Nematode Structure and Life

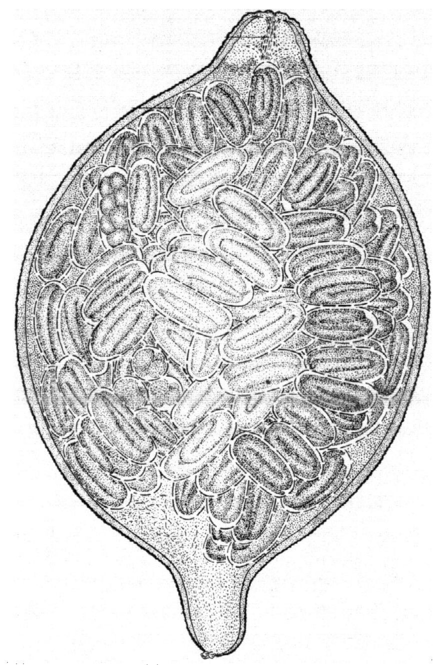
wide range of life habits requires combination of characters for identification of parasites classified among nematodes

A. R. Maggenti and M. W. Allen

The many thousands of species of nematodes in the phylum Nemata are a group of animals commonly placed into four categories: parasites of man and animals; parasites of plants; species living in marine and brackish water; and free-living soil and fresh-water species. No single character or criterion can be used to distinguish nematodes from other similar animals, although one feature—not structural—sets nematodes apart, and that is the tremendous variation in size. Nematodes vary in length from the 1/125″ ectoparasites of plants to the 25′ long parasite of whales.

Nematodes are generally elongate cylindrical and taper at both ends. Deviations in shape occur mainly in the animal and plant parasitic forms. In some forms the adult females may be obese, saccate, spherical or kidney-shaped. In addition to differences in size and shape, all nematodes have certain features in common regardless of whether marine, soil or fresh-water, animal or plant parasites. The alimentary canal begins with the oral opening which is anterior, terminal and usually surrounded by lips which bear the cephalic sensory structures: papillae, setae, amphids, and so forth. Following the oral opening is the buccal cavity or stoma which may or may not be armed by teeth, jaws or a stylet—spear. The esophagus, sometimes called the pharynx, is formed of one, two or three distinct parts in which a variety of valves and glands may be located. Anteriorly the tubular intestine is separated from the esophagus by the esophago-intestinal valve; posteriorly the intestine joins the rectum which ends in a terminal or subterminal anus in the female and a cloaca in the male. Externally nematodes are covered by a resistant cuticle which may or may not exhibit surface modifications. Internally nematodes are not segmented and the somatic musculature is limited to longitudinal fibers. As a result of this almost unique musculature nematodes move mainly in a dorso-ventral plane.

Sugar-beet nematode cyst containing eggs.



The excretory system in its simplest form can be described as consisting of collecting tubules located in or near the lateral hypodermal chords. The collecting tubules connect anteriorly with a renette cell which excretes its contents to the enviroment by way of an excretory duct. The system undergoes many variations. In some groups of nematodes there lated animals. The female genital opening is separate from the posterior opening—rectum and anus—of the alimentary canal but in the male the reproductive system and the alimentary canal join posteriorly to form a cloaca. Although is no evidence of the presence of an excretory system, in other groups there is only a single collecting tubule and in still others only the renette cell and excretory duct remain.

There are also features of the reproductive system of nematodes that can be utilized to separate them from other re-

Continued on next page

---

pests at least once in every 12-month period. Growers and sellers of nursery stock are required to maintain effective control over all plant pests. When a pest is found that is of limited distribution or is not known to be established in California the pest must be eradicated in a way satisfactory to the authorities.

To comply with the regulations, an infestation of a nematode—of known economic importance—must be determined to be under effective control, but there are no known practical and reliable methods of measuring nematode populations which may be present in nursery stock but not showing evidences of infection. Furthermore, there are no methods available to significantly reduce or to eliminate a nematode infestation in most nursery stock other than by destroying the stock itself.

