

Biochemical and molecular characterization of plant-parasitic nematodes

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Summary. Nematologists need correct species identification to carry out research, teaching, extension and other activities. Therefore, nematode taxonomy must be pursued diligently at all levels. The identification of plant-parasitic nematodes is not always easy and that of some species is especially difficult. Most of the information that nematologists use when characterizing and identifying specimens is based on morphological and morphometrical characters. Although these characters are of primary importance, in the last three decades they have been supplemented by biochemical/molecular characters. Biochemical approaches include the separation of proteins (general proteins and isozymes) by one-dimensional gel electrophoresis, isoelectric focusing, two-dimensional gel electrophoresis, and sodium dodecyl sulphate-capillary gel electrophoresis. Serology has also been found effective in the identification and quantification of nematodes, monoclonal antibodies being a more useful immunological tool than polyclonal antibodies. Identification based on the direct examination of DNA is potentially a more powerful method to characterize inter- and intra-specific variability. The development of techniques such as the polymerase chain reaction, restriction fragment length polymorphism, randomly amplified polymorphic DNA, and amplified fragment length polymorphism has increased the accuracy and speed of nematode characterization/identification. Progress continues to be made and more and more nematologists are using molecular techniques for diagnostic purposes and to assess genetic variation.

Key words: biochemistry, DNA, phytoparasitic nematodes, serology

Introduction

The identification of plant-parasitic nematodes is not always easy, particularly in the case of some taxa. Identification is even more complicated when two or more species occur in the same sample. The faulty characterization and identification

of species that are economically important may lead to inappropriate control measures being taken. To overcome these problems the characterization and identification of nematodes should be based not only on morphological and morphometrical characters and on host range bioassays, which are of primary importance, but also on protein and nucleic acid profiles.

Biochemical and molecular techniques have been a research priority with nematologists over the past 30 years, and several reviews on the application of such techniques to nematology have

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been published (Hussey, 1979; Platzer, 1981; Fox and Atkinson, 1986; Curran, 1991; Hyman and Powers, 1991; Williamson, 1991; Curran and Robinson, 1993; Hyman, 1996; Jones *et al.*, 1997; Powers and Fleming, 1998).

This review attempts to summarize the information available concerning biochemical and molecular markers that have been used in the characterization and identification of plant-parasitic nematodes.

Protein-based characterization

Since the 1960s a wide range of electrophoretic techniques have been developed to detect protein variation: one-dimensional gel electrophoresis for the separation of proteins (general proteins and isozymes); isoelectric focusing (IEF) for protein fractionation (general proteins and isozymes); two-dimensional gel electrophoresis (2-DGE) for electrophoretic resolution of proteins; and sodium dodecyl sulphate-capillary gel electrophoresis (SDS-CGE) for the separation of micro-amounts of proteins and peptides.

One-dimensional gel electrophoresis was the first of these techniques to be applied in nematology, in order to differentiate *Ditylenchus* from *Panagrellus* (Benton and Myers, 1966) and from four *Meloidogyne* species (Dickson *et al.*, 1970). Since then, there have been several studies based on proteins, using non-denaturing conditions, to differentiate species, races or pathotypes of: cyst nematodes (mainly *Heterodera avenae*, *H. glycines*, *H. schachtii* and *H. trifolii*); *Globodera* (especially the potato cyst nematodes [PCN] *G. pallida* and *G. rostochiensis*); root-knot nematodes (RKN) (especially the four common species, *Meloidogyne arenaria*, *M. hapla*, *M. incognita* and *M. javanica*); and some other plant-parasitic nematodes, *Aphelenchoides*, *Aphelenchus*, *Ditylenchus*, and *Radopholus* (Table 1).

One-dimensional SDS gel electrophoresis of proteins has also been used to distinguish species and races of several groups of plant-parasitic nematodes, including cyst nematodes, PCN, RKN, *Aphelenchoides*, *Ditylenchus*, *Pratylenchus*, and *Radopholus* (Table 2).

Protein profiles provide a wealth of information but they are often difficult to interpret. Specific enzymes or isozymes can be localized us-

ing the appropriate staining procedures and have been effective in discriminating species of several groups of plant-parasitic nematodes (Table 3), including infraspecific groups such as *Heterodera glycines* (Lee *et al.*, 1988) and *Radopholus similis* (Huettel *et al.*, 1983a, b). Analysis of a number of isozymes: 24 oxidoreductases; 8 transferases; 19 hydrolases; 7 lyases; and 5 isomerases (Table 4) has shown that characteristic isozyme patterns can identify species. Among all these enzymatic systems, the band patterns of carboxylesterase (EC 3.1.1.1), usually referred to as non-specific esterase, are particularly useful to differentiate plant-parasitic nematode species. Other isozymes, such as aspartate transaminase (EC 2.6.1.1), fumarate hydratase (EC 4.2.1.2), glucose-6-phosphate isomerase (EC 5.3.1.9), malate dehydrogenase (EC 1.1.1.37), phosphoglucosmutase (EC 5.4.2.2) and superoxide dismutase (EC 1.15.1.1), also distinguish some species.

Esterase phenotypes have been obtained from several populations of 36 species of *Meloidogyne*. The most common esterase phenotypes are designated A2, A3, H1, I1, and J3, according to Esben-shade and Triantaphyllou (1985). These phenotypes are associated with most of the populations in all the four major species, *M. arenaria* (A2, A3), *M. hapla* (H1), *M. incognita* (I1) and *M. javanica* (J3).

Another technique for nematode characterization and identification is isoelectric focusing (IEF), which is a modification of the standard electrophoretic technique. With IEF the proteins are separated on the basis of their charge and resolved into sharp bands. This technique does not register some of the variations observed with other methods, but still provides a large amount of data. IEF of proteins was sensitive enough to identify the two species of potato cyst nematodes. Two species-specific proteins, located at pI 5.7 and pI 5.9, can be used to identify *G. pallida* and *G. rostochiensis*. The intensity of the bands has been shown to be directly proportional to the number of eggs and second-stage juveniles in a sample of cysts. Thus it can be used to indicate the proportions of species present in a field, and potentially to determine the level of infestation in field soils (Fleming and Marks, 1982, 1983). Most IEF protein studies have concentrated on PCN, with oth-

er nematodes receiving less attention (Table 5).

The application of enzyme staining techniques to proteins differentiated by IEF limits the number of bands that are visualised. Several studies have been carried out on plant-parasitic nematodes using isozymes and IEF (Table 6).

Two-dimensional gel electrophoresis (2-DGE) is a considerably more informative representation of proteins in a nematode extract, although the preparation and analysis of the gels can be technically demanding. It has been used to examine inter- and intra-specific differences in proteins of *Ditylenchus*, *Globodera*, *Heterodera* and *Meloidogyne* (Table 7).

SDS-capillary gel electrophoresis (SDS-CGE) differentiates microscopic amounts of proteins and peptides. High-performance capillary electrophoresis is still in a developmental stage. When it was tried out to discriminate populations and pathotypes within *G. rostochiensis* and *G. pallida*, it detected differences in protein profiles between pathotypes Ro1, Ro2, Ro5, Pa1, and Pa2/3 (Hinch et al., 1998; Cunha et al., 2002). Capillary electrophoresis is simple and more reproducible than 2-DGE and is suitable for the automated analysis of large numbers of samples. This technique will be useful to identify polypeptides of interest for future sequencing and molecular cloning. It should thus lead more quickly to development of probes for species-specific or pathotype-specific components.

Immunological approaches to the nematode diagnostics of *Bursaphelenchus*, *Ditylenchus*, *Globodera*, *Heterodera*, and *Meloidogyne* have included those using polyclonal antibodies (PABs) which recognize multiple antigenic determinants in nematodes (Webster and Hooper, 1968; Scott and Riggs, 1971; Wharton et al., 1983; Davies and Lander, 1992; Lawler and Harmey, 1993; Kennedy et al., 1997; Masler, 2002). However, the general cross-reactivity of polyclonal antisera limits their value in species-diagnosis. Problems with PABs led to the development of tests based on monoclonal antibodies (MAbs), which exhibit greater antigenic specificity and need only small amounts of antigen (50–200 µg) to be produced (Torrance, 1995). Though monospecific, they can be mass-produced and purified, and frozen cell-lines can be stored for long periods of time. However, they have some disadvantages: a long

time is required to select useful MAbs, and the cell-lines from which they are produced are not stable.

Species-specific MAbs have been produced against: *H. avenae* and *H. glycines* (Atkinson et al., 1988; Curtis et al., 1997); *G. rostochiensis* and *G. pallida* (Bakker et al., 1988; Schots et al., 1989, 1992; Backett et al., 1993; Robinson et al., 1993; De Boer et al., 1996; Cotroneo and Gotta, 1997); *M. incognita* and *M. javanica* (Jones et al., 1988; Davies et al., 1996; Fujiwara et al., 1997). The serodiagnosis of RKN using MAbs appears to be less straightforward than that of PCN, probably because RKN reproduce parthenogenetically. From 281 MAbs produced to females of *M. javanica*, no antibody was found to be species-specific when screened against females of *M. arenaria*, *M. incognita* and *M. javanica* (Davies and Lander, 1992). In an attempt to differentiate *M. incognita* from *M. javanica*, species-specific esterase bands were purified and MAbs produced; although it is now possible to differentiate these 2 species, the MAbs also cross-react with other RKN (Davies et al., 1996; Ibrahim et al., 1996).

