Journal of Nematology 30(3):313–340. 1998.

Review of *Pasteuria penetrans:* Biology, Ecology, and Biological Control Potential[1]

Z. X. Chen and D. W. Dickson[2]

Abstract: Pasteuria penetrans is a mycelial, endospore-forming, bacterial parasite that has shown great potential as a biological control agent of root-knot nematodes. Considerable progress has been made during the last 10 years in understanding its biology and importance as an agent capable of effectively suppressing root-knot nematodes in field soil. The objective of this review is to summarize the current knowledge of the biology, ecology, and biological control potential of *P. penetrans* and other *Pasteuria* members. *Pasteuria* spp. are distributed worldwide and have been reported from 323 nematode species belonging to 116 genera of free-living, predatory, plant-parasitic, and entomopathogenic nematodes. Artificial cultivation of *P. penetrans* has met with limited success; large-scale production of endospores depends on in vivo cultivation. Temperature affects endospore attachment, germination, pathogenesis, and completion of the life cycle in the nematode pseudocoelom. The biological control potential of *Pasteuria* spp. have been demonstrated on 20 crops; host nematodes include *Belonolaimus longicaudatus, Heterodera* spp., *Meloidogyne spp.,* and *Xiphinema diversicaudatum. Pasteuria penetrans* plays an important role in some suppressive soils. The efficacy of the bacterium as a biological control agent has been examined. Approximately 100,000 endospores/g of soil provided immediate control of the peanut root-knot nematode, whereas 1,000 and 5,000 endospores/g of soil each amplified in the host nematode and became suppressive after 3 years.

Key words: bacterium, *Belonolaimus longicaudatus,* biological control, biology, cyst nematode, dagger nematode, ecology, endospore, *Heterodera* spp., *Meloidogyne* spp., nematode, *Pasteuria penetrans,* review, root-knot nematode, sting nematode, *Xiphinema diversicaudatum.*

HISTORICAL BACKGROUND

The genus *Pasteuria* Metchnikoff, 1888 was first described as a bacterial parasite of water fleas, *Daphnia magna* Straus. Metchnikoff (1888) named the bacterium *Pasteuria ramosa* and stated, "*Pasteuria* sp. was able to undergo as many as five longitudinal divisions at the same time, giving it a characteristic fan shape" (Sayre, 1993). Metchnikoff (1888) also tried to culture the bacterium but was unsuccessful.

Metchnikoff's paper, with its concept of longitudinal division of a microorganism and the accompanying drawings that showed "stalked" spores, intrigued other investigators. The bacterium, however, was not found again; consequently, Metchnikoff's work was considered erroneous until the 1970s (Hirsh, 1972; Migula, 1900), when Sayre et al. (1977, 1979) reported its rediscovery in *Moina rectirostris* Leydig, a member of Daphnidae.

Cobb (1906) was the first to report an organism resembling *Pasteuria* sp. infecting a nematode, *Dorylaimus bulbiferus.* He mistakenly suggested that the spores inside *D. bulbiferus* were "perhaps monads" of a parasitic sporozoan. The idea that these organisms were sporozoan parasites remained in the literature for nearly 70 years. Micoletzky (1925) suggested their placement in *Duboscqia* Perez, 1908. In 1940, a parasite from *Pratylenchus pratensis* (de Man) Filipjev was named *Duboscqia penetrans* on the assumption that it was similar to the nematode parasite described by Micoletzky (Thorne, 1940). It was not until the mid-1970s, when the nematode parasite was examined with electron microscopy, that its relatedness to bacteria rather than protozoa was recognized, and it was named *Bacillus penetrans* (Mankau 1975a, 1975b). However, *B. penetrans* was not included in the approved lists of bacterial names (Skerman et al., 1980).

Sayre and Starr (1985) drew attention to the fact that *B. penetrans* resembled the actinomycete *Pasteuria ramosa* (Metchnikoff, 1888; Sayre et al., 1979) and renamed the organism *Pasteuria penetrans.* Recently, Ebert

---

Received for publication 5 August 1997.

[1] Florida Agricultural Experiment Station Journal Series No. R-05899. Supported in part by a grant from the Southern Region IPM Grant No. 93-34103-8396.

[2] Post-Doctoral Research Associate and Professor, Entomology and Nematology Department, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL 32611-0620.

E-mail: dwd@gnv.ifas.ufl.edu

et al. (1996) rediscovered *P. ramosa* infecting *Daphnia magna,* the organism with which Metchnikoff originally worked, and the evidence presented suggested that the parasite infecting *Moina rectirostris* (Sayre et al., 1977, 1979) was not the type species of *Pasteuria* and belonged to another species. The genus *Pasteuria* as described by Metchnikoff has been conserved (Judicial Commission of the International Committee on Systematic Bacteriology, 1986; Starr et al., 1983). Current research emphasis is mostly on species of *Pasteuria* that parasitize plant-parasitic nematodes.

MEMBERS OF *PASTEURIA*

Pasteuria species are gram-positive, dichotomously branched, endospore-forming bacteria with septate mycelium (Mankau and Imbriani, 1975). Endospores are a nonmotile form of the organism that lie in the soil matrix. When a suitable nematode host enters its domain, the endospore attaches to the nematode's cuticle. One to several hundred endospores may attach per nematode; however, a single endospore is sufficient to infect the nematode host. The infection process involves the formation of a germ tube that penetrates the nematode body wall. Primary colonies are formed from the germinating tube after it penetrates inside the nematode pseudocoelom. These colonies are shaped like cauliflower florets or clusters of elongated grapes. Daughter colonies are formed by fragmentation of the mother colonies, and the daughter colonies in turn produce clusters of sporangia. The terminal hyphae of the mycelium elongate to form sporangia, and these give rise to endospores. Endospores are resistant to desiccation.

Pasteuria spp. have not been grown successfully in pure culture. Species of the genus must be cultured on a nematode or water-flea host. Four species of *Pasteuria* have been described; they are differentiated by their host preference, developmental characteristics, and size and shape of sporangia and endospores (Sayre and Starr, 1989). *Pasteuria ramosa,* which parasitizes water fleas of the genus *Daphnia,* is the type species of the genus (Ebert et al., 1996). The other three species of *Pasteuria* are parasites of plant-parasitic nematodes: *P. penetrans* on *Meloidogyne spp., P. thornei* on *Pratylenchus* spp., and *P. nishizawae* on cyst nematodes of the genera *Heterodera* and *Globodera* (Sayre and Starr, 1989). Two undescribed species of *Pasteuria* have been reported, one from *Heterodera goettingiana* Liebscher in Germany (Sturhan et al., 1994) and the other from *Belonolaimus longicaudatus* Rau in Florida (Giblin-Davis et al., 1990, 1995).

The taxon *Pasteuria penetrans* is often mistakenly used to represent other *Pasteuria* members (Ciancio, 1995b; Ciancio et al., 1992; Fattah et al., 1989; Singh and Dhawan, 1994; Vovlas et al., 1993). *Pasteuria penetrans* originally was suggested to mean 'members of *P. penetrans* group' (Sayre and Starr, 1985), but the species was later delineated to *P. penetrans sensu stricto,* which infects *M. incognita,* and *P. thornei,* which infects *Pratylenchus* spp. (Starr and Sayre, 1988). *Pasteuria penetrans* now is a valid taxon (Sayre and Starr, 1989), which according to the nomenclatural code (Lapage et al., 1975) must refer only to the parasite of *M. incognita.* We suggest that other indefinitive isolate(s) be addressed as *Pasteuria* sp. (spp.), or *Pasteuria* member(s).

There is still considerable confusion about the taxonomy of *Pasteuria* spp. because of the criteria currently used for differentiating species within the genus. These criteria (ultrastructure, morphology, life cycle, and host preference), once seemingly explicit, are challenged by the numerous new isolates of *Pasteuria* spp. collected from plant and soil nematodes. Some isolates of *Pasteuria* spp. display cross-generic parasitism of nematodes. Also, isolates from different nematode genera often appear superficially similar under light microscopy in regard to development within the nematode's pseudocoelom and endospore morphology. Furthermore, recent evidence indicates that morphology of sporangia and endospores of 69 *Pasteuria* members were correlated with some host characters (Ciancio, 1995a). Diameter of sporangia varied from 1.5 µm for an isolate from *Criconemella* sp. in Florida

(Z. X. Chen, pers. obs.) to 8 µm for an isolate from *Axonchium valvulatum* in Sri Lanka (Ciancio et al., 1994). Distinct groupings of *Pasteuria* spp. by sizing sporangia and endospores were not obtainable. It is apparent that the taxonomy of *Pasteuria* spp. will remain unclear until more efforts are allocated to the problem.

