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Changing Approaches in Nematode Taxonomy

Identifying, describing, and classifying plant-parasitic nematodes in relation to agriculture is essentially a practical art or science. In describing some practical aspects of plant nematode taxonomy, I will draw heavily on my interest in the taxonomy and biology of the cyst nematodes, *Globodera* and *Heterodera* spp. (Fig. 1).

The Changing Background

Biological control in the form of crop rotations, the farmer's traditional method of combating pests, has a scientific basis in the earliest studies of host ranges of plant-parasitic nematodes. Such studies depended then—and depend today—on recognizing a multiplicity of nematode species, many with specific host requirements. Taxonomic endeavor in the form of species descriptions and reliable identification of nematodes in field populations has been an essential adjunct to the development of host-based control measures. Furthermore, a large number of soil-dwelling nematodes have little or no importance as crop parasites, and these should be identified to ensure that control is not attempted where none is needed, since all control measures impose some penalty. The trend to utilize some aspect of the target species' biology is also increasing. The use of resistant and tolerant cultivars is an established approach of this type, whereas fungal antagonists of nematodes and behavior-modifying chemicals are more speculative examples. Figure 2 shows the increasing trend in the number of abstracts indexed under host resistance in *Helminthological Abstracts (Series B)* since 1970.

In much of the developed world during the second half of the 20th century, the major emphasis in plant nematode control has been on the use of chemical agents. Today, the increasing attention being paid to real or alleged dangers to health and the environment posed by nematicides is changing this emphasis. A number of well-established nematicides are under question or already banned in various parts of the world—DBCP and EDB in the United States, for example—and the likelihood of new compounds being developed is becoming less and less because of the cost involved. As a result, greater attention is being paid to biological control measures. Such methods, in the broadest sense, are most likely to succeed against the nematode species with the greatest adaptation to their hosts or the greatest specialization in their life histories.

Biologically based control measures are highly specific in action. The basis may be on the particular host requirement of a nematode species, the efficacy of crop resistance against a particular race or pathotype of a species, or the specificity of a behavior-modifying chemical. A hatching agent is such a chemical, since the eggs of many cyst nematode species require a specific stimulus from host plant roots to hatch; another is a mate-attracting pheromone, which some sedentary females secrete to attract males. Because the use of such chemicals in control measures requires specific characterization of the target organisms, the demand for taxonomic expertise is likely to increase rather than decline. Taxonomic research will need to be fully integrated with the plant pathology aspects of nematology.

Fig. 1. Cyst nematodes on host roots. Each female is the size of a pinhead.

Typically, these measures are used to control nematodes with high levels of adaptation to the parasitic habit. Resistance is effective only against species with a limited host range; fungal antagonists seem most effective when they decrease the reproductive potential of a species by destroying females adapted to producing large numbers of eggs; behavior-modifying chemicals are most likely to be effective where they interfere with the normal operation of specific triggers in a highly specialized life history. With resistance, for example, prospects are good for controlling nematodes with highly specialized host-parasite relations. Of the citations indexed under "resistance" in *Helmin-*

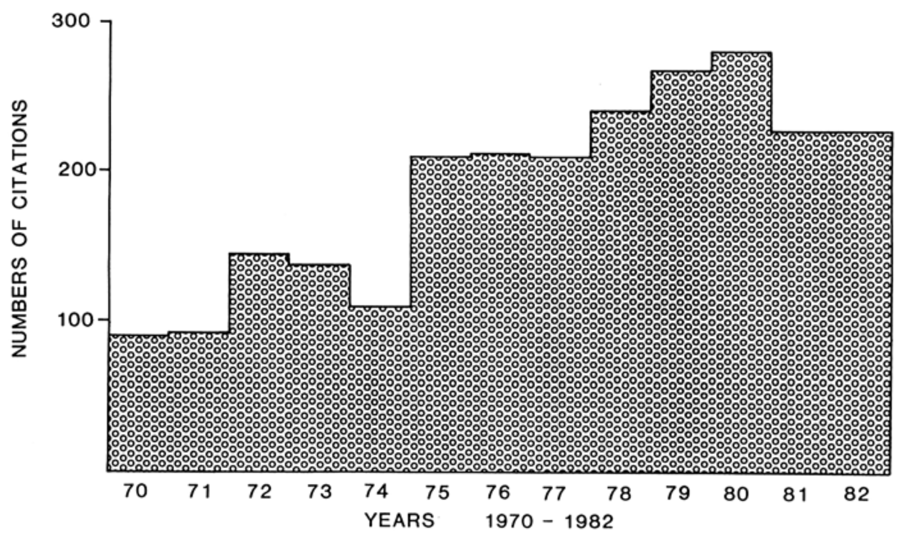

Fig. 2. Number of publications indexed under host resistance to plant-parasitic nematodes in *Helminthological Abstracts (Series B)*.