Immunoassays in the form of an ELISA are an excellent method to quantify plant-parasitic nematodes. MAbs were used to quantify the two species of PCN from clean extracts of cysts and from clean cysts (Schots et al., 1992; Robinson et al., 1993). Attempts have been made to quantify nematodes, mainly PCN, directly in soil homogenates, although some level of nematode extraction from the soil is necessary here (Davies and Carter, 1995; Evans et al., 1995; Davies, 1997; Curtis et al., 1998). MAbs that showed species-specific recognition of *H. avenae* and PCN identified and quantified cysts from processed soil samples and from soil samples containing up to 14–20% of organic matter (Curtis et al., 1997, 1998). The serological quantification of *Meloidogyne* spp. in roots has also been achieved using MAbs (Robinson, 1989).

DNA-based characterization

The first report of a DNA technique used for taxonomic purposes was probably in 1985 when Curran et al. analysed fragments of genomic DNA with restriction enzymes to differentiate

M. arenaria from *M. javanica* and other non-plant-parasitic nematodes. However, this method: 1) was time-consuming; 2) required a substantial amount of DNA; 3) was not sensitive; and 4) exploited only a small proportion of the genetic variation present in the genome. The development of the polymerase chain reaction (PCR) made it possible to discriminate when only minute amounts of material were available, such as, for example, single juveniles of RKN (Powers and Harris, 1993). PCR is characterized by the three Ss: selectivity, sensitivity and speed (Arnheim and Erlich, 1992).

A wide range of DNA-based techniques are available to detect genetic variations that can be exploited or adapted for taxonomic and diagnostic purposes (Curran, 1991; Curran and Robinson, 1993; De Giorgi *et al.*, 1994; Vrain and McNamara, 1994; Hyman and Whipple, 1996; Powers and Fleming, 1998).

The amplification of specific genomic regions is a highly effective way of detecting inter- and intra-specific variations between genera and species, and within species. The two most common repeated regions for taxonomic and diagnostic purposes are in ribosomal DNA (rDNA) and in mitochondrial DNA (mtDNA). PCR amplification of the Internal Transcribed Spacer Regions (ITS 1 and ITS 2) combined with restriction enzyme analysis (PCR-RFLP) is a powerful tool for nematode diagnostics. It has been used to characterize several species of Tylenchida, *Longidorus*, *Paralongidorus*, *Xiphidiorus*, and *Xiphinema* (Table 8).

Another technique, Randomly Amplified Polymorphic DNA (RAPD), extended DNA analysis to characterize a wide range of organisms (Williams *et al.*, 1990). The power of RAPD-PCR is in its ability to detect DNA sequence variation without the need for prior DNA sequence information.

RAPD-PCR has been used for interspecific, and especially intra-specific discrimination, particularly of *Globodera* and *Meloidogyne* species (Table 9).

Amplified fragment length polymorphism (AFLP) is used to detect and evaluate genetic variation and can screen the whole genome (Vos *et al.*, 1995). Qualitative and quantitative analysis has been used to assess genetic relationships mainly among populations of cyst nematodes, PCN and RKN (Xue *et al.*, 1993; Folkerstma *et al.*, 1996a, b; Jones and Harrower, 1998; Van der Beek *et al.*, 1998; Kaplan *et al.*, 1999; Semblat *et al.*, 1998, 2000; Wang *et al.*, 2001; Dautova *et al.*, 2002).

Other DNA-based techniques, such as Microsatellites or Single Sequence Repeats (SSRs), Satellite DNA (satDNA), Sequence Characterized Amplified Regions (SCARs), PCR-Single-Strand Conformational Polymorphism (PCR-SSCP), and DNA microarrays have been used to characterize *Bursaphelenchus*, *Ditylenchus*, *Globodera*, *Heterodera*, and *Meloidogyne* (Table 10).

Concluding remarks

Protein analysis is an effective tool for the characterization and identification of plant-parasitic nematodes; antibody-based systems offer a great potential for the qualitative and quantitative analysis of nematode samples and the direct examination of genetic material or DNA analysis is potentially the most powerful method for nematode diagnosis and the most sensitive means to measure genetic variability. It is expected that more accurate methods of nematode characterization and identification will be developed. For the differentiation of taxa, a multidisciplinary system is probably more appropriate than any single approach.

Table 1. Plant-parasitic nematode species characterized on the basis of proteins, using one-dimensional native gel electrophoresis.

Species	Reference
<i>Aphelenchoides fragariae</i>	Gysels, 1968 ^a
<i>A. ritzemabosi</i>	Eriksson and Granberg, 1969
<i>Aphelenchus avenae</i>	Dickson <i>et al.</i> , 1970; Evans, 1971
<i>Ditylenchus destructor</i>	Evans, 1971
<i>D. dipsaci</i>	Eriksson and Granberg, 1969; Dickson <i>et al.</i> , 1970; Hussey and Krusberg, 1971 ^b
<i>D. myceliophagus</i>	Evans, 1971
<i>D. triformis</i>	Benton and Myers, 1966; Dickson <i>et al.</i> , 1970; Hussey and Krusberg, 1971 ^b
<i>Globodera "mexicana"</i>	Greet, 1972 ^c ; Greet and Firth, 1977 ^d
<i>G. pallida</i>	Greet and Firth, 1977 ^d ; Franco, 1979 ^d ; Stegemann <i>et al.</i> , 1982 ^f
<i>G. rostochiensis</i>	Trudgill and Carpenter, 1971 ^e ; Greet, 1972 ^c ; Trudgill, 1972; Trudgill and Parrot, 1972 ^c ; Greet and Firth, 1977 ^d ; Franco, 1979 ^d ; Stegemann <i>et al.</i> , 1982 ^f
<i>G. solanacearum</i>	Greet, 1972 ^c ; Greet and Firth, 1977 ^d
<i>G. tabacum</i>	" "
<i>G. virginiae</i>	" "
<i>Heterodera avenae</i>	Trudgill and Carpenter, 1971 ^e ; Stone and Williams, 1974 ^d ; Shashi <i>et al.</i> , 1999
<i>H. cajani</i>	Shashi <i>et al.</i> , 1999
<i>H. carotae</i>	Trudgill and Carpenter, 1971 ^e
<i>H. glycines</i>	Dickson <i>et al.</i> , 1970; Ishibashi, 1970 ^d ; Pozdol <i>et al.</i> , 1981; Pozdol and Noel, 1984 ^b ; Lee <i>et al.</i> , 1988
<i>H. graminis</i>	Shashi <i>et al.</i> , 1999
<i>H. lespedezae</i>	Pozdol and Noel, 1984 ^b
<i>H. oryzae</i>	Ishibashi, 1970 ^d
<i>H. schachtii</i>	Trudgill and Carpenter, 1971 ^e ; Pozdol and Noel, 1984 ^b
<i>H. sorghi</i>	Shashi <i>et al.</i> , 1999
<i>H. trifolii</i>	Trudgill and Carpenter, 1971 ^e ; Pozdol and Noel, 1984 ^b
<i>H. zeae</i>	Shashi <i>et al.</i> , 1999
<i>Meloidogyne arenaria</i>	Dickson <i>et al.</i> , 1970; Hussey <i>et al.</i> , 1972 ^d ; Bergé and Dalmasso, 1975 ^e ; Dalmasso and Bergé, 1978 ^f
<i>M. hapla</i>	Dickson <i>et al.</i> , 1970; Ishibashi, 1970 ^d ; Bergé and Dalmasso, 1975 ^e , 1976; Dalmasso and Bergé, 1978 ^f
<i>M. incognita</i>	Dickson <i>et al.</i> , 1970; Ishibashi, 1970 ^d ; Hussey <i>et al.</i> , 1972 ^d ; Bergé and Dalmasso, 1975 ^e ; Dalmasso and Bergé, 1978 ^f ; Castagnone-Sereno <i>et al.</i> , 1995 ^b
<i>M. javanica</i>	Dickson <i>et al.</i> , 1970; Bergé and Dalmasso, 1975 ^e ; Dalmasso and Bergé, 1978 ^f ; Erba and Dickson, 1979
<i>M. mali</i>	Ishibashi, 1970 ^d
<i>M. naasi</i>	Dalmasso and Bergé, 1978 ^f
<i>Radopholus similis</i>	Huettel <i>et al.</i> , 1983 ^b

^a Cited in Platzer (1981).

^b Cited in Williamson (1991).

^c Cited in Hyman and Powers (1991).

^d Cited in Fox and Atkinson (1986).

^e Cited in Jones *et al.* (1997).

^f Cited in Powers and Fleming (1998).

Table 2. Plant-parasitic nematode species characterized on the basis of proteins, using one-dimensional SDS gel electrophoresis.