Some isolates of *Pasteuria* spp. display cross-generic host ranges and varying biological and ecological characteristics. Isolates of *P. penetrans* reported from China (Pan et al., 1993) and the United States (Mankau, 1975a; Mankau and Prasad, 1972; Oostendorp et al., 1990) parasitize both *Meloidogyne* spp. and *Pratylenchus* spp. An isolate reported from India parasitizes both *Heterodera* spp. and *M. incognita* (Bhattacharya and Swarup, 1988), whereas another Indian isolate parasitizes *Globodera* spp., *Heterodera* spp., and *Rotylenchulus reniformis* (Sharma and Davies, 1996).

Cross-generic attachment of *Pasteuria* sp. has been confirmed by laboratory experiments. The endospores obtained from second-stage juveniles (J2) of *H. avenae* attached to J2 of *H. schachtii, H. glycines, Globodera rostochiensis, G. pallida,* and *M. javanica,* but the completion of their development in females was not observed (Davies et al., 1990). Hewlett and Dickson (1994) tested endospores of *P. penetrans* collected from *M. arenaria* race 1 females for attachment to other nematode species. The endospores attached to *Aphelenchoides* sp., *Criconemella* sp., an unknown *Meloidogyne* sp., and *Tylenchus* sp., but it was not ascertained whether the bacterium completed its development in the latter three species. Many attempts were made to infect *Aphelenchoides* sp., but these attempts never met with success. Endospores of *Pasteuria* sp. obtained from *H. goettingiana* J2 were able to attach to J2 of *Cactodera cacti, G. artemisiae, G. pallida, G. rostochiensis, H. carotae, H. cruciferae, H. filipjevi, H. glycines, H. humuli, H. schachtii, H. trifolii, H. urticae,* and *Meloidodera alni* (Winkelheide and Sturhan, 1996), but, again, development of the bacterium in each of these species was not determined.

An isolate from the citrus nematode, *Tylenchulus semipenetrans,* appeared to be host-specific (Kaplan, 1994). Endospores of the isolate did not attach to the body of *M. incognita, M. javanica, Radopholus citrophilus,* or *R. similis,* whereas several *T. semipenetrans* J2 and males were observed with endospores developing inside their bodies after 20 days' incubation.

Pasteuria spp. are reported to selectively parasitize different developmental stages of nematodes (Abrantes and Vovlas, 1988; Davies et al., 1990; Noel and Stanger, 1994). Davies et al. (1990) reported a *Pasteuria* sp. isolate that completed its life cycle in J2 of *Heterodera avenae* but not in females and cysts. Abrantes and Vovlas (1988) reported an isolate of *Pasteuria* sp. parasitizing juveniles and males of *Meloidogyne* sp. An Illinois isolate of *Pasteuria* sp. was first reported to infect both J2 and males of *Heterodera glycines* but not females (Noel and Stanger, 1994); however, endospore-filled females are now recognized (Atibalentja and Noel, 1997). In *H. goettingiana, Pasteuria* sp. exclusively parasitized J2 (Sturhan et al., 1994), while in *Tylenchulus semipenetrans* J2 and males became infected with *Pasteuria* sp. (Kaplan, 1994).

Pasteuria penetrans has been reported to develop endospores only in females of *Meloidogyne* spp. (Sayre and Starr, 1989). However, endospore-filled J2 of a *Meloidogyne* sp. from turfgrass in south Florida has been reported (Giblin-Davis et al., 1990). Recently, we observed a high proportion of spore-filled J2 from populations of *Meloidogyne* sp. on turfgrass and *Meloidogyne* spp. (mixed population of *M. incognita* and *M. javanica*) on tobacco in northern Florida (D. W. Dickson, pers. obs.). Hatz and Dickson (1992) observed males of *M. arenaria* race 1 filled with mature endospores when infected tomato roots were incubated at temperatures above 35 °C. These workers suggested that the endospore-filled males were a result of sex reversal. No males with a single gonad were observed to be infected by *P. penetrans.* Furthermore, no attachment of endospores was observed on males of *M. arenaria* race 1 following exposure of the males to seven isolates of *P. penetrans* from

Florida (Freitas, 1997). However, all seven isolates attached readily to J2 of *M. arenaria* race 1. Page and Bridge (1985) reported an isolate of *Pasteuria* that developed mature endospores in juveniles, males, and females of *M. acronea;* however, the apparent thickness of the germ tube in their figure (ca. 5 µm in diameter) would be unusual for a member of *Pasteuria.*

Several genera of nematodes may be parasitized by *Pasteuria* members at the same field site. In a field survey in Puerto Rico, both *Pratylenchus* spp. and *Meloidogyne* spp. were parasitized by *Pasteuria* members, but there was no evidence that the *Pasteuria* member that parasitized *Pratylenchus* sp. also parasitized the *Meloidogyne* spp. or vice versa (Vargas and Acosta, 1990). Second-stage juveniles of *Heterodera avenae,* and juveniles and adults of *Pratylenchus* sp. and *Tylenchorhynchus* sp., were infected with *Pasteuria* members in a nematode-suppressive soil in England (Davies et al., 1990). Although the endospores from the three nematode hosts were similar in size, it was not clear whether they belonged to a single species of *Pasteuria.* Similarly, juveniles and adults of *Aphelenchoides* sp., *Helicotylenchus* sp., and *Pratylenchus* sp. were filled with *Pasteuria* endospores at an experimental site that had been infested previously with *P. penetrans* endospores (Z. X. Chen, pers. obs.). A survey of sugarcane fields in South Africa revealed that endospores of *Pasteuria* members attached to species of *Helicotylenchus, Meloidogyne, Pratylenchus, Scutellonema,* and *Xiphinema* (Spaull, 1981). Small endospores (2.9–4.4 × 1–2 µm) from *H. dihystera, M. incognita* J2, and *P. zeae* were assumed to be *P. penetrans,* and larger endospores (4.3–6.6 × 2.0 µm) from *Scutellonema* sp. and *Xiphinema* sp. were considered to be a different species. In a survey of turfgrass in southern Florida, the following nematodes were parasitized by *Pasteuria* spp. at various sites: *Belonolaimus longicaudatus, Helicotylenchus microlobus,* and *Meloidogyne* spp. in Collier County; *B. longicaudatus, Hoplolaimus galeatus, Meloidogyne* spp., and *Tylenchorhynchus annulatus* in Broward County; and *H. microlobus* and *Meloidogyne* spp. in Palm Beach County (Giblin-Davis et al., 1990).

In some cases two different isolates of *Pasteuria* spp. appeared to parasitize a single nematode species at the same location. Giblin-Davis et al. (1990) reported large-endospore and small-endospore isolates of *Pasteuria* spp. parasitizing both *B. longicaudatus* and *H. galeatus* in Broward County, Florida. A *Criconemella* sp. was parasitized by two morphologically different isolates of *Pasteuria* spp. in Florida (T. E. Hewlett, pers. comm.). These distinct endospores obtained from the same host nematode at the same location most likely belonged to different species of *Pasteuria.*

The current uncertainty in taxonomy of *Pasteuria* members probably will not be resolved until the bacterial genome properties, such as size, base composition, and DNA-sequence similarity, are revealed by hybridization. Recent success in DNA sequencing of *P. ramosa* might facilitate the molecular taxonomy of *Pasteuria* spp. (Ebert et al., 1996). In addition, artificial cultivation is crucial to helping us understand the complex biology and taxonomy of *Pasteuria* spp., but such cultivation has met with only limited success.