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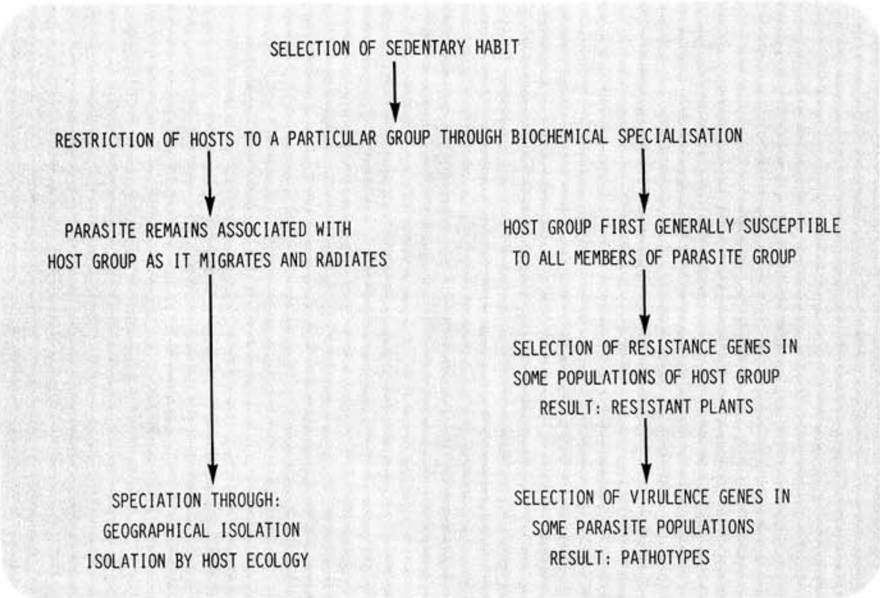

Fig. 3. Possible steps in the coevolution of sedentary plant-parasitic nematodes and their hosts.

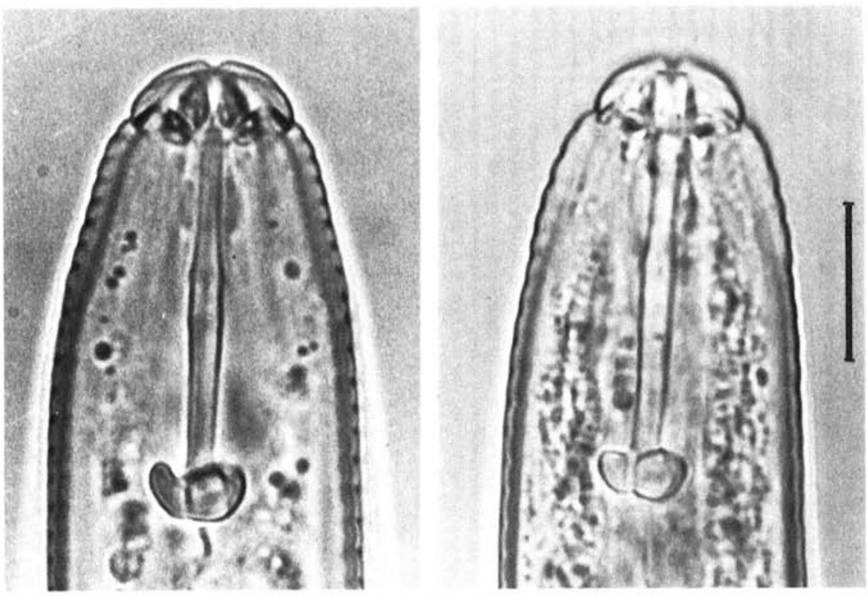

Fig. 4. *Heterodera mani* (left) and *H. avenae* (right) are members of a species complex distinguished by subtle differences in the shape of second-stage juvenile stylets. Only *H. avenae* is a significant crop pest. Scale bar = 10 μm.