Species	Reference
<i>Aphelenchoides arachidis</i>	Ibrahim <i>et al.</i> , 1994 ^b
<i>A. besseyi</i>	"
<i>A. bicaudatus</i>	"
<i>A. fragariae</i>	"
<i>A. hamatus</i>	"

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Table 2. (continued)

Species	Reference
<i>Ditylenchus angustus</i>	Ibrahim <i>et al.</i> , 1994b
<i>D. dipsaci</i>	Tenente and Evans, 1997
<i>D. myceliophagus</i>	Ibrahim <i>et al.</i> , 1994b
<i>Globodera pallida</i>	Den Nijs and Lock, 1990
<i>G. rostochiensis</i>	"
<i>Heterodera glycines</i>	Pozdol and Noel, 1984 ^a
<i>H. carotae</i>	Bossis, 1991
<i>H. cruciferae</i>	"
<i>H. lespedezae</i>	Pozdol and Noel, 1984 ^a
<i>H. schachtii</i>	"
<i>H. trifolii</i>	"
<i>Pratylenchus coffeae</i>	Jaumot <i>et al.</i> , 1997
<i>P. crenatus</i>	Ibrahim <i>et al.</i> , 1995
<i>P. fallax</i>	"
<i>P. goodeyi</i>	Jaumot <i>et al.</i> , 1997
<i>P. neglectus</i>	Ibrahim <i>et al.</i> , 1995
<i>P. penetrans</i>	"
<i>P. pinguicaudatus</i>	"
<i>P. scribneri</i>	Jaumot <i>et al.</i> , 1997
<i>P. thornei</i>	Ibrahim <i>et al.</i> , 1995; Jaumot <i>et al.</i> , 1997
<i>P. vulnus</i>	Jaumot <i>et al.</i> , 1997
<i>Radopholus similis</i>	Huettel <i>et al.</i> , 1983b; Jaumot <i>et al.</i> , 1997

^a□Cited in Wlliamson (1991).

Table 3. Plant-parasitic nematode species characterized on the basis of isozymes, using one-dimensional native gel electrophoresis.

Species	Reference
<i>Anguina agrostis</i>	Riley <i>et al.</i> , 1988 ^a
<i>A. funesta</i>	"
<i>A. tritici</i>	"
<i>Aphelenchoides arachidis</i>	Ibrahim <i>et al.</i> , 1994b
<i>A. besseyi</i>	"
<i>A. bicaudatus</i>	"
<i>A. fragariae</i>	"
<i>A. hamatus</i>	"
<i>Aphelenchus avenae</i>	Dickson <i>et al.</i> , 1970; Evans, 1971; Ali <i>et al.</i> , 1999b
<i>Bursaphelenchus mucronatus</i>	De Guiran <i>et al.</i> , 1985
<i>B. xylophilus</i>	"
<i>Ditylenchus angustus</i>	Ibrahim <i>et al.</i> , 1994b
<i>D. destructor</i>	Evans, 1971
<i>D. dipsaci</i>	Dickson <i>et al.</i> , 1971 ^b ; Hussey and Krusberg, 1971 ^a
<i>D. myceliophagus</i>	Evans, 1971; Ibrahim <i>et al.</i> , 1994b
<i>D. triformis</i>	Dickson <i>et al.</i> , 1971 ^b ; Hussey and Krusberg, 1971 ^a
<i>Heterodera avenae</i>	Bergé <i>et al.</i> , 1981 ^c ; Dalmasso <i>et al.</i> , 1982 ^c ; Bossis and Rivoal, 1989; Ganguly <i>et al.</i> , 1990; Molinari <i>et al.</i> , 1996; Romero <i>et al.</i> , 1996; Shashi <i>et al.</i> , 1999; Mokabli <i>et al.</i> , 2001
<i>H. cajani</i>	Ganguly <i>et al.</i> , 1990; Meher <i>et al.</i> , 1998; Shashi <i>et al.</i> , 1998a, b, c, 1999;
<i>H. cruciferae</i>	Molinari <i>et al.</i> , 1996
<i>H. elachista</i>	Nobbs <i>et al.</i> , 1992
<i>H. filipjevi</i>	Mokabli <i>et al.</i> , 2001
<i>H. glycines</i>	Dickson <i>et al.</i> , 1971 ^b ; Lee <i>et al.</i> , 1988; Molinari <i>et al.</i> , 1996
<i>H. goettingiana</i>	Molinari <i>et al.</i> , 1996

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Table 3. (continued)

Species	Reference
<i>H. graminis</i>	Meher <i>et al.</i> , 1998; Shashi <i>et al.</i> , 1999
<i>H. latipons</i>	Mokabli <i>et al.</i> , 2001
<i>H. mani</i>	Mokabli <i>et al.</i> , 2001
<i>H. oryzae</i>	Nobbs, 1992; Nobbs <i>et al.</i> , 1992
<i>H. oryzicola</i>	Nobbs <i>et al.</i> , 1992
<i>H. sacchari</i>	Nobbs, 1992; Nobbs <i>et al.</i> , 1992
<i>H. schachtii</i>	Molinari <i>et al.</i> , 1996
<i>H. sorghi</i>	Ganguly <i>et al.</i> , 1990; Meher <i>et al.</i> , 1998; Shashi <i>et al.</i> , 1999
<i>H. trifolii</i>	Molinari <i>et al.</i> , 1996
<i>H. zeae</i>	Meher <i>et al.</i> , 1998; Shashi <i>et al.</i> , 1998b, c, 1999
<i>Longidorus arthensis</i>	Lamberti <i>et al.</i> , 2001b
<i>L. elongatus</i>	"
<i>L. helveticus</i>	"
<i>L. macrosoma</i>	"
<i>L. profundorum</i>	"
<i>L. raskii</i>	"
<i>Meloidogyne ardenensis</i>	Karssen and Van Hoenselaar, 1998
<i>M. arenaria</i>	Dickson <i>et al.</i> , 1971 ^b ; Hussey <i>et al.</i> , 1972 ^c ; Bergé and Dalmasso, 1975 ^d , 1976; Starr, 1979 ⁱ ; Janati <i>et al.</i> , 1982 ^c ; Esbenshade and Triantaphyllou, 1985, 1986, 1987 ^b ; Lopez, 1985; Fargette, 1987b ^e , 1988; Pais and Abrantes, 1989 ^g ; Fargette and Braaksma, 1990 ^f ; Cenis <i>et al.</i> , 1992; Ibrahim and Perry, 1993; Davies and Beadle, 1995 ^e ; Carneiro <i>et al.</i> , 1996, 2000; Williamson <i>et al.</i> , 1997 ^e ; Yaegashi and Toida, 1997; Chen <i>et al.</i> , 1998; Semblat <i>et al.</i> , 2000; Navas <i>et al.</i> , 2001; Castro <i>et al.</i> , 2003; Cetintas <i>et al.</i> , 2003
<i>M. artiellia</i>	Karssen and Van Hoenselaar, 1998; Castillo <i>et al.</i> , 2003
<i>M. baetica</i>	Castillo <i>et al.</i> , 2003
<i>M. carolinensis</i>	Esbenshade and Triantaphyllou, 1985
<i>M. chitwoodi</i>	Esbenshade and Triantaphyllou, 1985, 1987 ^b ; Karssen, 1995, 1996 ^h ; Karssen <i>et al.</i> , 1995 ^e ; Van der Beek <i>et al.</i> , 1997 ^e ; Williamson <i>et al.</i> , 1997 ^e ; Karssen and Van Hoenselaar, 1998; Waeyenberge and Moens, 2001
<i>M. coffeicola</i>	Carneiro <i>et al.</i> , 2000
<i>M. cruciani</i>	Esbenshade and Triantaphyllou, 1985
<i>M. deconincki</i>	Karssen and Van Hoenselaar, 1998
<i>M. duytsi</i>	Karssen and Van Hoenselaar, 1998; Karssen <i>et al.</i> , 1998b ^h
<i>M. enterolobii</i>	Esbenshade and Triantaphyllou, 1985; Ibrahim and Perry, 1993
<i>M. exigua</i>	Lopez, 1985; Carneiro <i>et al.</i> , 1996, 2000
<i>M. fallax</i>	Karssen, 1996 ^h ; Van der Beek <i>et al.</i> , 1997 ^e ; Waeyenberge and Moens, 2001
<i>M. graminicola</i>	Esbenshade and Triantaphyllou, 1985, 1987 ^b ; Ibrahim and Perry, 1993; Carneiro <i>et al.</i> , 1996, 2000
<i>M. graminis</i>	Esbenshade and Triantaphyllou, 1987 ^b
<i>M. hainanensis</i>	Liao and Feng, 1995
<i>M. hapla</i>	Ishibashi, 1970 ^c ; Dickson <i>et al.</i> , 1971 ^b ; Bergé and Dalmasso, 1975 ^d , 1976; Dalmasso and Bergé, 1978 ^e ; Starr, 1979 ⁱ ; Esbenshade and Triantaphyllou, 1985, 1986, 1987 ^b ; Lopez, 1985; Ganguly and Dasgupta, 1989; Pais and Abrantes, 1989 ^g ; Cenis <i>et al.</i> , 1992; Ibrahim and Perry, 1993; Karssen <i>et al.</i> , 1995 ^e ; Carneiro <i>et al.</i> , 1996, 2000; Karssen and Van Hoenselaar, 1998; Van der Beek <i>et al.</i> , 1997 ^e ; Williamson <i>et al.</i> , 1997 ^e ; Chen <i>et al.</i> , 1998; Molinari, 2001; Navas <i>et al.</i> , 2001
<i>M. haplanaria</i>	Eisenback <i>et al.</i> , 2003
<i>M. hispanica</i>	Janati <i>et al.</i> , 1982 ^c ; Esbenshade and Triantaphyllou, 1985; Pais and Abrantes, 1989 ^g ; Fargette, 1987b ^e
<i>M. incognita</i>	Ishibashi, 1970 ^c ; Dickson <i>et al.</i> , 1971 ^b ; Hussey <i>et al.</i> , 1972 ^c ; Hussey and Sasser, 1973 ⁱ ; Bergé and Dalmasso, 1975 ^d ; Dalmasso and Bergé, 1978 ^e ; Starr, 1979 ⁱ ; Janati <i>et al.</i> , 1982 ^c ; Esbenshade and Triantaphyllou, 1985, 1986, 1987 ^b ; Lopez, 1985; Fargette, 1987a ^d , b ^e , 1988; Ganguly and Dasgupta, 1989; Pais and Abrantes, 1989 ^g ; Fargette and Braaksma, 1990 ^f ; Rajasekhar <i>et al.</i> , 1990; Cenis <i>et al.</i> , 1992; Ganguly and Sharma, 1992; Ibrahim and Perry, 1993; Davies and Beadle, 1995 ^e ; Carneiro <i>et al.</i> , 1996, 2000; Williamson <i>et al.</i> , 1997 ^e ; Chen <i>et al.</i> , 1998; Suchitra and Ganguly, 1999; Semblat <i>et al.</i> , 2000; Molinari, 2001; Navas <i>et al.</i> , 2001; Castro <i>et al.</i> , 2003

