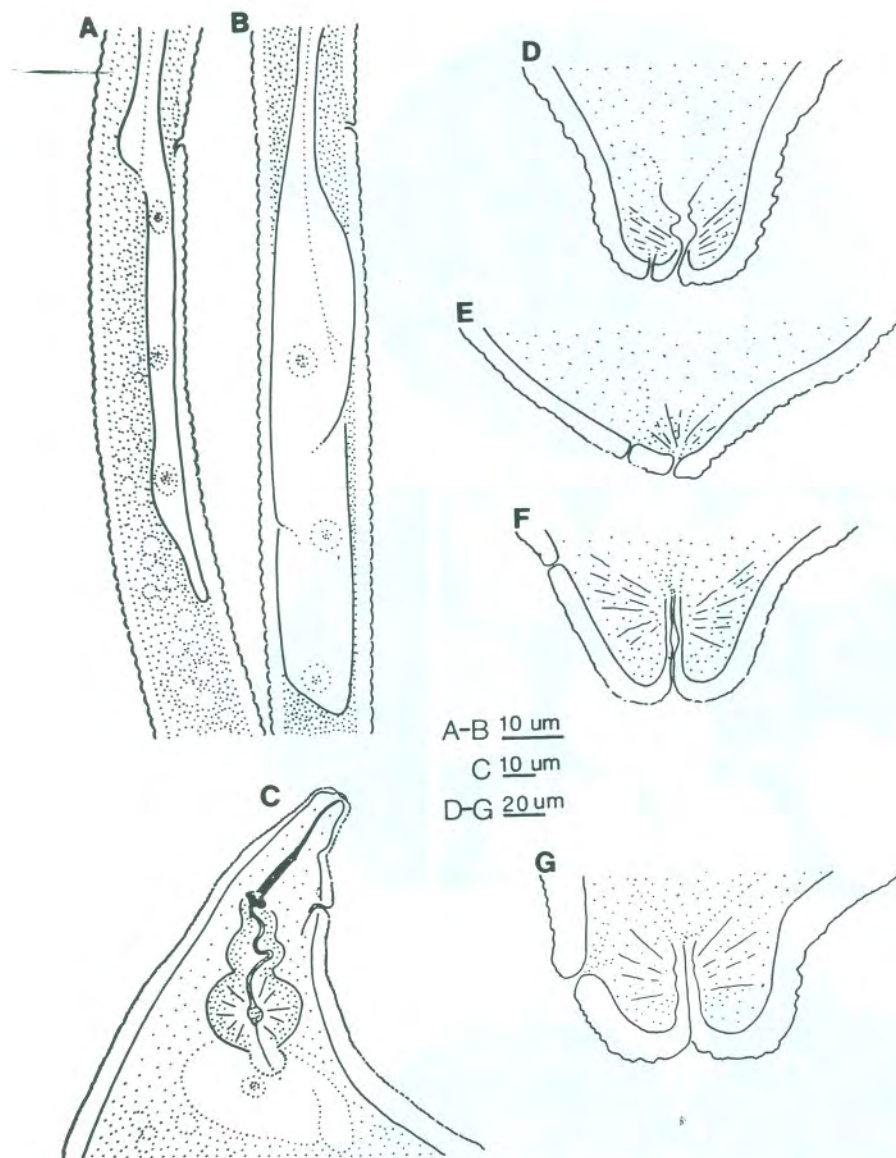


FIGURE 25 Characteristics for identification of ataloderines and sarisoderines. (A) Narrow esophageal gland region of second-stage juveniles (J2) typical of ataloderines. (B) Broad esophageal gland region of J2, typical of sarisoderines. (C) Head region of female of *Bellodera utahensis* showing anterior position of excretory pore, typical of this genus. (Redrawn after Baldwin et al., 1983.) (D) *Atalodera ucrici*, lateral view of terminal region of the female. (E) *Thecavermiculatus gracililancea*, lateral view of terminal region of female. (F) *Camellodera eremophila*, lateral view of terminal region of female. (Redrawn from Krall et al., 1988.) (G) *B. utahensis*, lateral view of terminal region of female.