In California, efforts are being directed toward resolving some of the problems presented by the growth and sale of nursery stock. If an effective pre-planting treatment of nursery growing grounds followed by protection of the plantings against further infection during growth can be accomplished, certification of California-grown nursery stock at origin should be possible.

To obtain a more accurate and complete picture of nematode distribution in California, records of the University and of the California Department of Agriculture are being compiled and coordinated. When complete the distribution patterns demonstrated should provide a firm basis for practical quarantine regulations affecting both California growers and importers of agricultural products.

A program of collection and collation of additional knowledge of nematodes established, and of those entering and moving within the state, is being attempted. In the program, a portion of the necessary laboratory work has been delegated to personnel of the County Agricultural Commissioners' offices. The California Department of Agriculture has prepared instructions for use by the counties in certain standardized methods to extract nematodes from plant tissue and from soil. Specimens of the nematodes are preserved and sent to Sacramento for identification.

The county laboratory program has shown promise of adding materially to the knowledge necessary for practical quarantine actions.

W. H. Hart is Extension Specialist in Plant Nematology, University of California, Davis.

STRUCTURE

Continued from preceding page

the reproductive system is basically similar in all nematodes the mode of reproduction varies from group to group. All reproduce sexually, the majority being bisexual—reproduction by fertilization from male—but some are parthenogenetic—reproduction without male fertilization—and others are hermaphroditic—female gonads produce sperm as well as ova.

The central nervous system is comprised of the circumesophageal nerve ring, its associated ganglia, and longitudinal nerves. The main longitudinal nerve runs the length of the body and is located in the ventral hypodermal cord. This ventral nerve cord is intermittently interrupted by ganglia which serve to innervate various structures throughout the body and the somatic muscles. There are also nerves running anteriorly from the nerve ring; these serve to innervate the various cephalic sensory structures and the esophagus.

Nematodes are also distinguished from other animals not only by the features that they possess, but also by those they lack. Nematodes have neither a definitive respiratory nor circulatory system. Morphologically—structurally—they are designated as pseudo-coelomate, that is, the organs and structures of the internal body are not bounded from the general body cavity by a continuous mesodermal membrane. Rather the internal organs and structures are bathed by the body fluid, which functions both as a respiratory and circulatory medium.

The life cycle of nematodes can be divided into six stages: an egg, four larval forms and the adult. Each larval stage is terminated by a molting of the cuticle, much the same as occurs in insects. The first larval molt may occur while the nematode is still within the egg. Larvae, except for a few animal and plant parasitic forms, superficially resemble the adult, lacking only the matured gonads. The time spent in any one stage or the time for complete development varies according to temperature, moisture, host and the individual species involved. Likewise, the stage best adapted to survive unfavorable conditions varies with the conditions prevailing, and with the species involved. *Ditylenchus* spp. survive best as fourth stage larvae, *Anguina* spp. as second stage larvae, and *Heterodera* spp. as eggs within cysts.

Plant parasitic nematodes classified according to their mode of parasitism can be assigned to two major groups: parasites of the aboveground plant parts and parasites of the belowground plant parts. Each group can be further subdivided into ecto- or endoparasites. An ectoparasitic nematode in either classification lies outside its host and feeds by inserting its stylet into the desired plant tissue. Its entire life cycle is spent outside the host and never does the entire body penetrate into the plant tissues. An endoparasitic nematode spends all or part of its life cycle within the plant tissue, either completely or partially embedded. Parasites in this group are either sessile or vagrant.

Ectoparasitic nematodes of aboveground parts of plants are seldom found on open leaves or stems, unless there is free moisture on the plant or the atmospheric humidity is very high. Normally parasites of this group are found in unopened leaf and flower buds where humidity remains relatively constant and high. The symptoms associated with ectoparasitic nematodes are the deformation or stunting of new plant tissue. Parasites of this type are seldom found in the soil. However, this can occur when infested parts come into contact with the soil. Because of this, detection is normally accomplished by dissection of the immature leaf and flower buds.

Some of the ectoparasitic nematodes can on occasion be endoparasitic. *Aphelenchoides ritzema-bosi* on blackberries is ectoparasitic in the buds, but endoparasitic in the leaves of the same host. This same nematode also shows differential mode of parasitism according to the host species: on strawberries it is ectoparasitic and on chrysanthemum it is endoparasitic.