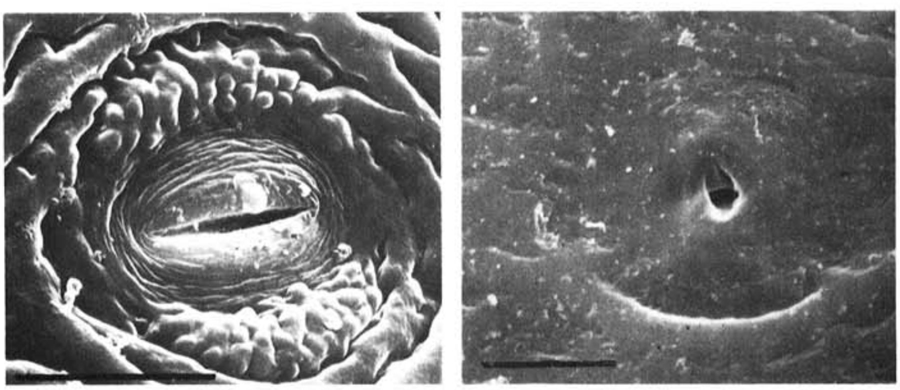

Fig. 5. Scanning electron micrographs showing morphological differences in the external genitalia of females of the *Globodera* spp. attacking potatoes (left) and yarrow (right). The species are otherwise virtually identical. Only the potato parasite is a pest. Scale bars = 10 μm.

thological Abstracts for 1970 through 1982, 9% were for *Anguina, Ditylenchus*, and *Aphelenchoides* spp. combined, 33% for cyst nematodes, 47% for root-knot nematodes (*Meloidogyne* spp.), 3% for other forms with sedentary females, and only 8% for vermiform root parasites.

Many of the most damaging and difficult to manage nematode pests are those with a high level of adaptation to the truly parasitic habit. Of the 14 economically most important genera in tropical African agriculture listed by Taylor (14), nine are highly specialized forms. Distributions elsewhere are similar, with *Meloidogyne* spp. predominating in the tropics and cyst nematodes predominating in temperate zones. Forms with obvious specializations in their life histories are those with sedentary, swollen females that induce specialized feeding sites (4), eg, root-knot and cyst nematodes and *Nacobbus* and *Rotylenchulus* spp., and those that are adapted to dispersal with their hosts, eg, *Anguina* spp. and the bulb and stem nematode *Ditylenchus dipsaci*. High levels of adaptive parasitism are also being found among less obviously specialized forms. Recently, the banana and citrus races of *Radopholus similis* were shown to be genetically isolated (2), and *Xiphinema* spp. are now known to induce specific morphological responses in their hosts (17).

The host-parasite relations we observe today are the products of coevolution of the parasites and their hosts in geological time, since nematode specialization to a particular host would have affected evolution of that host. This process (Fig. 3) has been demonstrated most clearly for cyst nematodes (5,11) but can be extended to other groups. Coevolution has important implications for taxonomy, especially in relation to nematode management. The coevolutionary process may produce a complex of species with very similar or even apparently identical morphology (sibling species sensu Mayr [7]), with morphological variants within a species, and with physiological variants that behave differently on resistant plants. Components of such complexes can be very difficult to distinguish (Fig. 4), but their identification by nontraditional taxonomic methods may be necessary because of agriculturally important differences in their biology.

New Concepts and Methods

Novel approaches to the taxonomy of species complexes do not necessarily yield simple solutions. None of the numerical analyses of host range or nematode morphology, both based on large numbers of populations, or hybridization experiments could resolve the complex of the *Globodera* spp. (12), and taxonomic decisions had to be made subjectively.

Numerical techniques are gradually

being applied, but considering the importance of measurements in differentiating nematodes, nematode taxonomists have been exceptionally slow to take up methods widely used in other branches of systematics. Multivariate analyses are particularly suitable for studies of population variation within species complexes but require corroborative evidence to aid interpretation.

For amphimictic species, the biological species concept, applied by demonstrating the ability or inability of nematodes assigned to putatively different species to hybridize, is theoretically important. In practice, the concept has been limited to matings of those nematodes experimentally suitable, then following the development of their progeny. The techniques are laborious and the results not necessarily easy to interpret. Failure to produce fertile hybrids is evidence of separate specific status, but the reverse is not always so; many true species of animals may produce hybrids under artificial conditions. Moreover, the biological species concept in zoology has been developed largely through observation of insects and vertebrates, the most "complex" members of the animal kingdom. Nematodes are indisputably less complex than higher animals, with correspondingly less complex burdens of genetic information and a greater expected frequency of successful hybridizations. Disparate species or even genera of cyst nematodes can hybridize (8), and it may be that for groups of nematodes with a close relationship, the classical biological species concept will be as difficult or inappropriate to apply as with some plants.