(continued on the next page)

Table 3. (continued)

Species	Reference
<i>M. javanica</i>	Dickson <i>et al.</i> , 1971 ^b ; Bergé and Dalmasso, 1975 ^d ; Dalmasso and Bergé, 1978 ^e ; Starr, 1979; Janati <i>et al.</i> , 1982 ^c ; Esbenshade and Triantaphyllou, 1985, 1986, 1987 ^b ; Fargette, 1987 ^e , 1988; Ganguly and Dasgupta, 1989; Pais and Abrantes, 1989 ^g ; Fargette and Baarksma, 1990 ^f ; Rajasekhar <i>et al.</i> , 1990; Cenis <i>et al.</i> , 1992; Ibrahim and Perry, 1993; Tomaszewski <i>et al.</i> , 1994; Abrantes <i>et al.</i> , 1995; Davies and Beadle, 1995 ^e ; Carneiro <i>et al.</i> , 1996, 2000; Williamson <i>et al.</i> , 1997 ^e ; Yaegashi and Toida, 1997; Chen <i>et al.</i> , 1998; Molinari, 2001; Castro <i>et al.</i> , 2003; Cetintas <i>et al.</i> , 2003
<i>M. konaensis</i>	Carneiro <i>et al.</i> , 2000
<i>M. kralli</i>	Karssen and Van Hoenselaar, 1998; Karssen and Grunder, 2002
<i>M. lusitanica</i>	Pais and Abrantes, 1989 ^g ; Abrantes and Santos, 1991 ^h
<i>M. mali</i>	Ishibashi, 1970 ^c
<i>M. maritima</i>	Karssen and Van Hoenselaar, 1998; Karssen <i>et al.</i> , 1998a ^h
<i>M. mayaguensis</i>	Carneiro <i>et al.</i> , 2000, 2001
<i>M. megadora</i>	Abrantes <i>et al.</i> , 1995
<i>M. microcephala</i>	Esbenshade and Triantaphyllou, 1985, 1986, 1987 ^b
<i>M. microtyla</i>	Esbenshade and Triantaphyllou, 1985, 1987 ^b
<i>M. naasi</i>	Dalmasso and Bergé, 1978 ^a ; Esbenshade and Triantaphyllou, 1985, 1987 ^b ; Karssen and Van Hoenselaar, 1998
<i>M. oryzae</i>	Esbenshade and Triantaphyllou, 1985; Carneiro <i>et al.</i> , 2000
<i>M. paranaensis</i>	Carneiro <i>et al.</i> , 2000; Castro <i>et al.</i> , 2003
<i>M. platani</i>	Esbenshade and Triantaphyllou, 1985
<i>M. querciana</i>	Esbenshade and Triantaphyllou, 1985
<i>M. salasi</i>	Lopez, 1985
<i>Nacobbus aberrans</i>	Baldwin and Cap, 1992; Doucet and Gardenal, 1992; Jatala <i>et al.</i> , 1993; Doucet <i>et al.</i> , 2002
<i>Pratylenchus crenatus</i>	Ibrahim <i>et al.</i> , 1995
<i>P. fallax</i>	"
<i>P. neglectus</i>	"
<i>P. penetrans</i>	"
<i>P. pinguicaudatus</i>	"
<i>P. thornei</i>	"
<i>Radopholus similis</i>	Huettel <i>et al.</i> , 1983a; Sarah, 1997
<i>Rotylenchulus reniformis</i>	Rao <i>et al.</i> , 1998

^a Cited in Williamson (1991).

^b Cited in Hyman and Powers (1991).

^c Cited in Fox and Atkinson (1986).

^d Cited in Jones *et al.* (1997).

^e Cited in Powers and Fleming (1998).

^f Cited in Hyman (1996).

^g Cited in Curran and Robinson (1993).

^h Cited in Karssen and van Hoenselaar (1998).

ⁱ Cited in Platzer (1981).

Table 4. Enzymes used in the electrophoretic analysis of plant-parasitic nematodes.

Enzyme	EC Number ^a
Oxidoreductases	
Alcohol dehydrogenase	1.1.1.1
Amine oxidase (flavin-containing) (= monoamine oxidase)	1.4.3.4
Catalase	1.11.1.6
Cytochrome-c oxidase	1.9.3.1
Cytochrome-b 5-reductase (= diaphorase)	1.6.2.2

(continued on the next page)

Table 4. (continued)

Enzyme	EC Number ^a
D-Aspartate oxidase	1.4.3.1
Dihydrolipoyl dehydrogenase (= lipoamide dehydrogenase)	1.8.1.4
Galactose 1-dehydrogenase	1.1.1.48
Glucose-6-phosphate 1-dehydrogenase	1.1.1.49
Glucose oxidase	1.1.3.4
Glutamate dehydrogenase	1.4.1.2
Glyceraldehyde-3-phosphate dehydrogenase(phosphorylating)	1.2.1.12
Glycerol-3-phosphate dehydrogenase (NAD ⁺) (= α -glycerophosphate dehydrogenase)	1.1.1.8
Isocitrate dehydrogenase (NADP ⁺)	1.1.1.42
L-Iditol 2-dehydrogenase (= sorbitol dehydrogenase)	1.1.1.14
L-Lactate dehydrogenase	1.1.1.27
Leucine dehydrogenase	1.4.1.9
Malate dehydrogenase	1.1.1.37
Malate dehydrogenase (oxaloacetate-decarboxylating) (NADP ⁺) (= malic enzyme)	1.1.1.40
Peroxidase	1.11.1.7
Phosphogluconate dehydrogenase (decarboxylating)	1.1.1.44
Succinate dehydrogenase (ubiquinone)	1.3.5.1
Superoxide dismutase	1.15.1.1
Xanthine dehydrogenase	1.1.1.204
Transferases	
Adenylate kinase	2.7.4.3
Alanine transaminase (= alanine aminotransferase = glutamate pyruvate transaminase)	2.6.1.2
Aspartate transaminase (= aspartate aminotransferase = glutamate-oxaloacetate transaminase)	2.6.1.1
Creatine kinase	2.7.3.2
Hexokinase	2.7.1.1
Nucleoside triphosphate adenylate kinase	2.7.4.10
Phosphoglycerate kinase	2.7.2.3
Pyruvate kinase	2.7.1.40
Enzyme	EC Number ^a
Hydrolases	
β -N-Acetylhexosaminidase (= β -N-acetylglucosaminidase)	3.2.1.52
Acid phosphatase	3.1.3.2
Adenosine deaminase	3.5.4.4
Alkaline phosphatase	3.1.3.1
α -Amylase	3.2.1.1
Carboxylesterase (= esterase)	3.1.1.1
Cellulose 1,4- β -cellobiosidase	3.2.1.91
Cholinesterase	3.1.1.8
Fructose-biphosphatase (D-fructose-1,6-diphosphatase)	3.1.3.11
α -L-Fucosidase	3.2.1.51
α -Galactosidase	3.2.1.22
β -Galactosidase	3.2.1.23
α -Glucosidase	3.2.1.20
β -Glucosidase	3.2.1.21
β -Glucuronidase	3.2.1.31
Hydroxyacylglutathione hydrolase (= glyoxalase II)	3.1.2.6
α -Mannosidase	3.2.1.24
β -Mannosidase	3.1.2.25
Urease	3.5.1.5
Lyases	
Aconitate hydratase	4.2.1.3
Fructose-bisphosphate aldolase	4.1.2.13
Fumarate hydratase	4.2.1.2
4-Hydroxy-2-oxoglutarate aldolase (= aldolase)	4.1.3.16
Lactoylglutathione lyase (= glyoxalase I)	4.4.1.5

(continued on the next page)

Table 4. (continued)

Enzyme	EC Number ^a
Phosphoenolpyruvate carboxylase	4.1.1.31
Phosphopyruvate hidratase (= enolase)	4.2.1.11
Isomerases	
Glucose-6-phosphate isomerase (= phosphoglucose isomerase)	5.3.1.9
Mannose-6-phosphate isomerase (= phosphomannose isomerase)	5.3.1.8
Phosphoglucomutase	5.4.2.2
Phosphoglycerate mutase	5.4.2.1
Triose-phosphate isomerase	5.3.1.1

^a Enzyme classification number recommended by the Nomenclature Committee of the International Union of Biochemistry and Molecular Biology.