Progressing from the transitional mode of ecto-endoparasitism are nematodes which are wholly endoparasitic and usually limited to aboveground plant parts. The symptoms associated with endoparasitism resemble the deformation and stunting of the ectoparasites. In addition, there is often galling and stunting of the entire plant and, in monocotyledonous plants, subsequent rotting and decay. Stem and bulb nematode exemplifies both types of damage: in alfalfa it causes swollen galled tissue which is associated with the shortening of internodes, resulting in a galled stunted plant. When the stem and bulb nematode attacks a monocotyledon such as onion or garlic the swellings are usually at the base of the leaves and later associated with a rotting or bloating of the plant tissue.

The first reported plant parasitic nematode, wheat nematode—*Anguina tritici*—belongs to the endoparasite group. The most important economic damage of the wheat nematode is the formation of galls in the floral parts. In addition to the galled kernels there is a stunting of the plant and a twisting and rolling of the leaf blades.

The second major grouping of plant parasitic nematodes of belowground plant parts is also subject to further subdivision into ecto- and endoparasites. The endoparasites can be subdivided into vagrant, sessile, non-gall forming, gall forming, and cyst forming endoparasites.

Plant parasitic nematodes discovered since the end of the 19th century have—for the major part—been ectoparasitic on roots. These parasites were not easily detected because they are rarely found attached to and feeding on the roots. The entire life cycle of ectoparasitic nematodes is spent in the soil. Therefore, all stages of development can be found in soil samples. Eggs are normally laid randomly in the soil. Even though the type of damage induced by these forms is characteristic of nematodes—stunting of roots, hypertrophy, hyperplasia and stunted, nutritionally deficient plants with impaired roots—the cause of such damage is still often attributed to other factors.

Probably the most important factor contributing to the discovery of damage by ectoparasitic nematodes was the discovery of the nematocidal activity of D-D — 1,3-dichloropropene-1,2-dichloropropane mixture—and ethylene dibromide. Because of the low cost and the relative ease of application large areas of soil were fumigated.

Many areas where plants showed symptoms of reduced yield and vigor—but where known plant parasites were not found—showed remarkable reaction to fumigation. In many instances the stimulus was attributed to some indirect action of the fumigant and was commonly called increased-growth-response. However, closer observation in most cases revealed ectoparasitic nematodes were being controlled by fumigation, which was the fundamental cause of the plants' response.

The vagrant endoparasites represent what is probably the most primitive form of endoparasitism among nematodes. The life cycle is rather direct and uncomplicated. Females, males and larvae penetrate completely into the host tissue. Eggs are laid randomly as the female wanders within the root tissue from feeding site to feeding site. Larvae hatching from eggs may either leave the root seeking new feeding sites or they may spend their entire life within the host. The ability to leave the root is not limited to larvae; adults may also spend some time in the soil seeking new roots to feed upon. The meadow or root-lesion nematodes—*Pratylenchus* spp.—are the most widely known representatives of this group. The feeding activities result in the formation of necrotic lesions in the roots; the nematodes themselves are only in the living tissue at margin of lesion.