BIOLOGY OF *PASTEURIA PENETRANS*

Life cycle: The first step in the life cycle of *P. penetrans* is the attachment of endospores to the cuticle of J2 of *Meloidogyne* spp. This occurs when the J2 move through soil infested with endospores of *P. penetrans.* Endospores that attach to the nematode cuticle germinate within 4 to 10 days after the endospore-encumbered J2 enters a plant root and begins to feed (Sayre and Wergin, 1977b; Serracin et al., 1997). The germ tube emerges through a central opening in the basal layer of the endospore and penetrates the nematode body wall. The process of penetration seems to be enzymatic (Mankau, 1975a, 1975b; Mankau et al., 1976), but the trigger mechanism for germ tube penetration is unknown. After entering the nematode pseudocoelom, the germ tube develops into a cauliflower-like microcolony consisting of a dichotomously branched septate mycelium. Daughter colonies form when the intercalary cells in the microcolony lyse (Sayre and Starr, 1989). Due to unknown triggers, the colony fragments, and the terminal cells of each fragment enlarge and undergo sporogenesis. Eventually, doublets and quartets of developing sporangia predominate in the nematode body cavity and finally separate into single sporangia, each containing an endospore (Hatz and Dickson, 1992; Serracin et al., 1997). The mature endospores are released into soil when the plant root, with its complement of parasitized root-knot nematode females, decomposes.

Sporogenesis: Although the endospore ultrastructure of each *Pasteuria* spp. appears to be unique, all species that have been studied share the typical sequence of a gram-positive, endospore-forming bacterium (Chen et al., 1997b; Sayre, 1993). Sporogenesis has been divided into seven stages (Figs. 6,7, and 9 in Chen et al., 1997b). In stage I, mycelial terminal cells elongate and become fully septate. Stage II is characterized by the formation of a transverse septum that separates the forespore from the endospore mother cell. In stage III, the forespore is engulfed by the endospore mother cell and condensation of the forespore protoplasm occurs. Parasporal fibers are initiated in stage III. Formation of the cortex, coat, and exosporium occurs in stages IV to VI. Mature endospores are formed in stage VII. The dichotomously branched vegetative mycelium of *P. penetrans* has been assigned as stage 0, which is similar to the vegetative cells of *Bacillus* spp.

Systematics and phylogeny: Modern bacterial systematics depends on both phenotypic and molecular biological characters. The phenotypic characters are currently more important than molecular biological characters in classification and identification of prokaryotes. In recent years, nucleic-acid techniques have been used to determine bacterial genome properties, such as size, base composition, and DNA-sequence similarity as revealed by hybridization. It is now commonly accepted that bacteria with DNA base compositions differing by more than 10 mol percent of guanine (G) plus cytosine (C) content (%GC) should not be regarded as members of the same genus, and populations differing by more than 5% GC values should not be regarded as the same species (Bull et al., 1992). A genomic method of separation for species is based on strains having ≥70% relatedness and ≥5% divergence of DNA; both parameters must be used (Goodfellow and O'Donnell, 1993).

Currently, endospore-forming bacteria are placed in 13 genera, which are separated by morphology, physiology, and genetic diversity (Table 1). When the %GC rule is applied, the three genera *Bacillus, Clostridium,* and *Desulfotomaculum* are heterogeneous. Because *Pasteuria* spp. have not been cultured axenically, their DNA base composition remains unknown. However, some molecular evidence indicates that *P. penetrans* is a deeply rooted member of the *Clostridium-Bacillus* line of descent, neither related to the actinomycetes nor closely related to the true endospore-formers (Berkeley and Ali, 1994). The 16S rDNA of *P. ramosa* was sequenced and compared with those of other endospore-forming bacteria using maximum likelihood and maximum parsimony analysis (Ebert et al., 1996). *Pasteuria ramosa* belongs to the low GC branch of eubacteria and is phylogenetically close to *Alicyclobacillus cycloheptanicus, A. acidocaldarius,* and *Bacillus tusciae.* Recently, the 16S rDNA of *P.*

TABLE 1. Described genera of endospore-forming bacteria and their DNA base composition.[a]

Genus	Mol % GC[b]
Alicyclobacillus	52–60
Amphibacillus	36–38
Bacillus	32–69
Clostridium	22–54
Desulfotomaculum	38–52
Sporohalobacter	30–32
Sporolactobacillus	38–40
Sporosarcina	40–42
Sulfobacillus	54
Syntrophosphora	38
Thermoactinomyces	52–55

[a] From Berkeley and Ali, 1994.

[b] Mol %GC = mol % guanine (G) plus cytosine (C) content; no information available for *Oscillospira* and *Pasteuria.*

penetrans isolate P-100 that originated from an unknown *Meloidogyne* sp. in Florida was sequenced and showed a 92% similarity with *P. ramosa* (J. Anderson, pers. comm.).

Host records and geographical distribution: From comprehensive reviews, we find host records of *Pasteuria*-like organisms associated with 196 species of soilborne nematodes belonging to 96 genera, from 51 countries on five continents and on various islands in the Atlantic, Pacific, and Indian oceans (Ciancio et al., 1994; Sayre and Starr, 1988; Sturhan, 1988). An updated host nematode record list includes 20 new genera, 127 new species plus unidentified species, and 29 new countries (Table 2). The new host records include free-living, predacious, plant-parasitic, and entomopathogenic (*Steinernema glaseri*) nematodes (K. Nguyen, pers. comm.).

Very little research emphasis has been directed to understanding the mechanism of the cosmopolitan distribution of *Pasteuria* spp. A survey in the Hawaiian Islands may provide a unique insight for the distribution and dispersal of *Pasteuria* spp. (Ko et al., 1995). Occurrence of *Pasteuria* spp. was more abundant in lowlands (moist-wet areas, <900 m in elevation) and on the older islands of Kauai and Oahu than in subalpine and alpine regions (dry areas, >900 m in elevation) and on the young islands of Maui and Hawaii. *Pasteuria* spp. were not found in areas with a mean annual temperature below 10 °C, and the occurrence was more abundant in areas with a mean annual temperature >21 °C compared with 10 °C to 21 °C. *Pasteuria* spp. also were more frequently associated with introduced plant species than endemic plants (Ko et al., 1995). These results suggest an ancient presence of *Pasteuria* spp. in the Hawaiian Islands and an enhanced dispersal of *Pasteuria* spp. by human activities.

Endospore attachment and host preference: Most reports on *Pasteuria* spp. are based on attachment of endospores to the cuticle of nematodes rather than parasitism, where it is established that the bacterium develops and produces endospores inside the nematode's pseudocoelom. Host specificity should be based on established parasitism, whereby a given parasite-isolate infects a nematode, develops, and produces viable mature endospores. We use the term 'host preference' to cover the context of endospore attachment and host specificity.

Starr and Sayre (1988) concluded that the host range of *P. penetrans* isolates is limited to *Meloidogyne* spp. Stirling (1985) speculated that host preference of *P. penetrans* might be related to nematode populations rather than species. Recent studies showed that *P. penetrans* can produce heterogeneous endospores (Davies et al., 1994; Davies and Redden, 1997). These heterogeneous subpopulations of endospores showed preferences to various nematode populations. Therefore, *P. penetrans* may develop numerous genomic variations that undergo a host-adoptive process that allows endospores to attach and infect nematodes present in a given environment (Davies et al., 1994).

Host preference of a particular isolate of *Pasteuria* sp. can be induced experimentally to shift from one host to another by continually propagating the bacterium on a new host nematode (Davies et al., 1988b; Oostendorp et al., 1990). However, studies with some isolates from *M. javanica* and *M. incognita* showed that endospore attachment is not always related to the species from which the endospores were obtained, nor to the species of the recipient nematode (Stirling, 1985).

The true nature of host preferences among isolates of *P. penetrans* still remains to be elucidated. Recent results suggest that proteins on the nematode and endospore surface may be involved (Davies, 1994; Davies et al., 1992). In-vitro binding of endospore extracts has been attributed to a 190-kDa glycoprotein derived from a cuticle extract of *M. javanica* J2 (Davies, 1994). Different protein antigens were observed in different isolates of *P. penetrans* (Chen et al., 1997a), and concanavalin A and wheat-germ agglutinin were reported to inhibit endospore attachment to *M. javanica* J2 (Bird et al., 1989). Recent work showed that fibronectin in the nematode cuticle is involved in endospore attachment through hydropho-

TABLE 2. Host nematodes associated with *Pasteuria* spp. and geographical distribution.