Table 5. Plant-parasitic nematode species characterized on the basis of proteins, using isoelectric focusing.

Species	Reference
<i>Globodera achilleae</i>	Doneghan and McKenzie, 1987
<i>G. hypolysi</i>	Sumiya <i>et al.</i> , 2002
<i>G. pallida</i>	Fleming and Marks, 1982, 1983; Ohms and Heinicke, 1983 ^a ; Fox and Atkinson, 1984a ^b ; Marks and Fleming, 1985 ^b ; Fleming and Dolan, 1986 ^a ; Doneghan and McKenzie, 1987; Santos <i>et al.</i> , 1989, 1995; Jatala and Gavilano, 1991; Karssen <i>et al.</i> , 1995 ^a ; Zaheer <i>et al.</i> , 1996a; Ibrahim <i>et al.</i> , 2001
<i>G. rostochiensis</i>	Fleming and Marks, 1982, 1983; Ohms and Heinicke, 1983 ^a ; Fox and Atkinson, 1984a ^b ; Marks and Fleming, 1985 ^b ; Fleming and Dolan, 1986 ^a ; Doneghan and McKenzie, 1987; Santos <i>et al.</i> , 1989, 1995; Jatala and Gavilano, 1991; Karssen <i>et al.</i> , 1995 ^a ; Zaheer <i>et al.</i> , 1996a; Subbotin <i>et al.</i> , 1999a; Ibrahim <i>et al.</i> , 2001; Sumiya <i>et al.</i> , 2002
<i>G. tabacum</i>	Sumiya <i>et al.</i> , 2002
<i>Heterodera australis</i>	Subbotin <i>et al.</i> , 2002
<i>H. avenae</i>	Rumpfenhorst, 1985; Fleming and Dolan, 1986 ^a ; Subbotin <i>et al.</i> , 1996; Subbotin <i>et al.</i> , 2002
<i>H. bifenestra</i>	Rumpfenhorst, 1985
<i>H. carotae</i>	Fleming and Dolan, 1986 ^a
<i>H. fici</i>	Trindade <i>et al.</i> , 1992
<i>H. filipjevi</i>	Subbotin <i>et al.</i> , 1996
<i>H. glycines</i>	Lawson <i>et al.</i> , 1984
<i>H. goettingiana</i>	Trindade <i>et al.</i> , 1992
<i>H. hordecalis</i>	Rumpfenhorst, 1985
<i>H. humuli</i>	Fleming and Dolan, 1986 ^a
<i>H. latipons</i>	Rumpfenhorst, 1985
<i>H. mani</i>	Rumpfenhorst, 1985; Fleming and Dolan, 1986 ^a ; Subbotin <i>et al.</i> , 1996
<i>H. schachtii</i>	Fleming and Dolan, 1986 ^a ; Trindade <i>et al.</i> , 1992
<i>Hoplolaimus columbus</i>	Lawson <i>et al.</i> , 1984
<i>Meloidogyne arenaria</i>	Lawson <i>et al.</i> , 1984
<i>M. exigua</i>	Rodrigues and Abrantes, 1992
<i>M. hapla</i>	Lawson <i>et al.</i> , 1984
<i>M. hispanica</i>	Rodrigues and Abrantes, 1992
<i>M. incognita</i>	Lawson <i>et al.</i> , 1984; Rodrigues and Abrantes, 1992
<i>M. javanica</i>	" "
<i>Punctodera punctata</i>	Rumpfenhorst, 1985; Fleming and Dolan, 1986 ^a

^a Cited in Powers and Fleming (1998).

^b Cited in Jones *et al.* (1997).

Table 6. Plant-parasitic nematodes species characterized on the basis of enzymes, using isoelectric focusing.

Species	Reference
<i>Ditylenchus dipsaci</i>	Ibrahim, 1991
<i>Globodera pallida</i>	Fleming and Marks, 1983; Wharton <i>et al.</i> , 1983; Fox and Atkinson, 1984a ^a , b ^b , 1985 ^c , 1988 ^d ; Marks and Fleming, 1985 ^a ; Fox <i>et al.</i> , 1986 ^b ; Ibrahim, 1991; Zaheer <i>et al.</i> , 1992, 1996a, b
<i>G. rostochiensis</i>	
<i>Heterodera avenae</i>	Bergé <i>et al.</i> , 1981 ^b ; Rumpenhorst, 1985; Bossis and Rivoal, 1989; Molinari <i>et al.</i> , 1996; Andrés <i>et al.</i> , 2001
<i>H. bifenestra</i>	Rumpenhorst, 1985
<i>H. cruciferae</i>	Molinari <i>et al.</i> , 1996
<i>H. glycines</i>	Huettel, 1986; Esbenshade and Triantaphyllou, 1988; Radice <i>et al.</i> , 1988 ^d ; Noel and Stanger, 1991; Molinari <i>et al.</i> , 1996; Noel and Liu, 1998
<i>H. goettingiana</i>	Molinari <i>et al.</i> , 1996
<i>H. filipjevi</i>	Andrés <i>et al.</i> , 2001
<i>H. hordecalis</i>	Rumpenhorst, 1985
<i>H. latipons</i>	Rumpenhorst, 1985; Andrés <i>et al.</i> , 2001
<i>H. mani</i>	" "
<i>H. schachtii</i>	Molinari <i>et al.</i> , 1996
<i>H. trifolii</i>	" "
<i>Longidorus arthensis</i>	Lamberti <i>et al.</i> , 2001b
<i>L. elongatus</i>	Lamberti <i>et al.</i> , 1999b, 2001b
<i>L. helveticus</i>	Lamberti <i>et al.</i> , 2001b
<i>L. latocephalus</i>	Molinari <i>et al.</i> , 1997
<i>L. macrosoma</i>	Lamberti <i>et al.</i> , 2001b
<i>L. pauli</i>	Lamberti <i>et al.</i> , 1999b
<i>L. profundorum</i>	Lamberti <i>et al.</i> , 2001b
<i>L. raskii</i>	" "
<i>Meloidogyne arenaria</i>	Venkatachari <i>et al.</i> , 1991 ^e
<i>M. exigua</i>	Rodrigues and Abrantes, 1992
<i>M. hapla</i>	Venkatachari <i>et al.</i> , 1991 ^e
<i>M. hispanica</i>	Rodrigues and Abrantes, 1992
<i>M. incognita</i>	Ibrahim, 1991; Venkatachari <i>et al.</i> , 1991 ^e ; Rodrigues and Abrantes, 1992
<i>M. javanica</i>	Ibrahim, 1991; Venkatachari <i>et al.</i> , 1991 ^e ; Rodrigues and Abrantes, 1992; Abrantes <i>et al.</i> , 1995
<i>M. megadora</i>	Abrantes <i>et al.</i> , 1995
<i>Nacobbus aberrans</i>	Ibrahim <i>et al.</i> , 1997 ^c
<i>Paralongidorus halepensis</i>	Lamberti <i>et al.</i> , 1999b
<i>Pratylenchus agilis</i>	Andrés <i>et al.</i> , 2000
<i>P. brachyurus</i>	Payan and Dickson, 1990
<i>P. coffeae</i>	Andrés <i>et al.</i> , 2000
<i>P. goodeyi</i>	" "
<i>P. penetrans</i>	" "
<i>P. scribneri</i>	Payan and Dickson, 1990; Andrés <i>et al.</i> , 2000
<i>P. thornei</i>	Andrés <i>et al.</i> , 2000
<i>P. vulnus</i>	" "
<i>Punctodera punctata</i>	Rumpenhorst, 1985
<i>Radopholus similis</i>	Fallas <i>et al.</i> , 1996; Kaplan and Opperman, 1997; Andrés <i>et al.</i> , 2000
<i>Xiphidorus minor</i>	Lamberti <i>et al.</i> , 1999a
<i>Xiphinema chambersi</i>	Lamberti <i>et al.</i> , 2002a
<i>X. citricolum</i>	Lamberti <i>et al.</i> , 2002b
<i>X. diversicaudatum</i>	Lamberti <i>et al.</i> , 1999c
<i>X. floridae</i>	Lamberti <i>et al.</i> , 2002b
<i>X. georgianum</i>	Molinari <i>et al.</i> , 1997
<i>X. index</i>	" "

(continued on the next page)

Table 6. (continued)

Species	Reference
<i>X. italiae</i>	Lamberti <i>et al.</i> , 1999c
<i>X. laevistriatum</i>	Lamberti <i>et al.</i> , 2002b
<i>X. naturale</i>	Lamberti <i>et al.</i> , 2002a
<i>X. pachtaicum</i>	Lamberti <i>et al.</i> , 1999c
<i>X. santos</i>	Molinari <i>et al.</i> , 1997
<i>X. simile</i>	Lamberti <i>et al.</i> , 1999c
<i>X. taylori</i>	Molinari <i>et al.</i> , 1997; Lamberti <i>et al.</i> , 1999c
<i>X. vuittenezi</i>	" "
<i>X. vulgare</i>	Lamberti <i>et al.</i> , 2001a

^a□Cited in Jones *et al.* (1997).