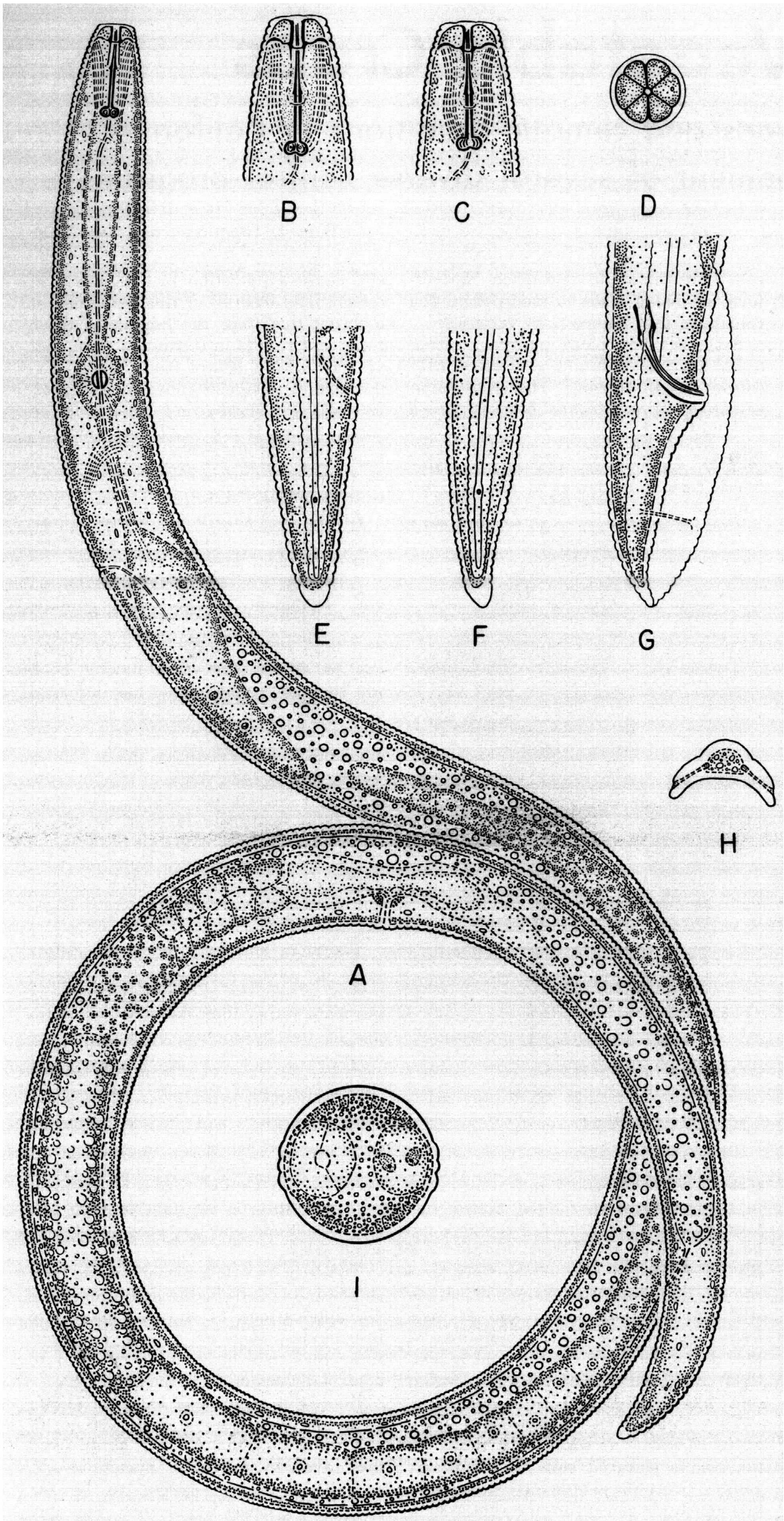
Sessile endoparasitic nematodes which feed on underground parts of plants differ from the vagrant endoparasites, in that in the adult stage they never move from the feeding site. It may be debatable as to whether or not some of the nematodes included here are truly endoparasites. Those nematodes that are always found with the head and neck embedded in plant tissues are considered here to be endoparasites as opposed to nematodes that only penetrate the cells with the spear.

In this debatable group of exposed endoparasites are placed two important plant parasites: the citrus nematode—*Tylenchulus semipenetrans*—and the reniform nematode—*Rotylenchulus reniformis*. Both of these nematodes are characterized by the swollen to saccate adult females and also by the production of a gelatinous egg sac. The larvae of citrus nematode feed upon cortical cells, the juvenile females penetrating partially into root tissues. All stages of the citrus nematode—with the exception of the fully mature reproductive female—can be found in the soil. An essential difference between these two species is the fact that the reniform nematode can develop from egg to young female without feeding on roots. Both species are similar in that the adult male has a degenerate spear and esophagus and, therefore, does not feed on root tissue.