Nematode	Location	Reference
Achromadora micoletzkyi	Germany	Sturhan, 1988
Acrobeloides buetschlii	Germany	Sayre and Starr, 1988
A. nanus	Germany	Sturhan, 1988
Acrobeloides sp.	Germany	Steiner, 1938
	Italy	Ciancio et al., 1994
	USA (California)	Ciancio and Mankau, 1989a
Actinca sp.	Nicaragua	Sturhan, 1988
Aglenchus agricola	England	Sturhan, 1988
	Germany	Sayre and Starr, 1988
Alaimus sp.	Germany	Sturhan, 1988
Amplimerlinius globigerus	Germany	Sturhan, 1988
A. icarus	Belgium	Sturhan, 1988
	Germany	Sayre and Starr, 1988
A. macrurus	Germany	Sayre and Starr, 1988
Amplimerlinius sp.	Germany	Sayre and Starr, 1988
Anaplectus grandipapillatus	Germany	Sayre and Starr, 1988
	USA	Sturhan, 1988
A. granulosus	Germany, Iceland	Sayre and Starr, 1988
Aphanolaimus sp.	Germany	Sayre and Starr, 1988
Aphasmatylenchus nigeriensis	Liberia	Ciancio et al., 1994
Aphelenchoides bicaudatus	Iran	Sayre and Starr, 1988
	Russia	Subbotin et al., 1994
A. composticola	Germany	Sturhan, 1988
	Iran	Sayre and Starr, 1988
A. dactylocercus	Italy	Roccuzzo and Ciancio, 1991
A. megadorus	USA	Allen, 1941
A. parietinus	Germany	Steiner, 1938
A. rutgersi	Italy	Ciancio et al., 1994
A. saprophilus	Germany	Sturhan, 1988
Aphelenchoides sp.	Germany	Sayre and Starr, 1988
	Russia	Subbotin et al., 1994
	Turkey	Elekcioglu, 1995
Aphelenchus avenae	Germany	Sayre and Starr, 1988
	Turkey	Elekcioglu, 1995
Aphelenchus sp.	Mozambique	Sturhan, 1988
Aporcelaimellus simplex	Germany	Sturhan, 1988
A. obtusicaudatus	Germany	Sturhan, 1988
Aporcelaimellus sp.	Russia	Subbotin et al., 1994
Aporcelaimus eurydorus	Germany	Sturhan, 1988
	USA (South Dakota)	Sayre and Starr, 1988
Aulolaimus bathybius	Germany	Sturhan, 1988
A. nannocephalus	Germany	Sturhan, 1988
A. oxycephalus	Germany	Sturhan, 1988
Aulolaimus sp.	Germany	Sayre and Starr, 1988
Axonchium nairi	Germany	Sturhan, 1988
A. valvulatum	Sri Lanka	Ciancio et al., 1994
Basiria gracilis	Germany	Sturhan, 1988
Basiria sp.	Finland, Germany	Sayre and Starr, 1988
Basirotyleptus penetrans	Nicaragua	Sturhan, 1988
Basirotyleptus sp.	Nicaragua	Sayre and Starr, 1988
Bastiania longicaudata	Germany	Sturhan, 1988
Belondirella sp.	Nicaragua	Sturhan, 1988
Belonolaimus gracilis	USA (Florida)	Sayre and Starr, 1988
B. longicaudatus	USA (Florida)	Sayre and Starr, 1988
Belonolaimus spp.	USA (Florida)	Hewlett et al., 1994
Boleodorus thylactus	France	Sturhan, 1988
	Italy	Ciancio et al., 1994
Cactodera cacti	Bolivia	Sturhan, 1988
Cephalenchus leptus	Russia	Subbotin et al., 1994
Cephalobus persegnis	Germany	Sayre and Starr, 1988

TABLE 2. *Continued*

Nematode	Location	Reference
Clarkus papillatus	Germany	Sturhan, 1988
Coslenchus acceptus	Russia	Subbotin et al., 1994
C. andrassyi	Germany	Sturhan, 1988
C. costatus	Germany	Sayre and Starr, 1988
	Italy	Ciancio et al., 1994
C. multigyrus	Germany	Sturhan, 1988
C. turkeyensis	Italy	Ciancio et al., 1994
Criconemella onoensis	Nicaragua	Sayre and Starr, 1988
Criconemella spp.	USA (Florida)	Hewlett et al., 1994
Cylindrolaimus communis	Germany	Sturhan, 1988
	Italy	Ciancio et al., 1994
	Russia	Subbotin et al., 1994
Diphtherophora sp.	Germany, Iran	Sayre and Starr, 1988
Discocriconemella mauritiensis	South Africa	Sayre and Starr, 1988
	Mauritius	Ciancio et al., 1994
Discolaimus bulbiferus	Iran	Sturhan, 1988
	USA (Hawaii)	Sayre and Starr, 1988
D. major	Italy	Ciancio et al., 1994
Discolaimus sp.	Zaire	Sayre and Starr, 1988
Ditylenchus sp.	Germany	Sayre and Starr, 1988
Dolichodorus obtusus	USA (California, Florida)	Sayre and Starr, 1988
Dolichodorus sp.	Mozambique	Sayre and Starr, 1988
	USA	Mankau et al., 1976
Dorylaimellus demani	Germany	Sturhan, 1988
	Russia	Subbotin et al., 1994
Dorylaimellus sp.	Chile	Sturhan, 1988
D. virginianus	Switzerland	Sayre and Starr, 1988
Dorylaimida	Azores, Germany, Iran, Madeira Islands, Nicaragua	Sayre and Starr, 1988
Dorylaimoides mitis	Ethiopia	Ciancio et al., 1994
Dorylaimus carteri	Denmark	Sayre and Starr, 1988
Dorylaimus sp.	Switzerland	Sayre and Starr, 1988
Doryllium minor	Germany	Sturhan, 1988
Doryllium sp.	Nicaragua	Sturhan, 1988
Ecumenicus monohystera	USSR	Sturhan, 1988
Encholaimus taurus	Nicaragua	Sturhan, 1988
Epidorylaimus consobrinus	England	Sturhan, 1988
Eucephalobus oxyuroides	Germany	Sturhan, 1988
	Uzbekistan	Subbotin et al., 1994
Eucephalobus sp.	USA (California)	Ciancio and Mankau, 1989a
E. striatus	Germany	Sayre and Starr, 1988
Eudorylaimus morbidus	Venezuela	Sayre and Starr, 1988
E. parvus	Germany	Sayre and Starr, 1988
Eudorylaimus sp.	Scotland	Sayre and Starr, 1988
	Brazil, France, Nicaragua	Sturhan, 1988
	Russia	Subbotin et al., 1994
Eumonhystera vulgaris	Germany	Sturhan, 1988
Eutobrilus husmanni	Ukraine	Subbotin et al., 1994
Filenchus attenuatus	France	Sturhan, 1988
F. helenae	Germany	Sturhan, 1988
F. misellus	Russia	Subbotin et al., 1994
Filenchus sp.	Austria, Germany, Switzerland	Sturhan, 1988
	Russia	Subbotin et al., 1994
F. thornei	Germany	Sturhan, 1988
F. vulgaris	Germany	Sturhan, 1988
	Russia	Subbotin et al., 1994
Funaria maryanneae	Germany	Sturhan, 1988
Geocenamus nanus	Russia	Subbotin et al., 1994
G. rugosus	Tadzhikistan	Subbotin et al., 1994
G. tartuensis	Russia	Subbotin et al., 1994
G. tenuidens	Germany	Sayre and Starr, 1988