^b□Cited in Fox and Atkinson (1986).

^c□Cited in Powers and Fleming (1998).

^d□Cited in Williamson (1991).

^e□Cited in Curran and Robinson (1993).

Table 7. Plant-parasitic nematodes species characterized on the basis of proteins, using two-dimensional gel electrophoresis.

Species	Reference
<i>Ditylenchus dipsaci</i>	Bossis <i>et al.</i> , 1998
<i>Globodera pallida</i>	Bakker and Gommers, 1982 ^a ; Stegemann <i>et al.</i> , 1982 ^b ; Bakker and Bouwman-Smits, 1988b ^c ; Bakker <i>et al.</i> , 1992 ^b ; De Boer <i>et al.</i> , 1992b; Bossis and Mugniéry, 1993 ^b ; Fullaondo <i>et al.</i> , 1997 ^b , 2001; Cunha <i>et al.</i> , 2000; Folkertsma <i>et al.</i> , 1996a
<i>G. "mexicana"</i>	Bossis and Mugniéry, 1993 ^b
<i>G. rostochiensis</i>	Bakker and Gommers, 1982 ^a ; Stegemann <i>et al.</i> , 1982 ^b ; Ohms and Heinicke, 1985; Bakker and Bouwman-Smits, 1988a ^c , b ^c ; De Boer <i>et al.</i> , 1992a; Bossis and Mugniéry, 1993 ^b ; Fullaondo <i>et al.</i> , 1997 ^b ; Cunha <i>et al.</i> , 2000
<i>G. solanacearum</i>	Bossis and Mugniéry, 1993 ^b
<i>G. tabacum</i>	"
<i>G. virginiae</i>	"
<i>Heterodera avenae</i>	Ferris <i>et al.</i> , 1989 ^b , 1994 ^d ; Bossis and Rivoal, 1996; Romero <i>et al.</i> , 1996
<i>H. glycines</i>	Ferris <i>et al.</i> , 1985 ^c , 1986; Bakker and Bouwman-Smits, 1988b ^c
<i>H. schachtii</i>	Bakker and Bouwman-Smits, 1988b ^c ; Bossis <i>et al.</i> , 1997
<i>H. trifolii</i> f. sp. <i>beta</i>	Bossis <i>et al.</i> , 1997
<i>Meloidogyne arenaria</i>	Premachandran <i>et al.</i> , 1984 ^e ; Van der Beek <i>et al.</i> , 1998; Tastet <i>et al.</i> , 2000
<i>M. chitwoodi</i>	Van der Beek <i>et al.</i> , 1997 ^b , 1998; Tastet <i>et al.</i> , 1999
<i>M. fallax</i>	"
<i>M. hapla</i>	Van der Beek <i>et al.</i> , 1997 ^b , 1998
<i>M. incognita</i>	Premachandran <i>et al.</i> , 1984 ^e ; Dalmasso <i>et al.</i> , 1991; Castagnone-Sereno <i>et al.</i> , 1995b; Van der Beek <i>et al.</i> , 1998; Tastet <i>et al.</i> , 2000
<i>M. javanica</i>	Premachandran <i>et al.</i> , 1984; Van der Beek <i>et al.</i> , 1998; Tastet <i>et al.</i> , 2000
<i>M. mayaguensis</i>	Tastet <i>et al.</i> , 2000
<i>M. naasi</i>	Van der Beek <i>et al.</i> , 1998

^a Cited in Jones *et al.* (1997).

^b Cited in Powers and Fleming (1998).

^c Cited in Hyman and Powers (1991).

^d Cited in Hyman and Whipple (1996).

^e Cited in Williamson (1991).

Table 8. Plant-parasitic nematodes characterized by PCR-RFLP of ITS regions.

Species	Reference
<i>Anguina agropyronifloris</i>	Powers <i>et al.</i> , 2001
<i>A. agrostis</i>	"
<i>A. funesta</i>	"
<i>A. graminis</i>	"
<i>A. pacificae</i>	"
<i>A. microlaenae</i>	"
<i>A. tritici</i>	"
<i>A. wevelli</i>	"
<i>Aphelenchoides arachidis</i>	Ibrahim <i>et al.</i> , 1994a
<i>A. besseyi</i>	Ibrahim <i>et al.</i> , 1994a; Iwahori <i>et al.</i> , 1998
<i>A. bicaudatus</i>	Ibrahim <i>et al.</i> , 1994a
<i>A. composticola</i>	"
<i>A. fragariae</i>	Ibrahim <i>et al.</i> , 1994a; Iwahori <i>et al.</i> , 1998
<i>A. hamatus</i>	Ibrahim <i>et al.</i> , 1994a
<i>A. nechaleos</i>	"
<i>A. paranechaleos</i>	"
<i>Aphelenchus avenae</i>	Ali <i>et al.</i> , 1999a; Iwahori <i>et al.</i> , 1998
<i>Belonolaimus longicaudatus</i>	Cherry <i>et al.</i> , 1997
<i>Bursaphelenchus abietinus</i>	Braasch and Burgermeister, 2002
<i>B. borealis</i>	Braasch <i>et al.</i> , 1999
<i>B. eggersi</i>	"
<i>B. fraudulentus</i>	Hoyer <i>et al.</i> , 1998; Braasch <i>et al.</i> , 1999
<i>B. fungivorus</i>	Braasch <i>et al.</i> , 1999
<i>B. hellenicus</i>	Braasch <i>et al.</i> , 1999; Braasch and Burgermeister, 2002
<i>B. hofmani</i>	Braasch <i>et al.</i> , 1999
<i>B. hyalobianum</i>	Braasch <i>et al.</i> , 1999; Braasch and Burgermeister, 2002
<i>B. leoni</i>	Hoyer <i>et al.</i> , 1998; Braasch <i>et al.</i> , 1999
<i>B. mucronatus</i>	Hoyer <i>et al.</i> , 1998; Iwahori <i>et al.</i> , 1998, 1999; Braasch <i>et al.</i> , 1999; Mota <i>et al.</i> , 1999; Liao <i>et al.</i> , 2000, 2001; Abelleira <i>et al.</i> , 2003; Zheng <i>et al.</i> , 2003
<i>B. poligraphi</i>	Braasch <i>et al.</i> , 1999
<i>B. rainulfi</i>	Braasch <i>et al.</i> , 1999; Braasch and Burgermeister, 2002
<i>B. sexdentati</i>	Hoyer <i>et al.</i> , 1998; Braasch <i>et al.</i> , 1999
<i>B. xylophilus</i>	Hoyer <i>et al.</i> , 1998; Iwahori <i>et al.</i> , 1998, 1999; Braasch <i>et al.</i> , 1999; Mota <i>et al.</i> , 1999; Liao <i>et al.</i> , 2000, 2001; Zheng <i>et al.</i> , 2003
<i>Cactodera cacti</i>	Maafi <i>et al.</i> , 2003
<i>C. estonica</i>	Subbotin <i>et al.</i> , 2000b
<i>Ditylenchus africanus</i>	Wendt <i>et al.</i> , 1995
<i>D. angustus</i>	Ibrahim <i>et al.</i> , 1994a
<i>D. destructor</i>	Wendt <i>et al.</i> , 1993 ^a , 1995
<i>D. dipsaci</i>	Wendt <i>et al.</i> , 1993 ^a , 1995; Zouhar <i>et al.</i> , 2002
<i>D. myceliophagus</i>	Wendt <i>et al.</i> , 1993 ^a , 1995
<i>Globodera pallida</i>	Thiéry and Mugniéry, 1996 ^a ; Gonzalez <i>et al.</i> , 1997; Subbotin <i>et al.</i> , 1999a, 2000a; Fleming <i>et al.</i> , 2000; Grenier <i>et al.</i> , 2001
<i>G. "mexicana"</i>	Thiéry and Mugniéry, 1996 ^a
<i>G. rostochiensis</i>	Gonzalez <i>et al.</i> , 1997; Orui, 1997; Subbotin <i>et al.</i> , 1999a, 2000a; Fleming <i>et al.</i> , 2000; Grenier <i>et al.</i> , 2001; Radivojevic <i>et al.</i> , 2001
<i>G. tabacum</i>	Thiéry and Mugniéry, 1996 ^a ; Fleming <i>et al.</i> , 2000; Subbotin <i>et al.</i> , 2000a
<i>Heterodera arenaria</i>	Subbotin <i>et al.</i> , 1999b, 2000b
<i>H. aucklandica</i>	"
<i>H. australis</i>	Subbotin <i>et al.</i> , 2002
<i>H. avenae</i>	Bekal <i>et al.</i> , 1997; Subbotin <i>et al.</i> , 1999b, 2000b, 2002; Peng <i>et al.</i> , 2000; Zheng <i>et al.</i> , 2000; Maafi <i>et al.</i> , 2003
<i>H. betae</i>	Wouts <i>et al.</i> , 2001; Saïd <i>et al.</i> , 2002
<i>H. cajani</i>	Subbotin <i>et al.</i> , 2000b
<i>H. carotae</i>	Fleming <i>et al.</i> , 2000; Subbotin <i>et al.</i> , 2000b
<i>H. ciceri</i>	Subbotin <i>et al.</i> , 2000b
<i>H. cruciferae</i>	"
<i>H. cyper</i>	"