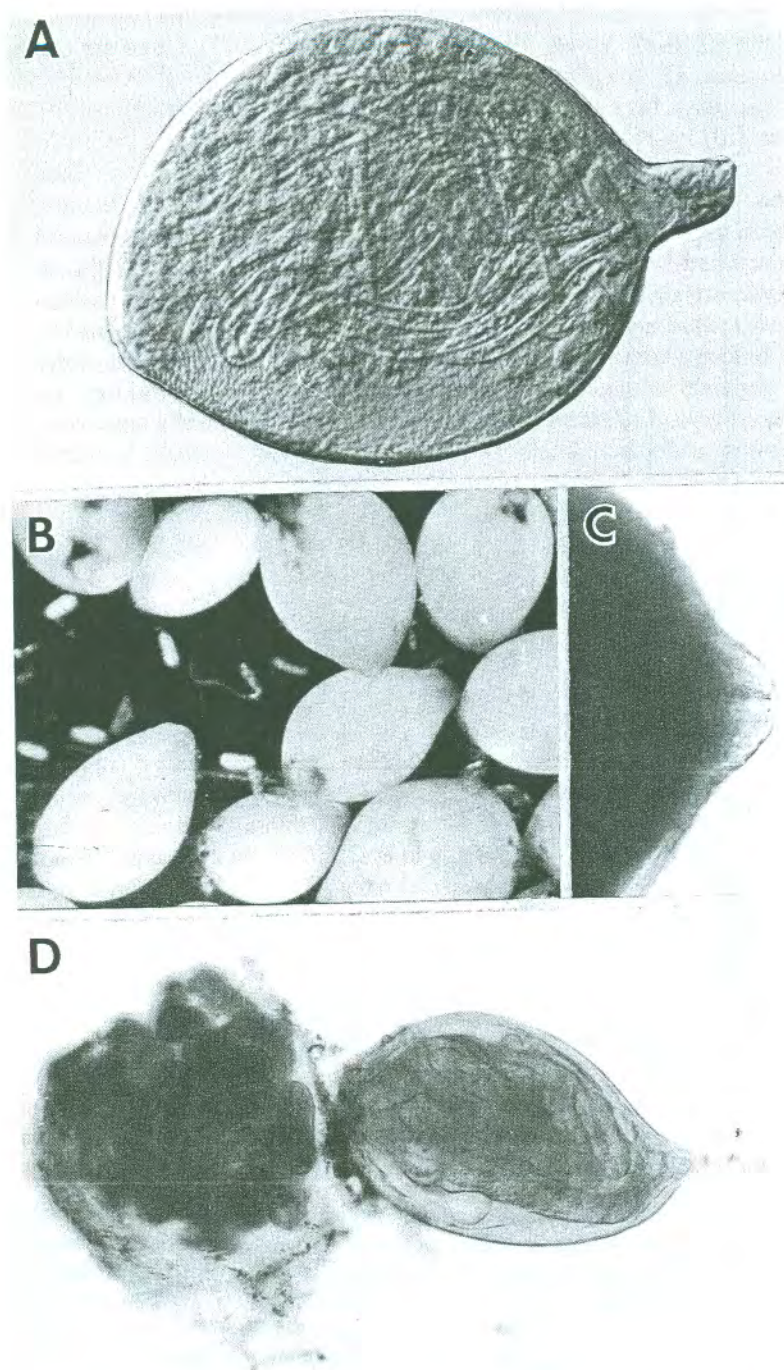


FIGURE 26 Females of ataloderines and sarisoderines. (A) *Thecavermiculatus gracililancea*, female full of second-stage juveniles. (B) *Sarisodera hydrophila* females. (C) *S. hydrophila* female, terminal cone region. (D) *Ekphymatodera thomasoni* with egg mass.