TABLE 2. *Continued*

Nematode	Location	Reference
Globodera pallida	England	Davies et al., 1990
	India	Sharma and Davies, 1996
G. rostochiensis	Japan	Sayre and Starr, 1988
	England	Davies et al., 1990
	India	Sharma and Davies, 1996
Helicotylenchus californicus	Peru	Ciancio et al., 1994
H. canadensis	Germany	Sayre and Starr, 1988
H. crenacauda	Algeria	Ciancio et al., 1994
H. depressus	New Zealand	Yeates, 1967
H. digonicus	Algeria, Croatia, Hungary, Italy, Malta	Ciancio et al., 1994
	Estonia, Kyrgystan, Russia	Subbotin et al., 1994
	Germany, Switzerland	Sayre and Starr, 1988
H. dihystera	Azores, South Africa, USA (Florida)	Sayre and Starr, 1988
	Algeria	Ciancio et al., 1994
	USA (California)	Mankau and Imbriani, 1975
H. erythrinae	Madeira Islands	Sayre and Starr, 1988
H. krugeri	South Africa	Sayre and Starr, 1988
H. lobus	USA (California)	Ciancio et al., 1992
H. microcephalus	Mozambique	Sturhan, 1988
H. microlobus	USA (Florida)	Sayre and Starr, 1988
H. paxilli	Germany	Sayre and Starr, 1988
H. pseudodigonicus	Germany	Sayre and Starr, 1988
	Russia	Subbotin et al., 1994
H. pseudorobustus	Algeria, Italy, Peru	Ciancio et al., 1994
	Azores, Germany, Iran, Madeira Islands	Sayre and Starr, 1988
	Greece	Vovlas et al., 1993
	Russia	Subbotin et al., 1994
Helicotylenchus sp.	Azores, Brazil, Canary Islands, Dominican Republic, Germany, Haiti, India, Iran, Mozambique, Nigeria, Samoa, USA	Sayre and Starr, 1988
	Ivory Coast	Sturhan, 1988
	Kyrgystan, Russia	Subbotin et al., 1994
	Turkey	Elekcioglu, 1995
	USA (California)	Mankau and Imbriani, 1975
	USA (Florida)	Hewlett et al., 1994
H. varicaudatus	Germany	Sayre and Starr, 1988
	Ivory Coast	Sturhan, 1988
H. vulgaris	Germany, Romania	Sayre and Starr, 1988
	Algeria, Italy	Ciancio et al., 1994
Hemicycliophora spp.	USA (Florida)	Hewlett et al., 1994
Heterodera avenae	Germany	Sayre and Starr, 1988
	England	Davies et al., 1990
H. cacti	Bolivia	Ciancio and Mankau, 1989a
H. cajani	India	Sharma and Sharma, 1989
H. elachista	Japan	Sayre and Starr, 1988
H. fici	Italy	Abrantes and Vovlas, 1988
H. glycines	Japan	Sayre and Starr, 1988
	India	Sharma and Davies, 1996
	USA (Illinois)	Noel and Stanger, 1994
H. goettingiana	Germany	Sayre and Starr, 1988
H. leuceilyma	USA (Florida)	Sayre and Starr, 1988
H. schachtii	Germany	Sturhan, 1988
	India	Sharma and Davies, 1996
Heterodera sp.	Germany, Nicaragua	Sayre and Starr, 1988
	India	Sturhan, 1988
	USA (Florida)	Hewlett et al., 1994
H. trifolii	India	Sharma and Davies, 1996
Hirschmanniella gracilis	Germany, USA (Florida)	Sayre and Starr, 1988
H. mucronata	Philippines	Sturhan, 1988
H. oryzae	Philippines	Sturhan, 1988

TABLE 2. *Continued*

Nematode	Location	Reference
Histotylenchus histoides	South Africa	Sayre and Starr, 1988
Hoplolaimus galeatus	USA (Florida)	Sayre and Starr, 1988
H. indicus	India	Sayre and Starr, 1988
Hoplolaimus sp.	USA (California, Florida)	Sayre and Starr, 1988
H. tylenchiformis	USA (Florida)	Sayre and Starr, 1988
H. uniformis	Netherlands	Sayre and Starr, 1988
Hoplotylus montanus	Japan	Sturhan, 1988
H. silvaticus	USA	Sturhan, 1988
Hypsoperine spp.	USA (Florida)	Hewlett et al., 1994
Ironus ignavus	Sweden	Sayre and Starr, 1988
Isolaimium nigeriense	Nigeria	Sayre and Starr, 1988
Labronemella sp.	Russia	Subbotin et al., 1994
Laimydorus reversus	USA (South Dakota)	Sayre and Starr, 1988
Leptonchus sp.	Russia	Subbotin et al., 1994
Limonchulus bryophilus	Nicaragua	Sturhan, 1988
Longidorella europaea	Germany	Sturhan, 1988
L. parva	Italy	Ciancio et al., 1994
Longidorella sp.	Germany	Sayre and Starr, 1988
	Italy	Ciancio et al., 1994
Longidorus attenuatus	Romania	Ciancio et al., 1994
L. caespiticola	Germany	Sayre and Starr, 1988
L. elongatus	Germany	Sayre and Starr, 1988
L. euonymus	Bulgaria	Sturhan, 1988
	Italy	Ciancio et al., 1994
L. laevicapitatus	Ethiopia, Liberia	Ciancio et al., 1994
L. leptocephalus	Germany	Sayre and Starr, 1988
L. profundorum	Germany	Sayre and Starr, 1988
Longidorus sp.	Sri Lanka	Ciancio et al., 1994
L. vineacola	Germany	Sayre and Starr, 1988
Malenchus bryophilus	Russia	Subbotin et al., 1994
Megadorus megadorus	USA (Utah)	Sayre and Starr, 1988
Meloidodera floridensis	USA (Florida)	Sayre and Starr, 1988
Meloidodera spp.	USA (Florida)	Hewlett et al., 1994
Meloidoderita sp.	Iran	Sayre and Starr, 1988
Meloidogyne acrita	USA (Florida)	Sayre and Starr, 1988
M. acronea	Malawi	Sturhan, 1988
M. ardenensis	Germany	Sayre and Starr, 1988
M. arenaria	China	Pan et al., 1993
	Netherlands, USA (California, Florida)	Sayre and Starr, 1988
	Spain	Verdejo-Lucas, 1992
	Turkey	Elekcioglu, 1995
M. coffeicola	Brazil	Sayre and Starr, 1988
M. exigua	Colombia	Sayre and Starr, 1988
M. fujianensis	China	Pan et al., 1993
M. graminicola	Sénégal	Duponnois et al., 1997
M. graminis	Germany	Sayre and Starr, 1988
M. hapla	China	Pan et al., 1993
	Japan, USA (California, Maryland)	Sayre and Starr, 1988
	Spain	Verdejo-Lucas, 1992
M. incognita	China	Pan et al., 1993
	Colombia	Ciancio and Mankau, 1989a
	Germany	Sturhan, 1988
	India	Bhattacharya and Swarup, 1988
	Japan, Mauritius, South Africa, Togo, USA (California, Florida, Louisiana, Maryland)	Sayre and Starr, 1988
	Pakistan	Maqbool and Zaki, 1990
	Puerto Rico	Vargas et al., 1992
	Sénégal	Duponnois et al., 1997
	Spain	Verdejo-Lucas, 1992
	Turkey	Elekcioglu, 1995

TABLE 2. *Continued*

Nematode	Location	Reference
M. javanica	Australia, Brazil, India, Japan, Mauritius, USA (California, Florida, Maryland)	Sayre and Starr, 1988
	China	Pan et al., 1993
	Pakistan	Maqbool and Zaki, 1990
	Turkey	Elekcioglu, 1995
M. lusitanica	Portugal	Abrantes and Vovlas, 1988
M. naasi	Finland, Germany	Sayre and Starr, 1988
Meloidogyne sp.	Germany, Nicaragua	Sayre and Starr, 1988
	Cuba	Sturhan, 1988
Meloidogyne spp.	China	Lin and Chen, 1992
	Puerto Rico	Vargas and Acosta, 1990
Merlinius bavaricus	Germany	Sayre and Starr, 1988
M. brevidens	Germany, Italy, Madeira Islands	Sayre and Starr, 1988
	Turkey	Elekcioglus, 1995
M. joctus	USA	Sturhan, 1988
	Germany	Sayre and Starr, 1988
M. macrurus	USA (California)	Mankau and Imbriani, 1975
	USA (Florida)	Sayre and Starr, 1988
M. microdorus	Germany, Iran	Sayre and Starr, 1988
M. nanus	Germany	Sayre and Starr, 1988
M. nothus	Germany	Sayre and Starr, 1988
M. processus	Germany	Sayre and Starr, 1988
Merlinius sp.	Germany, Iran	Sayre and Starr, 1988
	Italy	Ciancio et al., 1994
M. stegus	Iran	Barooti, 1989
M. tessellatus	USA, Netherlands	Mankau et al., 1976 Sayre and Starr, 1988
Mesodorylaimus bastiani	Germany	Sturhan, 1988
Mesorhabditis sp.	Germany	Sayre and Starr, 1988
Monhystera paludicola	Denmark	Micoletzky, 1925
Mononchus papillatus	Scotland	Sayre and Starr, 1988
Mumtazium mumtazae	Uganda	Sayre and Starr, 1988
Mylonchulus boveyi	SUA	Ciancio et al., 1994
M. brachyuris	Germany	Sayre and Starr, 1988
Nagelus camelliae	Iran	Sayre and Starr, 1988
N. leptus	Germany, Iceland	Sayre and Starr, 1988
	Russia	Subbotin et al., 1994
Neopsilenchus magnidens	France	Sturhan, 1988
Nygolaimus parabrachyurus	USA (South Dakota)	Sayre and Starr, 1988
Nygolaimus sp.	Germany	Sayre and Starr, 1988
Opisthodorylaimus sylphoides	Italy	Ciancio et al., 1994
Oxydirus oxycephalus	Germany	Sayre and Starr, 1988
Paralongidorus citri	Sri Lanka	Ciancio et al., 1994
P. hortensis	Russia	Subbotin et al., 1994
P. sali	India, USA (Florida)	Sayre and Starr, 1988
Paraphelenchulus pseudoparietinus	Germany	Sayre and Starr, 1988
Paratrichodorus minor	USA	Sturhan, 1988
Paratrichodorus spp.	USA (Florida)	Hewlett et al., 1994
Paratrophurus anomalus	Algeria, São Tomé	Ciancio et al., 1994
Paratylenchus bukowinensis	Germany	Sayre and Starr, 1988
P. mutabilis	Australia	Sturhan, 1988
P. pandata	Nigeria	Sturhan, 1988
Paratylenchus sp.	Canada, Nicaragua	Sturhan, 1988
	Germany	Sayre and Starr, 1988
	Turkey	Elekcioglu, 1995
P. straeleni	Germany	Sayre and Starr, 1988
Plectus acuminatus	Germany	Sayre and Starr, 1988
	Russia	Subbotin et al., 1994
P. cirratus	Germany	Sayre and Starr, 1988
P. parvus	Russia	Subbotin et al., 1994