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Table 8. (continued)

Species	Reference
<i>H. elachista</i>	Orui, 1997; Maafi <i>et al.</i> , 2003
<i>H. fici</i>	Subbotin <i>et al.</i> , 1997, 2000b; Maafi <i>et al.</i> , 2003
<i>H. filipjevi</i>	Bekal <i>et al.</i> , 1997; Subbotin <i>et al.</i> , 1999b, 2000b; Fleming <i>et al.</i> , 2000; Maafi <i>et al.</i> , 2003
<i>H. glycines</i>	Orui, 1997; Szalanski <i>et al.</i> , 1997; Fleming <i>et al.</i> , 2000; Subbotin <i>et al.</i> , 2000b; Zheng <i>et al.</i> , 2000; Maafi <i>et al.</i> , 2003
<i>H. goettingiana</i>	Szalanski <i>et al.</i> , 1997; Fleming <i>et al.</i> , 2000; Subbotin <i>et al.</i> , 2000b; Maafi <i>et al.</i> , 2003
<i>H. hordecalis</i>	Subbotin <i>et al.</i> , 1999b, 2000b; Maafi <i>et al.</i> , 2003
<i>H. humuli</i>	Subbotin <i>et al.</i> , 1997, 2000b; Eroshenko <i>et al.</i> , 2001; Maafi <i>et al.</i> , 2003
<i>H. iri</i>	Subbotin <i>et al.</i> , 2000b
<i>H. latipons</i>	Bekal <i>et al.</i> , 1997; Subbotin <i>et al.</i> , 1999b, 2000b; Maafi <i>et al.</i> , 2003
<i>H. litoralis</i>	Subbotin <i>et al.</i> , 1999b, 2000b
<i>H. mani</i>	Bekal <i>et al.</i> , 1997; Fleming <i>et al.</i> , 2000
<i>H. medicaginis</i>	Subbotin <i>et al.</i> , 2000b; Saïd <i>et al.</i> , 2002
<i>H. mothi</i>	Maafi <i>et al.</i> , 2003
<i>H. oryzicola</i>	Subbotin <i>et al.</i> , 2000b
<i>H. riparia</i>	Subbotin <i>et al.</i> , 1997, 2000b; Eroshenko <i>et al.</i> , 2001
<i>H. salixophila</i>	Subbotin <i>et al.</i> , 2000b
<i>H. schachtii</i>	Szalanski <i>et al.</i> , 1997; Subbotin <i>et al.</i> , 1999b, 2000b; Fleming <i>et al.</i> , 2000; Saïd <i>et al.</i> , 2002; Maafi <i>et al.</i> , 2003
<i>H. trifolii</i>	Orui, 1997; Szalanski <i>et al.</i> , 1997; Subbotin <i>et al.</i> , 2000b; Wouts <i>et al.</i> , 2001; Saïd <i>et al.</i> , 2002; Maafi <i>et al.</i> , 2003
<i>H. turcomanica</i>	Maafi <i>et al.</i> , 2003
<i>H. urticae</i>	Subbotin <i>et al.</i> , 2000b
<i>H. vallicola</i>	Eroshenko <i>et al.</i> , 2001
<i>H. zaeae</i>	Szalanski <i>et al.</i> , 1997
<i>Longidorus arthensis</i>	Lamberti <i>et al.</i> , 2001b
<i>L. elongatus</i>	Lamberti <i>et al.</i> , 1999b, 2001b
<i>L. helveticus</i>	Lamberti <i>et al.</i> , 2001b
<i>L. macrosoma</i>	"
<i>L. pauli</i>	Lamberti <i>et al.</i> , 1999b
<i>L. profundorum</i>	Lamberti <i>et al.</i> , 2001b
<i>L. raskii</i>	"
<i>Meloidodera alni</i>	Subbotin <i>et al.</i> , 2000b
<i>Meloidogyne arenaria</i>	Orui, 1998
<i>M. camelliae</i>	"
<i>M. chitwoodi</i>	Zijlstra <i>et al.</i> , 1995, 1997; Schmitz <i>et al.</i> , 1998; Waeyenberge and Moens, 2001
<i>M. fallax</i>	"
<i>M. hapla</i>	Zijlstra <i>et al.</i> , 1995, 1997; Orui, 1998; Schmitz <i>et al.</i> , 1998
<i>M. incognita</i>	"
<i>M. javanica</i>	Zijlstra <i>et al.</i> , 1995; Orui, 1998; Schmitz <i>et al.</i> , 1998
<i>M. mali</i>	Orui, 1998
<i>M. marylandi</i>	"
<i>M. naasi</i>	Schmitz <i>et al.</i> , 1998
<i>M. suginamiensis</i>	Orui, 1998
<i>Nacobbus aberrans</i>	Ibrahim <i>et al.</i> , 1997 ^a ; Reid <i>et al.</i> , 2003
<i>Paralongidorus halepensis</i>	Lamberti <i>et al.</i> , 1999b
<i>Pratylenchus agilis</i>	Waeyenberge <i>et al.</i> , 2000
<i>P. bolivianus</i>	"
<i>P. brachyurus</i>	Orui and Mizukubo, 1999c; Waeyenberge <i>et al.</i> , 2000
<i>P. coffeae</i>	Orui, 1996; Orui and Mizukubo, 1999a, c; Pourjame <i>et al.</i> , 1999; Waeyenberge <i>et al.</i> , 2000
<i>P. crenatus</i>	Orui and Mizukubo, 1999b, c; Waeyenberge <i>et al.</i> , 2000
<i>P. fallax</i>	Waeyenberge <i>et al.</i> , 2000
<i>P. goodeyi</i>	"
<i>P. japonicus</i>	Mizukubo <i>et al.</i> , 1997
<i>P. loosi</i>	Pourjame <i>et al.</i> , 1999; Waeyenberge <i>et al.</i> , 2000
<i>P. macrostylus</i>	Mizukubo <i>et al.</i> , 1997
<i>P. mediterraneus</i>	Waeyenberge <i>et al.</i> , 2000

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Table 8. (continued)

Species	Reference
<i>P. negletus</i>	Hafez <i>et al.</i> , 1999; Orui and Mizukubo, 1999a, b, c; Waeyenberge <i>et al.</i> , 2000
<i>P. penetrans</i>	Orui, 1996; Orui and Mizukubo, 1999a, b, c; Waeyenberge <i>et al.</i> , 2000
<i>P. pratensis</i>	Waeyenberge <i>et al.</i> , 2000
<i>P. pseudocoffeae</i>	"
<i>P. scribneri</i>	"
<i>P. subranjani</i>	"
<i>P. thornei</i>	"
<i>P. vulnus</i>	Orui, 1996; Orui and Mizukubo, 1999a; Waeyenberge <i>et al.</i> , 2000
<i>P. zaeae</i>	Orui and Mizukubo, 1999b, c; Waeyenberge <i>et al.</i> , 2000
<i>Punctodera punctata</i>	Fleming <i>et al.</i> , 2000
<i>Radopholus similis</i>	Sarah, 1997; Elbadri <i>et al.</i> , 2002
<i>Xiphidiorus minor</i>	Lamberti <i>et al.</i> , 1999a
<i>Xiphinema americanum</i>	Vrain <i>et al.</i> , 1992 ^a ; Vrain, 1993; Knoetze <i>et al.</i> , 2000
<i>X. bricolensis</i>	Vrain <i>et al.</i> , 1992 ^a ; Vrain, 1993
<i>X. chambersi</i>	Lamberti <i>et al.</i> , 2002a
<i>X. citricolum</i>	Lamberti <i>et al.</i> , 2002b
<i>X. diffusum</i>	Knoetze <i>et al.</i> , 2000
<i>X. diversicaudatum</i>	Lamberti <i>et al.</i> , 1999c
<i>X. elongatum</i>	Knoetze <i>et al.</i> , 2000
<i>X. floridiae</i>	Lamberti <i>et al.</i> , 2002b
<i>X. index</i>	Knoetze <i>et al.</i> , 2000
<i>X. italiae</i>	Lamberti <i>et al.</i> , 1999c; Knoetze <i>et al.</i> , 2000
<i>X. laevistriatum</i>	Lamberti <i>et al.</i> , 2002b
<i>X. naturale</i>	Lamberti <i>et al.</i> , 2002a
<i>X. pachtaicum</i>	Lamberti <i>et al.</i> , 1999c
<i>X. pacificum</i>	Vrain <i>et al.</i> , 1992 ^a ; Vrain, 1993
<i>X. rivesi</i>	"
<i>X. simile</i>	Lamberti <i>et al.</i> , 1999c
<i>X. taylori</i>	"
<i>X. vuittenezi</i>	"
<i>X. vulgare</i>	Lamberti <i>et al.</i> , 2001a

^a□ Cited in Powers and Fleming (1998).

Table 9. Plant-parasitic nematodes species characterized by RAPD-PCR.