Scanning electron microscopy has become an almost routine extension of the morphological approach to differentiating nematode species (Fig. 5). At first, devising adequate preparation techniques for soft-bodied nematodes was an obstacle, but critical point drying has largely overcome this (16). The increasing use of scanning electron microscopy is a rare example of a new technique being taken up from inception and applied in plant nematode taxonomy. Numbers of previously unrecognized characters are now available to the taxonomist, and the trend will undoubtedly continue.

Another relatively new class of techniques adopted by plant nematologists is chemical differentiation, the subject of a major review in 1979 (3) and a tool that will increase in importance as analytical power and ease of application improve. Serological methods were applied to cyst nematode taxonomy in the late 1960s and protein electrophoresis, in the early 1970s. Differences in protein or isoenzyme composition are proving to be powerful taxonomic tools. Their importance lies in their providing another set of criteria for elucidating taxa and in their reproducibility and speed of application. Species of potato cyst nematodes can be identified and even quantified faster in a field population by electrophoresis than by light or electron microscopy. Increased sensitivity also makes characterization of single specimens a possibility.

A further development is characterization of nematodes by their nucleic acids. Because they relate most closely to the basic genetic composition of an organism, nucleic acids offer, in theory at least, great potential. This seems likely to be research tool rather than a routine aid for some time to come, however.

Host Races and Pathotypes

The number of studies of infraspecific variation in relation to nematode behavior on hosts has increased steadily during the last decade as an adjunct to the control of plant-parasitic nematodes by crop rotation and use of resistant cultivars. At first, such forms were loosely described as races, biological races, biotypes, and so forth. The nomenclature is becoming more organized, however, and the following definitions are now widely accepted: *Host races* are races of a nematode species distinguished by inherited ability or inability to successfully parasitize certain *species* of plant. *Pathotypes* are races of a nematode species distinguished by inherited ability or inability to reproduce on specified *lines* of a host plant species that embody different genes for resistance to the nematode species. Pathotypes may exist within a host race. This simple nomenclature provides all the definitions needed and is self-explanatory and free from jargon. Proposals such as that by Maas et al (6) to substitute forma specialis for host race only add to the burden of terms. Examples of host races can be readily found among host-specialized nematodes, such as bulb and stem, cyst, and root-knot nematodes and other forms with sedentary females.

Pathotypes, also products of the coevolutionary process, are attracting increasing attention as field populations of nematodes able to overcome resistance bred into crop species are encountered. Pathotypes are now part of the informal taxonomy of several agriculturally important species of cyst nematode, and as plant breeding for resistance intensifies, more will be recognized among cyst nematodes and other host-specific groups. As additional sources of resistance to a particular nematode are utilized, the number of pathotypes recognized within that species will inevitably increase too. Pathotypes evolve from the selection of specific genes for resistance in a host species and of specific genes for virulence in the nematode species, with virulence defined as the ability to overcome the effects of a resistance gene (15). Such gene-for-gene interactions seem common in nematode host-parasite interactions (9) and are a logical outcome of the coevolutionary process (11).

Classification of a field population of a nematode species into pathotypes is laborious, depending on assessing nematode reproduction on several differential hosts. Morphological recognition of pathotypes within a species has generally not succeeded. This is not surprising, since pathotypes are not separate biological entities but are part of the gene pool of a species and not likely to be the subject of isolating mechanisms that might lead to the evolution of morphologically distinct forms. Pathotypes of a species that show significant and consistent morphological differences are most likely distinct species, as is the case with potato cyst nematodes (10) and is probably also the case with cereal cyst nematodes (13). Characterization by more subtle means, such as detecting differences in enzyme complement related to dissimilarities in pathogenicity of various pathotypes, may prove more successful.

Taxonomy and Classification

Agricultural nematologists require stable names for the organisms with which they work. Taxonomic specialists are concerned with describing and characterizing those same organisms effectively but are also concerned with producing a scientifically satisfactory classification. Agricultural nematologists cannot do their job properly without the taxonomists but frequently find changes in nomenclature irritating. Constant revision of generic and family-level taxa on the basis of trivial morphological differences is an unfortunate trait of a few scientists in this field. New taxa should be proposed only when supported by a consensus of evidence from several aspects of the nematode's biology. Only by increasing the involvement of taxonomists in the plant pathology aspects of nematology will this approach be fostered. The use of objective methods in forming classifications, a field of great interest in zoology but one only now being considered for plant nematodes (1), will be of further benefit.