The cyst-forming nematodes of the genus *Heterodera* can also be classed as exposed endoparasitic in the adult stage. The complete penetration of the second stage infective larvae into the root tissue is a distinctive feature of *Heterodera*. It is only the fully mature saccate female that is exposed to the surface and this results not from partial penetration but from the rupture of the root by the swelling female. In contrast to the other plant parasitic nematodes, most *Heterodera* species deposit some eggs into a gelatinous egg sac but the majority of eggs are retained inside the female in such large numbers that eventually her entire body is filled. At this time the cyst is formed by an enzymatic tanning process of the female cuticle.

The cyst probably serves as an effective means of survival by providing the enclosed eggs with some protection from desiccation and natural enemies. Eggs of the cyst-forming species are also protected by some internal mechanism against hatching in the absence of a host plant. At present this mechanism is not completely understood, but has been demonstrated for the golden nematode of potato where eggs hatch in large numbers only in the presence of certain root exudates. Because of these phe-

Concluded on page 12



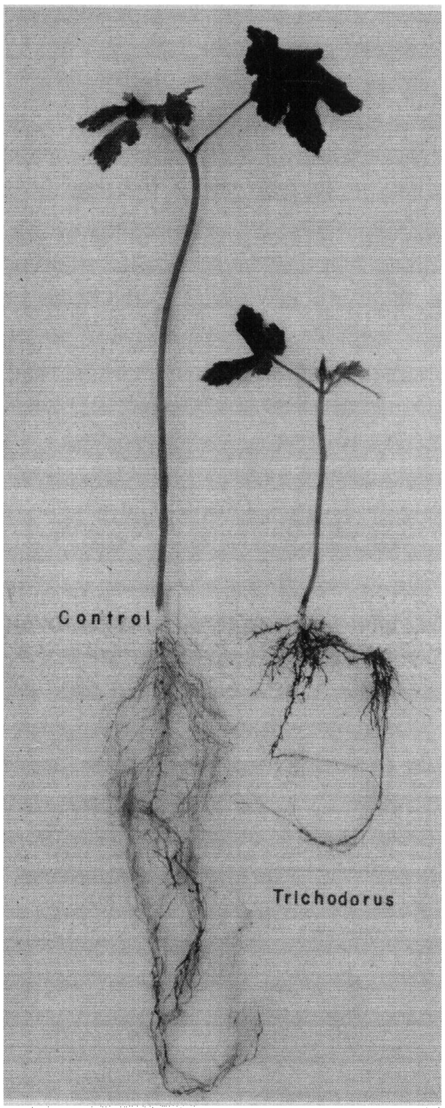
Structure of root-lesion nematode, *Pratylenchus vulnus*. A—Adult female. B and C—Heads of females. D—Face view of female. E and F—Female tails. G—Male tail. H—Diagrammatic cross-section through male tail. I—Cross-section through female body. Greatly magnified.

FIELD

Continued from preceding page

However, severe injury has been observed in cases where these crops were grown on heavily infested soils during periods when soil temperatures were warm enough for rapid nematode development.

Stubby-root nematode injury to okra. Greenhouse test.



The crucifers are particularly important as hosts of the sugar-beet nematode in that they should not be included in rotations designed to control that nematode.

The cabbage cyst nematode—*Heterodera cruciferae*—has been reported from a number of fields in the Half Moon Bay area, but little is known concerning the economic importance of this pest.

Pepper and eggplant also are injured by one or more of the species of root-knot nematodes.