Species	Reference
<i>Aphelenchus avenae</i>	Ali <i>et al.</i> , 1999a
<i>Bursaphelenchus mucronatus</i>	Braasch <i>et al.</i> , 1995; Irdani <i>et al.</i> , 1995 ^a ; Kusano <i>et al.</i> , 1999; Irdani, 2000; Wang <i>et al.</i> , 2001
<i>B. fraudulentus</i>	Braasch <i>et al.</i> , 1995
<i>B. sexdentati</i>	Irdani, 2000
<i>B. tusciae</i>	Braasch <i>et al.</i> , 1995; Irdani <i>et al.</i> , 1995 ^a ; Kusano <i>et al.</i> , 1999; Wang <i>et al.</i> , 2001
<i>B. xylophilus</i>	"
<i>Ditylenchus dipsaci</i>	Esquibet <i>et al.</i> , 1998
<i>Globodera "mexicana"</i>	Thiéry <i>et al.</i> , 1997 ^a
<i>G. pallida</i>	Fleming <i>et al.</i> , 1993; Roosien <i>et al.</i> , 1993 ^a ; Chacon <i>et al.</i> , 1994 ^a ; Folkertsma <i>et al.</i> , 1994 ^a , 1996a; Pastrik <i>et al.</i> , 1995 ^a ; Burrows <i>et al.</i> , 1996 ^a ; Blok <i>et al.</i> , 1997a; Fullaondo <i>et al.</i> , 1997 ^a , 1999; Thiéry <i>et al.</i> , 1997 ^a ; Bendezu <i>et al.</i> , 1998; Subbotin <i>et al.</i> , 1999b; Bendezu and Evans, 2001; Conceição <i>et al.</i> , 2003
<i>G. rostochiensis</i>	Fleming <i>et al.</i> , 1993; Roosien <i>et al.</i> , 1993 ^a ; Chacon <i>et al.</i> , 1994 ^a ; Folkertsma <i>et al.</i> , 1994 ^a ; Blok <i>et al.</i> , 1997a; Fullaondo <i>et al.</i> , 1997 ^a , 1999; Thiéry <i>et al.</i> , 1997 ^a ; Bendezu <i>et al.</i> , 1998; Subbotin <i>et al.</i> , 1999b; Bendezu and Evans, 2001; Conceição <i>et al.</i> , 2003

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Table 9. Plant-parasitic nematodes species characterized by RAPD-PCR.

Species	Reference
<i>G. tabacum</i>	Thiéry <i>et al.</i> , 1997 ^a
<i>Heterodera avenae</i>	López-Braña <i>et al.</i> , 1996 ^a ; Romero <i>et al.</i> , 1996
<i>H. cruciferae</i>	Caswell-Chen <i>et al.</i> , 1992 ^a
<i>H. daverti</i>	Ambrogioni and Irdani, 2001
<i>H. glycines</i>	Erickson <i>et al.</i> , 1993; Li <i>et al.</i> , 1996 ^a ; Silva <i>et al.</i> , 2000; Zheng <i>et al.</i> , 2000
<i>H. schachtii</i>	Caswell-Chen <i>et al.</i> , 1992 ^a ; Kaplan <i>et al.</i> , 1999
<i>H. trifolii</i>	Ambrogioni and Irdani, 2001
<i>H. trifolii</i> f. sp. beta	"
<i>Meloidogyne arenaria</i>	Cenis, 1993 ^a ; Castagnone-Sereno <i>et al.</i> , 1994 ^a ; Guirao <i>et al.</i> , 1995 ^a ; Blok <i>et al.</i> , 1997b; Yu <i>et al.</i> , 1998; Lecouls <i>et al.</i> , 1999; Orui, 1999; Randig <i>et al.</i> , 2001; Xu <i>et al.</i> , 2001
<i>M. camelliae</i>	Orui, 1999
<i>M. chitwoodi</i>	Williamson <i>et al.</i> , 1997 ^a ; Waeyenberge and Moens, 2001
<i>M. fallax</i>	Waeyenberge and Moens, 2001
<i>M. hapla</i>	Cenis, 1993 ^a ; Castagnone-Sereno <i>et al.</i> , 1994 ^a ; Guirao <i>et al.</i> , 1995 ^a ; Blok <i>et al.</i> , 1997b; Williamson <i>et al.</i> , 1997 ^a ; Yu <i>et al.</i> , 1998; Orui, 1999; Waeyenberge and Moens, 2001
<i>M. incognita</i>	Cenis, 1993 ^a ; Castagnone-Sereno <i>et al.</i> , 1994 ^a ; Guirao <i>et al.</i> , 1995 ^a ; Blok <i>et al.</i> , 1997b; Yu <i>et al.</i> , 1998; Orui, 1999; Swain <i>et al.</i> , 1999; Randig <i>et al.</i> , 2001; Xu <i>et al.</i> , 2001; Meher <i>et al.</i> , 2003
<i>M. javanica</i>	Powers <i>et al.</i> , 1991 ^b ; Cenis, 1993 ^a ; Castagnone-Sereno <i>et al.</i> , 1994 ^a ; Guirao <i>et al.</i> , 1995 ^a ; Blok <i>et al.</i> , 1997b; Carneiro <i>et al.</i> , 1998; Yu <i>et al.</i> , 1998; Orui, 1999; Boiteux <i>et al.</i> , 2000; Randig <i>et al.</i> , 2001; Xu <i>et al.</i> , 2001
<i>M. mali</i>	Orui, 1999
<i>M. marylandi</i>	"
<i>M. mayaguensis</i>	Blok <i>et al.</i> , 1997b
<i>M. suginamensis</i>	Orui, 1999
<i>Nacobbus aberrans</i>	Ibrahim <i>et al.</i> , 1997 ^a
<i>Radopholus similis</i>	Hahn <i>et al.</i> , 1994 ^a , 1996; Siddiqi and Hahn, 1995; Kaplan and Opperman, 1997; Sarah, 1997
<i>R. bridgei</i>	Siddiqi and Hahn, 1995; Hahn <i>et al.</i> , 1996
<i>R. citri</i>	Hahn <i>et al.</i> , 1996

^a□Cited in Powers and Fleming (1998).

^b□Cited in Curran and Robinson (1993).

Table 10. Plant-parasitic nematodes species characterized by other DNA-based techniques.

Technique	Species	Reference
Microsatellites or Single Sequence Repeats (SSRs)	<i>Globodera "mexicana"</i>	Thiéry and Mugniéry, 2000
	<i>G. pallida</i>	Blok and Phillips, 1995 ^a ; Fullaondo <i>et al.</i> , 1997 ^a ; Thiéry and Mugniéry, 2000
	<i>G. rostochiensis</i>	Blok and Phillips, 1995 ^a ; Fullaondo <i>et al.</i> , 1997 ^a
Satellite DNA (SatDNA)	<i>Bursaphelenchus xylophilus</i>	Tarès <i>et al.</i> , 1994 ^a ; Abad, 2000
	<i>Meloidogyne arenaria</i>	Castagnone-Sereno <i>et al.</i> , 2000
	<i>M. chitwoodi</i>	Castagnone-Sereno <i>et al.</i> , 1998, 1999; Castagnone-Sereno, 2000
	<i>M. exigua</i>	Randig <i>et al.</i> , 2002b
	<i>M. fallax</i>	Castagnone-Sereno <i>et al.</i> , 1999; Castagnone-Sereno, 2000
	<i>M. hapla</i>	Castagnone-Sereno <i>et al.</i> , 1995a, 1998; Piotte <i>et al.</i> , 1995 ^a
Sequence Characterized	<i>Meloidogyne arenaria</i>	Zijlstra <i>et al.</i> , 2000; Fourie <i>et al.</i> , 2001

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Table 10. (continued)

Technique	Species	Reference
Amplified Regions (SCARs)	<i>M. chitwoodi</i>	Zijlstra, 2000; Fourie <i>et al.</i> , 2001
	<i>M. exigua</i>	Randig <i>et al.</i> , 2002a
	<i>M. fallax</i>	Zijlstra, 2000; Fourie <i>et al.</i> , 2001
	<i>M. hapla</i>	
	<i>M. incognita</i>	Zijlstra <i>et al.</i> , 2000; Fourie <i>et al.</i> , 2001; Randig <i>et al.</i> , 2002a
	<i>M. javanica</i>	Zijlstra <i>et al.</i> , 2000; Fourie <i>et al.</i> , 2001
	<i>M. paranaensis</i>	Randig <i>et al.</i> , 2002a
PCR-Single-Strand Conformational Polymorphism (PCR-SSCP)	<i>Bursaphelenchus mucronatus</i>	Zhang <i>et al.</i> , 2001
	<i>B. xylophilus</i>	
	<i>Ditylenchus dipsaci</i>	Zouhar <i>et al.</i> , 2002
	<i>Globodera pallida</i>	Clapp <i>et al.</i> , 2000
	<i>G. rostochiensis</i>	
	<i>Heterodera arenaria/avenae</i>	Clapp <i>et al.</i> , 2000
	<i>H. ciceri</i>	
	<i>H. daverti</i>	
	<i>H. hordecalis</i>	
	<i>H. mani</i>	
	<i>H. schachtii</i>	
	<i>H. trifolii</i>	
<i>Meloidogyne ardenensis</i>		
	<i>M. duytsi</i>	
	<i>M. maritima</i>	
DNA-microarrays	<i>Heterodera glycines</i>	De Boer <i>et al.</i> , 2002

^a□Cited in Powers and Fleming (1998).

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