TABLE 2. *Continued*

Nematode	Location	Reference
P. rhizophilus	Germany	Sayre and Starr, 1988
Plectus sp.	Germany	Sayre and Starr, 1988
Pratylenchoides bacilisemenus	Canada	Sturhan, 1988
P. crenicauda	Germany	Sayre and Starr, 1988
	Kyrgystan, Russia, Tadzhikistan	Subbotin et al., 1994
P. laticauda	Germany	Sayre and Starr, 1988
Pratylenchoides sp.	Canada, Finland, Germany, Iran, Italy	Sayre and Starr, 1988
Pratylenchus brachyurus	USA (Florida, Georgia, Maryland, South Carolina)	Sayre and Starr, 1988
	Ivory Coast	Sturhan, 1988
P. convallariae	Germany	Sayre and Starr, 1988
P. crenatus	Germany	Sayre and Starr, 1988
P. fallax	Germany	Sayre and Starr, 1988
P. flakkensis	England	Sturhan, 1988
	Germany	Sayre and Starr, 1988
P. neglectus	Austria, Germany	Sayre and Starr, 1988
	Croatia, Italy	Ciancio et al., 1994
P. penetrans	Germany, Netherlands, USA (Florida)	Sayre and Starr, 1988
	Turkey	Elekcioglu, 1995
P. pratensis	Germany, Netherlands	Sayre and Starr, 1988
P. scribneri	USA (California)	Sayre and Starr, 1988
	USA (Florida)	Oostendorp et al., 1990
Pratylenchus sp.	China	Pan et al., 1993
	Germany, Greece, USA (Florida, Illinois, Maryland, Oregon)	Sayre and Starr, 1988
P. thornei	Germany	Sayre and Starr, 1988
	Turkey	Elekcioglu, 1995
P. zeae	Dominican Republic, Mozambique, South Africa, USA (Florida)	Sayre and Starr, 1988
Prionchulus sp.	Germany	Sayre and Starr, 1988
Pungentus engadinensis	Germany	Sturhan, 1988
P. silvaticus	Azores	Sturhan, 1988
Pungentus sp.	Germany	Sayre and Starr, 1988
Quinisulcius curvus	Dominican Republic	Sayre and Starr, 1988
Q. sulcatus	Israel	Sayre and Starr, 1988
Radopholus gracilis	Germany	Sayre and Starr, 1988
Rhabditis sp.	Germany	Sayre and Starr, 1988
Rotylenchulus macrosomus	Turkey	Elekcioglu, 1995
R. parvus	Turkey	Elekcioglu, 1995
R. reniformis	India	Sharma and Davies, 1996
Rotylenchus capensis	Greece	Vovlas et al., 1993
R. fallorobustus	Germany	Sayre and Starr, 1988
R. goodeyi	Germany	Sayre and Starr, 1988
R. incultus	South Africa	Sayre and Starr, 1988
R. laurentinus	Italy	Ciancio et al., 1994
R. quartus	Germany	Sayre and Starr, 1988
R. robustus	Switzerland, Netherlands, USA (Florida)	Sayre and Starr, 1988
Rotylenchus sp.	Germany, Israel	Sayre and Starr, 1988
R. unisexus	South Africa	Sayre and Starr, 1988
Scutellonema brachyurum	South Africa	Ciancio et al., 1994
S. clathrycaudatum	Sierra Leone	Ciancio et al., 1994
S. quadrifer	Germany	Sayre and Starr, 1988
S. rugosus	Iran	Sayre and Starr, 1988
Scutellonema sp.	Nigeria	Sayre and Starr, 1988
	Malawi	Sturhan, 1988
Scutellonema spp.	USA (Florida)	Sayre and Starr, 1988
S. truncatum	South Africa	Sayre and Starr, 1988
Scutylenchus sp.	Germany, Iran	Sayre and Starr, 1988
S. tessellatus	Germany	Sayre and Starr, 1988
Seinura tenuicaudata	Germany	Sturhan, 1988
Semitobrilus gagarini	Ukraine	Subbotin et al., 1994

TABLE 2. *Continued*

Nematode	Location	Reference
Sphaeronema californicum	Canada	Sayre and Starr, 1988
S. rumicis	Germany	Sayre and Starr, 1988
Tanzanius coffeae	Tanzania	Siddiqi, 1991
Thonus circulifer	Germany	Sturhan, 1988
Tobrilus gracilus	Armenia	Subbotin et al., 1994
Trichodorus similis	Germany	Sayre and Starr, 1988
T. sparsus	Germany	Sayre and Starr, 1988
Tripyla monohystera	USA	Cobb, 1916
Trophonema okamotoi	USA (Florida)	Inserra et al., 1992
Tylencholaimus minimus	Germany	Sayre and Starr, 1988
Tylencholaimus sp.	Azores	Sturhan, 1988
Tylenchorhynchus annulatus	USA (Florida)	Giblin-Davis et al., 1990
	USA	Sturhan, 1988
T. brassicae	Canary Islands	Sayre and Starr, 1988
T. dubius	Belgium, Germany, Netherlands, Scotland, USA (Florida)	Sayre and Starr, 1988
T. lamelliferus	Germany	Sayre and Starr, 1988
T. maximus	Austria	Sturhan, 1988
	Germany, USA (Maryland)	Sayre and Starr, 1988
T. microphasmis	Germany	Sayre and Starr, 1988
T. nanus	Belgium, USA (Florida)	Sayre and Starr, 1988
T. nudus	USA (South Dakota)	Sayre and Starr, 1988
Tylenchorhynchus sp.	Cuba	Sturhan, 1988
	USA (Colorado)	Sayre and Starr, 1988
Tylenchorhynchus spp.	USA (Florida)	Hewlett et al., 1994
Tylenchulus semipenetrans	France	Sturhan, 1988
	Iran	Maafi, 1993
	Iraq, Italy	Ciancio et al., 1994
	Samoa	Sayre and Starr, 1988
	Turkey	Elekcioglu, 1995
	USA (Florida)	Kaplan, 1994
Tylenchulus sp.	South Africa, Finland, Iceland, Netherlands, Romania, USA (Florida)	Sayre and Starr, 1988
Tylenchus elegans	Iceland	Sturhan, 1988
Tylenchus sp.	Iran	Sturhan, 1988
	Turkey	Elekcioglu, 1995
Tylenchus spp.	Azores, Germany	Sayre and Starr, 1988
Tylolaimophorus minor	Germany	Sturhan, 1988
Xiphinema americanum	Peru	Ciancio and Mankau, 1989b
	Sri Lanka, USA	Sayre and Starr, 1988
X. bakeri	Canada	Sayre and Starr, 1988
	Peru	Ciancio and Mankau, 1989b
X. basiri	Liberia	Ciancio et al., 1994
X. bergeri	South Korea	Ciancio et al., 1994
X. brasiliense	Peru	Ciancio and Mankau, 1989b
X. brevicolle	Poland	Ciancio et al., 1994
X. chambersi	Peru	Ciancio and Mankau, 1989b
	USA (South Dakota)	Sayre and Starr, 1988
X. coxi	Germany	Sayre and Starr, 1988
	Peru	Ciancio and Mankau, 1989b
X. diversicaudatum	Germany	Sayre and Starr, 1988
	Italy	Ciancio, 1995b
	Peru	Ciancio and Mankau, 1989b
X. ebriense	Liberia	Ciancio et al., 1994
X. elongatum	Mauritius, South Africa, USA (Florida)	Sayre and Starr, 1988
	Philippines, Sri Lanka	Ciancio et al., 1994
X. ifacolum	Liberia	Ciancio et al., 1994
X. imitator	South Africa	Sayre and Starr, 1988
X. index	Iran	Sayre and Starr, 1988
X. ingens	Ethiopia	Ciancio et al., 1994