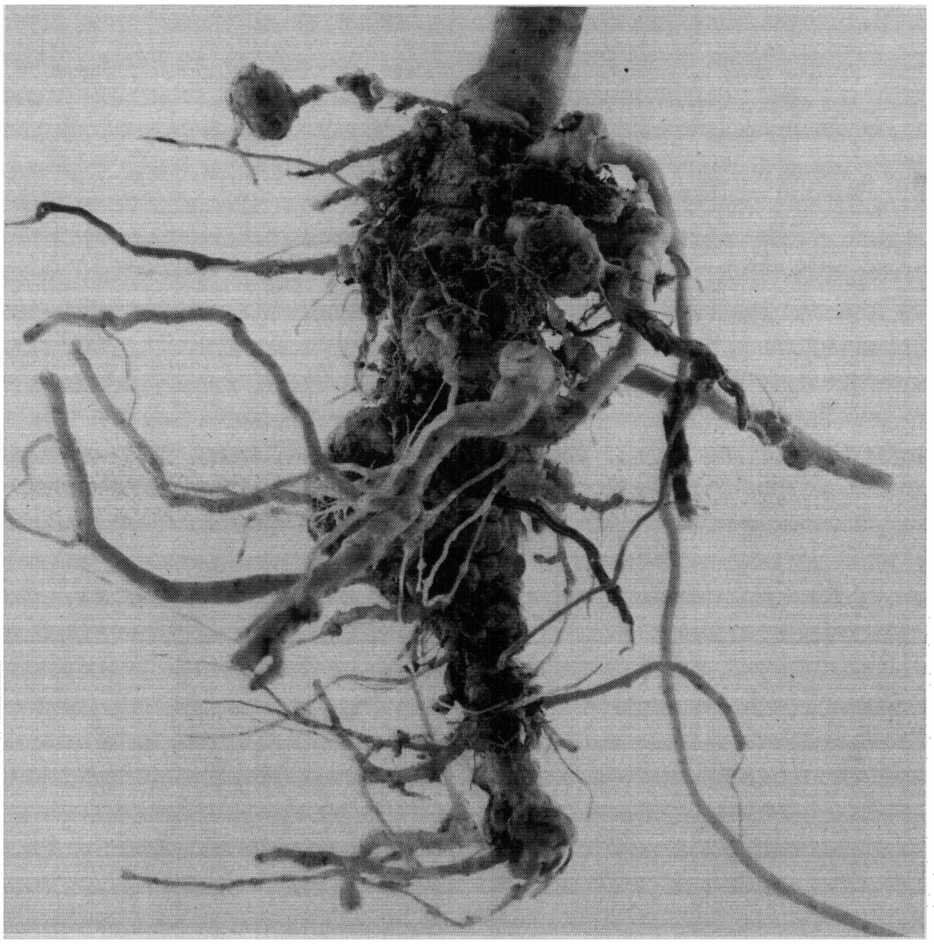
Okra is extremely susceptible to root-knot nematodes and can be severely stunted or killed on infested soil. Okra is also attacked by the stubby-root nematode, and crop injury has been observed in the Coachella Valley.

Celery grown during the winter months usually escapes severe injury by root-knot, but the nematodes must be controlled if the crop is to be grown on infested fields during the summer. Use of nematode-free celery transplants is important.

Ivan J. Thomason is Assistant Nematologist, University of California, Riverside.

Bert Lear is Associate Nematologist, University of California, Davis.

Root-knot nematode, *Meloidogyne javanica*, galling on watermelon roots.



STRUCTURE

Continued from page 7

nomena eggs within the cyst can remain viable in the soil for many years.

Endoparasitic sessile and gall forming nematodes include the most widely known and important root-knot nematode genus, *Meloidogyne*. Superficially the species in this group have a life cycle very similar to the cyst forming *Heterodera* and differ mainly by the absence of cyst production. As with *Heterodera*, only the second stage infective larvae and males are found free in the soil. All other stages are restricted to and develop in the roots of plants. In addition to not forming a cyst the adult females differ from *Heterodera* in that they are usually completely enclosed within the root, and eggs are always deposited in a gelatinous egg sac. All of the root-knot nematodes incite the formation of root galls in the process of feeding upon host tissues.

When females are in small galls the eggs are deposited on the surface of the root in a gelatinous egg sac that is an effective mechanism against egg desiccation. In large galls both females and their egg sacs may be completely inside the gall. The second stage larvae are not well adapted to withstand desiccation and they die rather quickly under conditions of low moisture. This lack of ability to withstand desiccation as second stage larvae does not interfere with larval survival under conditions of favorable moisture and temperature. Second stage larvae, under such conditions, and in the absence of a host, can remain viable in the soil for at least three years.

A. R. Maggenti is Assistant Nematologist, University of California, Davis.

M. W. Allen is Professor of Plant Nematology, University of California, Davis.