Plant nematode taxonomists are not alone in experiencing difficulty working with parasites with relatively uniform morphological characters. Monotypic genera (containing only one species and reckoned to indicate bad taxonomic practice when occurring too frequently) form about 38% of all plant and soil nematode genera. The figure for cestode parasites of mammals and fish is about 44%.

A Greater Concern

The image of the nematode taxonomist working only at the laboratory bench with a microscope and dead specimens is, in my view, increasingly outdated. Today, to meet the demands created by the increasing emphasis on control methods dependent on biological interactions, the nematode taxonomist must be concerned with many aspects of nematode biology, particularly the relationship of parasite to host. The coevolutionary hypothesis is the unifying theory for this approach. A greater concern for the plant pathology aspects of nematology, together with the application of exciting and powerful new techniques, may revive interest in nematode taxonomy, return it to its central position, and reverse the trend of recent years.

Literature Cited

1. Coomans, A. 1983. General principles for phylogenetic systematics of nematodes. Pages 1-10 in: Concepts in Nematode Systematics. A. R. Stone, H. M. Platt, and L. F. Khalil, eds. Academic Press, New York. 388 pp.
2. Huettal, R. N., Dickson, D. W., and Kaplan, D. T. 1983. Biochemical identification of the two races of *Radopholus similis* by starch gel electrophoresis. J. Nematol. 15:338-344.
3. Hussey, R. S. 1979. Biochemical systematics of nematodes—a review. Helminthol. Abstr. Ser. B. 48:141-148.
4. Jones, M. G. K. 1981. The development and function of plant cells modified by endoparasitic nematodes. Pages 255-279 in: Plant Parasitic Nematodes. Vol. 3. B. M. Zuckerman and R. A. Rohde, eds. Academic Press, New York. 508 pp.
5. Krall, E., and Krall, H. 1978. [The revision of plant nematodes of the family Heteroderidae (Nematoda: Tylenchida) by using a comparative ecological method of studying their phylogeny.] Pages 39-56 in: Printsipy i methody izucheniya vzaimootnoshenii mezhdu paraziticheskimi nematodami i rasteniyami. Akademiya Nauk Estonoskoi SSR, Tartu. 195 pp.
6. Maas, P. W. Th., du Bois, E., and Dede, J. 1982. Morphological and host range variation in the *Heterodera trifolii* complex. Nematologica 28:263-270.
7. Mayr, E. 1942. Systematics and the Origin of Species. Columbia University Press, New York. 334 pp.
8. Miller, L. I. 1983. Diversity of selected taxa of *Globodera* and *Heterodera* and their interspecific and intergeneric hybrids. Pages 207-220 in: Concepts in Nematode Systematics. A. R. Stone, H. M. Platt, and L. F. Khalil, eds. Academic Press, New York. 388 pp.
9. Sidhu, G. S., and Webster, J. M. 1981. The genetics of plant-nematode parasitic systems. Bot. Rev. 47:387-419.
10. Stone, A. R. 1973. *Heterodera pallida* n.sp. (Nematoda: Heteroderidae), a second species of potato cyst nematode. Nematologica 18(1972):591-606.
11. Stone, A. R. 1979. Co-evolution of nematodes and plants. Symb. Bot. Ups. 22(4):46-61.
12. Stone, A. R. 1983. Three approaches to the status of a species complex, with a revision of some species of *Globodera* (Nematoda: Heteroderidae). Pages 221-233 in: Concepts in Nematode Systematics. A. R. Stone, H. M. Platt, and L. F. Khalil, eds. Academic Press, New York. 388 pp.
13. Stone, A. R., and Hill, A. J. 1982. Some problems posed by the *Heterodera avenae* complex. EPPO Bull. 12:317-320.
14. Taylor, D. P. 1976. Plant nematology problems in tropical Africa. Helminthol. Abstr. Ser. B. 45:269-284.
15. Vanderplank, J. E. 1978. Genetic and Molecular Basis of Plant Pathogenesis. Springer-Verlag, Berlin. 167 pp.
16. Wergin, P. W., and Stone, A. R. 1981. Techniques for preparation and examination of plant parasitic nematodes in the scanning electron microscope. Scanning Electron Microsc. 1981. 3:169-176.
17. Wyss, U. 1981. Ectoparasitic root nematodes: Feeding behavior and plant cell responses. Pages 325-351 in: Plant Parasitic Nematodes. Vol. 3. B. M. Zuckerman and R. A. Rohde, eds. Academic Press, New York. 508 pp.

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