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species, all described from California, and most species are only known from one or a few localities (Baldwin et al., 1989; Wouts, 1973c; Wouts and Sher, 1971). Hosts are native plants including grasses, sage (*Haplopappus*), and honeysuckle (*Lonicera*). Four species of *Thecavermiculatus* have been described. These occur in California (Robbins, 1978, 1986), Alaska (Bernard, 1981), and Peru (Golden et al., 1983). The species are all from grasses with the exception of *T. andinus* from Peru, which is described from *Oxalis*. However, the taxonomic position of *T. andinus* is controversial (Wouts, 1985; Luc et al., 1988) and may prove to be a separate genus, with many characteristics ancestral to other ataloderines (Baldwin and Schouest, 1990). *Camelodera* was recently described from a woody shrub in the deserts of Turkmenian, USSR and closely resembles *T. andinus* by the relatively narrow esophagus in second-stage juveniles, the broad vulval-anal distance (Fig. 25F), and obscure surface pattern of females. A population of *Thecavermiculatus*, which is an undescribed new species, was recovered from cultivated potato in Alaska and may prove to be agriculturally important (Bernard, pers. commun.). Luc et al. (1988) reviewed the history and synonyms of *Atalodera* and *Thecavermiculatus* and included a complete diagnosis.

#### Sarisoderines

*Sarisodera* Wouts and Sher, 1971

*Rhizonema* Cid Del Prado Vera, Lownsbey, and Maggenti, 1983

*Bellodera* Wouts, 1985

*Hylonema* Luc, Taylor, and Cadet, 1978

*Ekphymatodera* Baldwin, Bernard, and Mundo, 1988

Sarisoderines are a diverse group of non-cyst-forming heteroderines which are distinct from other heteroderines by the lip patterns of juveniles and males as viewed with the scanning electron microscope; in each case the submedial lips are very thin in relation to the labial disc (Fig. 13I) (Othman and Baldwin, 1986; Baldwin et al., 1989; Baldwin and Schouest, 1990). Each genus is monospecific and all the species have a terminal cone (Fig. 26B, C). All the genera, except *Hylonema* described from Ivory Coast, are known only in the western USA. Contrary to ataloderines, all (with the possible exception of *Ekphymatodera*) induce a single uninucleate giant cell. *Sarisodera*, *Rhizonema*, and *Hylonema* are all parasites of trees, *Bellodera* occurs on a woody shrub, whereas *Ekphymatodera* is a parasite of rushes (Fig. 26D). An undescribed sarisoderine genus which is a parasite of trees in Brazil (Hirschmann, pers. commun.) suggests that these nematodes are more widely distributed than was previously indicated. *Sarisodera* is distinctive by the zig-zag cuticle pattern and very close vulval-anal distance, with the anus located on the inner lip of the vulva. *Rhizonema* and *Bellodera* both have annulated cuticles in the females, but the vulval-anal distance in the former is 15–33  $\mu\text{m}$ , whereas in *Bellodera* it is 53–88  $\mu\text{m}$ . Unlike other Heteroderinae in which the excretory pore is near the level of the esophageal glands, in *Bellodera* the opening is near the level of the stylet knobs (Fig. 25C). Unlike other sarisoderines, *Hylonema* and *Ekphymatodera* both have lip patterns in males and juveniles, in which the submedial lips are fused with the labial disc (Othman and Baldwin, 1986; Baldwin et al., 1989). Also the hyaline portion of the tail of second-stage juveniles is unusually long in both genera. The body wall pattern of females of *Ekphymatodera* is full of uneven protuberances (Fig. 10E), whereas the cuticle of *Hylonema* is relatively smooth or faintly striated. Luc et al. (1988) reviewed the history and synonyms of sarisoderines and included a complete diagnosis of each except *Ekphymatodera* (Baldwin et al., 1989).



## Ancestral heteroderines

*Cryphodera* Colbran, 1966syn. *Zelandodera* Wouts, 1973*Verutus* Esser, 1981*Meloidodera* Chitwood, Hannon, and Esser, 1956