TABLE 2. *Continued*

Nematode	Location	Reference
X. insigne	Ethiopia	Ciancio et al., 1994
X. longicaudatum	Liberia	Ciancio et al., 1994
X. magaliesmontanum	South Africa	Sturhan, 1988
X. pachtaicum	Canary Islands	Sturhan, 1988
	Iran	Sayre and Starr, 1988
	Hungary, Italy	Ciancio et al., 1994
X. pseudocoxi	Germany	Sayre and Starr, 1988
X. radicicola	Sri Lanka	Ciancio et al., 1994
X. rivesi	USA	Sturhan, 1988
X. rotundatum	Liberia	Ciancio et al., 1994
X. setariae	Ethiopia, Sri Lanka	Ciancio et al., 1994
Xiphinema sp.	Azores, Zaire	Sayre and Starr, 1988
	Liberia, Somalia	Ciancio et al., 1994
	USA (Florida)	Hewlett et al., 1994
X. turcicum	Israel	Ciancio et al., 1994
X. vuittenezi	Hungary	Ciancio et al., 1994
Zeldia odontocephala	Germany	Steiner, 1938
Zygotylenchus guevarai	Germany	Sturhan, 1988

bic interactions (Davies et al., 1996). Furthermore, Davies and Danks (1993) demonstrated that a carbohydrate-protein mechanism is involved in endospore attachment to *M. incognita;* N-acetylglucosamine residues on the endospore surface recognized carbohydrate-recognition domains on the nematode surface. Carbohydrate residues, carbohydrate-recognition domains, and a 250-kDa antigen on the cuticle surface of *M. javanica* juveniles were shown to be involved in *P. penetrans* endospore attachment (Spiegel et al., 1996). Therefore, variations in endospore attachments may be attributed to differences in the surface composition of nematode species, races, and populations, as well as to the heterogeneity of the endospore surfaces.

Cultivation: Current methods of mass-producing *P. penetrans* rely on the multiplication of the pathogen in its nematode host on greenhouse-grown plants (Stirling and Wachtel, 1980). The plant system has been optimized (Sharma and Stirling, 1991), and recently a hydroponic cultivation system has been reported (Serracin et al., 1994). Suggested improvements for the plant system include culturing the nematode and pathogen in excised or transformed root cultures (Verdejo and Jaffee, 1988; Verdejo and Mankau, 1986). For example, Verdejo and Mankau (1986) developed a method to grow *P. penetrans* in *M. incognita* on excised tomato roots. A *P. penetrans*-infected female was placed on a small block of agar close to the roots and squashed to release the endospores and then a single *M. incognita* egg mass was placed on the agar block. Endospores attached to J2, which, in turn, invaded the roots. Diseased females were found after 58 days. The culture was improved using a four-element system containing *M. incognita, P. penetrans,* and tomato roots transformed with *Agrobacterium rhizogenes* (Verdejo and Jaffee, 1988). Unfortunately, the process is not cyclic. The spore-filled females do not readily break down, thereby releasing endospores back into the media because of the aseptic conditions of the culture. It appears that commercial use of the pathogen will most likely require cultivation in axenic culture.

Various media have been tested for their ability to support the growth of isolates of *Pasteuria* spp. from *Pratylenchus brachyurus, Heterodera glycines,* and *Meloidogyne incognita* (Reise et al., 1988). Diseased nematodes were surface-sterilized and then crushed in various media that were modified by addition of organic and mineral supplements. Increased production of mature endospores, sporangia, and vegetative cells was observed. Growth closely resembling bacterial structures found in diseased nematodes gradually decreased to marginal growth and ceased after three to five transfers (Reise et al., 1988). However, Reise et al. (1988) did not give the details of the media that they used for cultivation of *Pasteuria* spp., and their study was published only as an abstract. Williams et al. (1989) and Bishop and Ellar (1991) gave detailed descriptions of several microbial media for cultivation of *P. penetrans* outside the nematode host. Williams et al. (1989) screened a wide range of simple and complex media that were developed to cultivate fastidious organisms; media containing root extract, soil extract, or crushed nematodes; media suitable for the growth of nematodes; and media containing sterol compounds. Endospores and vegetative mycelial bodies were used as the initial inoculum, but the cultivation was not successful (Williams et al., 1989). Bishop and Ellar (1991) reported two defined media: one maintained inoculated 'ball-mycelia' of *P. penetrans* in an apparently viable state for up to 1 month with low yields of mature endospores, and another gave a small increase in the number of inoculated 'ball mycelia,' but lysis resulted. A patent was obtained for a cultivation system that involved adding explanted tissue from *Ascaris suum* to an enriched medium, but this work was never published (Previc and Cox, 1992).

ECOLOGY OF *PASTEURIA PENETRANS*

Temperature: Pasteuria penetrans is a mesophilic bacterium, with an optimal growth temperature between 28 °C and 35 °C (Hatz and Dickson, 1992; Serracin et al., 1997). Based on this established temperature range, Chen and Dickson (1997a) reported the minimum temperature at which *P. penetrans* will develop as 17 °C. Ko et al. (1995) reported that *Pasteuria* spp. did not occur in the Hawaiian Islands in areas with a mean annual temperature below 10 °C. However, different temperature requirements may exist for different isolates of the bacterium because of its cosmopolitan distribution. As an example, an Indian isolate of *P. penetrans* that infects both *Heterodera* spp. and *M. incognita* completed its life cycle in *M. incognita* in 49 days at 10 °C to 17 °C (Bhattacharya and Swarup, 1988). In contrast, two different Florida isolates of *P. penetrans* developed more quickly within their host at 30 °C and 35 °C than at 25 °C or below (Hatz and Dickson, 1992; Serracin et al., 1997). Mature endospores of an isolate from *M. arenaria* race 1 were obtained from females after they were incubated for 35, 40, 81, and 116 days at 35, 30, 25, and 20 °C, respectively (Hatz and Dickson, 1992). An isolate from *M. arenaria* race 2 produced mature endospores after they were incubated for 28, 35, and 90 days at 35, 28, and 21 °C, respectively (Serracin et al., 1997). Growth of *P. penetrans* within females of *M. javanica* and *M. arenaria* was not observed at 10 °C (Hatz and Dickson, 1992).

Endospore attachment to J2 increased with increasing temperature, up to ca. 30 °C (Ahmed, 1990; Singh and Dhawan, 1990; Stirling et al., 1990). The rate of endospore attachment at 27 °C was approximately double that at 18 °C (Stirling et al., 1990), but the maximum number of *P. penetrans* endospores attaching to *Meloidogyne* spp. J2 was observed at 30 °C (Ahmed, 1990; Hatz and Dickson, 1992; Orui, 1997). Above 30 °C, the number of endospores attached per J2 declined (Hatz and Dickson, 1992). An isolate of *Pasteuria* sp. parasitic on *H. cajani* showed higher numbers of endospores attached to *H. cajani* at 25 °C than at 15 °C or 35 °C (Singh and Dhawan, 1990). Suspending *M. arenaria* J2 in 30 °C water before exposure to endospores increased J2 receptivity to endospores when compared to treatments at 25 °C and 35 °C (Freitas et al., 1997). Higher temperatures (35 °C to 40 °C) decreased J2 receptivity to endospore attachment. In *P. penetrans*-infested soil, highest attachment occurred when soil was maintained at 20 °C to 30 °C for 4 days. Higher temperatures (>30 °C) greatly reduced endospore attachment. After sonication in water, the number of endospores that attached to J2 increased markedly, with increases in temperature from 15 °C to 30 °C (Orui, 1997).