Although *Cryphodera*, *Verutus*, and *Meloidodera* apparently do not form a cohesive taxonomic group (Baldwin and Schouest, 1989), they nevertheless are considered together because they share a number of ancestral similarities. All have striated cuticles and lack a distinct posterior protuberance. *Verutus* and *Meloidodera* have a subequatorial vulva and terminal anus (Figs. 6; 14A); in *Cryphodera* the vulva and anus are also widely separated. The four species of *Cryphodera* are all from trees in Australia and New Zealand. The uniquely large vulval lips and elongate-reniform shape of females of *Verutus* readily distinguish it from *Meloidodera* with smaller vulval lips and more ovoid females. Two species of *Verutus* occur in the USA, one in Japan, and a fourth undescribed species is present in West Germany; apparently the genus favors marshy habitats and grass or herbaceous hosts (Baldwin et al., 1989). *Meloidodera*, a diverse genus with six species, is widely distributed in the USSR as well as the United States, including Alaska. Most are parasites of woody plants including forest trees. However, *M. eurytyla* from Alaska parasitizes dunegrass, and *M. charis*, while often found on woody desert hosts such as *Mesquite*, also parasitizes a number of herbaceous plants including corn (*Zea mays*), sorghum, okra (*Abelmoschus esculentus*), and turf grass (Heald and Golden, 1969; Heald, 1984). *Meloidodera charis* is apparently widely distributed on field corn in Nebraska, where in recent years it appears to be pathogenic (Minton and Golden, 1971; Dappen and Powers, pers. commun.). Luc et al. (1988) reviewed the history and synonyms of *Cryphodera*, *Verutus*, and *Meloidodera* and included a complete diagnosis of each.

## KEY TO GENERA OF HETERODERINAE

|  |                    |
|--|--------------------|
| 1. Vulval subequatorial  | 2                  |
| Vulva terminal   | 3                  |
| 2. Female reniform   | <i>Verutus</i>     |
| Female not reniform  | <i>Meloidodera</i> |
| 3. Cyst absent; eggs not retained in<br>body of dead female                | 4                  |
| Cyst present; at least some eggs retained in<br>tanned body of dead female | 13                 |
| 4. Vulval anal distance 15–35 $\mu$ m                                      | 5                  |
| Vulval anal distance greater than 35 $\mu$ m                               | 10                 |
| 5. Esophageal gland lobe of J2 nearly fills<br>diameter of body cavity     | 6                  |
| Esophageal gland lobe of J2 narrow;<br>about one-third body diameter       | 7                  |
| 6. Female with rounded terminus  | <i>Hylonema</i>    |
| Female with distinct cone  | 8                  |



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| 7. Little or no terminal cone  | <i>Thecav-</i><br><i>miculatus</i>                     |
| Distinct terminal cone   | <i>Atalodera</i>                                       |
| 8. Cuticle pattern of female striated at midbody   | <i>Rhizonema</i>                                       |
| Cuticle pattern of female not striated at midbody  | 9  |
| 9. Cuticle pattern of female zig-zag   | <i>Sarisodera</i>                                      |
| Cuticle pattern of female not zig-zag but with<br>rough surface and longitudinal furrows | <i>Ekphy-</i><br><i>matodera</i>                       |
| 10. Female cuticle with prominent striae at midbody                                      | 11   |
| Female cuticle without prominent striae at midbody                                       | 12   |
| 11. Mature female lemon-shaped;<br>prominent vulval cone                                 | <i>Bellodera</i>                                       |
| Mature female nearly spherical<br>little or no vulval cone                               | <i>Cryphodera</i>                                      |
| 12. Mature female nearly spherical,<br>little or no terminal prominence                  | <i>Thecaver-</i><br><i>miculatus</i><br><i>andinus</i> |
| Mature female with distinct terminal prominence  | <i>Camelodera</i>                                      |
| 13. Cyst lacking fenestration of vulval region   | <i>Afenestrata</i>                                     |
| Cyst with fenestration of vulval region  | 14   |
| 14. Cyst with fenestration of anal region  | <i>Punctodera</i>                                      |
| Cyst lacking fenestration of anal region   | 15   |
| 15. Cyst with two semifenestrae in vulval region   | <i>Heterodera</i>                                      |
| Cyst with one fenestrae (circumfenestrae)<br>in vulval region                            | 16   |
| 16. Terminal cone of female prominent to<br>slightly reduced                             | <i>Cactodera</i>                                       |
| Terminal cone of female absent, rounded terminus   | 17   |
| 17. Cuticle of female zig-zag  | <i>Globodera</i>                                       |
| Cuticle of female striated   | <i>Dolichodera</i>                                     |

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Hetero

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Vovla

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Willia

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