Relatively high temperatures generally favor endospore germination. Germ tubes formed and penetrated the body wall of J2 of *M. arenaria* race 2 approximately 9 to 10, 6, and 4 to 5 days after inoculation at 21, 28, and 35 °C, respectively (Serracin et al., 1997). Endospores attached to *M. incognita* germinated 6 to 8 days after inoculation at 25 °C (Sayre and Wergin, 1977a). The mechanism by which temperature causes these effects is unclear; however, temperature effects on the host nematodes may influence germination of endospores.

Pathogenesis also was favored by high temperature. At 30 °C, *P. penetrans* proliferated extensively within the pseudocoelom of female nematodes before they reached maturity, whereas, at 20 °C, females often developed mature gonads containing eggs before infection prevented further development (Stirling, 1981).

Numbers of endospores per root system also were related to temperature. At temperatures of 20, 25, 30, and 35 °C, the average number of endospores per root system was 12.5, 14.7, 115, and 113 million, respectively (Hatz and Dickson, 1992). The number of endospores per female also increased with increasing degree-days between 469 and 684 degree-days, based on a threshold temperature of 17 °C (Chen and Dickson, 1997a, 1997b).

Moisture: Little is known about the effect of soil moisture on endospore attachment and development of *P. penetrans;* however, endospores in soil are resistant to desiccation (Williams et al., 1989). Endospores of *P. penetrans* are not motile, and attachment to J2 is dependent on nematode movement in soil (Stirling et al., 1990). Because the movement of nematodes through soil is affected by soil moisture conditions (Van Gundy, 1985), endospore attachment also should be affected. However, studies on soil moisture and endospore attachment have produced variable results. In one investigation, no correlation was observed between the number of endospores attached per J2 and the soil pore size or moisture levels (Dutky and Sayre, 1978). Conversely, moistening air-dried soil containing *P. penetrans* for 3 days before adding *M. incognita* J2 increased endospore attachment (Brown and Smart, 1984). Isolates of *P. penetrans* survived for several weeks in dry, moist, and wet soils and in a soil with fluctuating moisture levels without loss of their ability to attach to their nematode hosts (Oostendorp et al., 1990).

Interestingly, soil moisture was reported to affect the growth of *P. penetrans* within *Meloidogyne* sp. females (Davies et al., 1991). The number of *P. penetrans*-infected females per root system decreased with increasing soil moisture. The development of *P. penetrans* in infected females also was delayed in high soil moisture treatments. However, *P. penetrans* developed normally in *Meloidogyne* females grown on tomato in a hydroponic solution (Serracin et al., 1994, 1997).

Soil texture: In field surveys, *P. penetrans* occurred more frequently in sand and loamy sand than sandy loam, loam, and clay (Spaull, 1984). Mateille et al. (1995) reported that sandy soils favored endospore attachment to *Meloidogyne* spp. and retention of endospores in the upper soil horizon. However, *P. penetrans* was determined to be more abundant in sandy loam than loamy sand in kiwi orchards (Verdejo-Lucas, 1992). A sandy soil (>92% sand) allowed endospores to be distributed readily with percolating water (Oostendorp et al., 1990).

pH: Endospore attachment was affected by pH (Ahmed, 1990; Davies et al., 1988b; Orui, 1997). Attachment was highest at pH 9 and decreased at low pH values (Ahmed, 1990). However, Davies et al. (1988b) observed that attachment was higher at pH 7 than at pH 4 or 9 in tap water, but lower at pH 7 than at pH 4 or 9 in distilled water. With sonicated endospores, attachment was higher at pH 7 than at pH 4 or 9 either in distilled water or tap water, and sonicated endospores attached in higher numbers per J2 in tap water than in distilled water (Davies et al., 1988b). Orui (1997) reported that attachment was generally greater at a higher pH after spore sonication. Recent studies have demonstrated that the endospore surface has a net negative charge, which is greatest at neutral pH and is reduced with a change of pH away from neutral (Afolabi et al., 1995). Electrostatic forces between the nematode cuticle and the endospore surface opposed attachment because the charges on the nematode cuticle also were negative. Reasons for the pH effects remain unclear (Afolabi et al., 1995).

Survival: Little is known about the long-term survival of endospores of *P. penetrans* in soil. In a peanut field in Florida, *P. penetrans* endospores maintained suppressive levels for *M. arenaria* over 10 years (D. W. Dickson, unpubl.). Microplots initially infested with relatively low numbers of *P. penetrans* and *M. arenaria* became suppressive to the nematode after 3 years and were highly suppressive in years 4 through 7 (E. Weibalzahl-Fulton, pers. comm.).

Laboratory studies have shown that *P. penetrans* endospores resist various chemicals and environmental conditions (Bird et al., 1990; Williams et al., 1989). In the laboratory, endospores of *Pasteuria* sp. were viable for a period of more than 1 year at 10 °C to 36 °C (Mani, 1988). Endospores subjected to a prolonged storage of up to 6 years were able to attach to the host nematodes, but infection did not occur (Español et al., 1997). However, an isolate of *P. penetrans* remained infective after 11 years of storage at room temperature, but the number of individuals infected were less than that which occurred with fresh *P. penetrans.* The ability to attach was not affected by storage (Giannakou et al., 1997).

It has been documented that endospores can survive high temperature and desiccation. Williams et al. (1989) observed that infectivity of *P. penetrans* endospores was reduced after heating endospores at 100 °C for 5 minutes, but attachment was not markedly affected by heating at 100 °C for 15 minutes. Endospores also were resistant to desiccation and sonication (Williams et al., 1989). Another test revealed that endospore attachment occurred at up to 80 °C, but infection did not occur at this temperature (Dutky and Sayre, 1978). Freitas et al. (1997) reported that suspending endospores in water at temperatures higher than 30 °C for 5 hours daily over a 10-day period decreased attachment from 61 endospores/J2 at 30 °C to $\geq$8 endospores/J2 at 60 °C to 100 °C. Heating of J2 above 40 °C, either in water or in endospore-infested soil, decreased their receptivity to endospores to almost zero. Conversely, Giannakou et al. (1997) observed that endospore attachment was greater when endospore suspensions were heated 2 hours daily for 8 days at 60 °C than at 40 °C and 50 °C. However, the high-temperature treatment decreased the incidence of *P. penetrans* infection of root-knot nematode females.

Mechanisms for the long-term survival of bacterial endospores include lack of high-energy compounds (ATP and NADH); high content of 3-phosphoglycerate, dipicolinic acid, and divalent cations (Ca^{2+}, Mg^{2+}, and Mn^{2+}); dormancy of enzymes; dehydration of protoplasm; and presence of a thick cortex and coat (Setlow, 1994). Heat resistance can be predicted from the optimal growth temperature of the bacterium, endospore protoplasm water content, total and specific mineral content, temperature for optimum sporulation, and cortex size (Gerhardt and Marquis, 1989). Chemical resistance is related to the impermeability of the protoplasm membrane and endospore coat layers (Setlow, 1994). Endospores of some bacteria survive in soil for periods of up to 9,000 years (Nilsson and Renberg, 1990; Setlow, 1994). To date, the ultrastructure, morphology, sporogenesis, and chemical properties of *Pasteuria* spp. endospores appear similar to those of other endospore-formers (Bird et al., 1990; Chen et al., 1997b; Williams et al., 1989), which suggests that they have the ability for prolonged survival in soil.

Natural enemies: Endospores appear to be resistant to various environmental conditions; thus, their survival in soil may be affected largely by biotic factors. Natural enemies of *P. penetrans* endospores in soil have not been reported, but there have been some observations of hyperparasites attacking endospores (M. A. McClure, pers. comm.). We have observed rod-shaped, gram-negative bacteria adhering to endospores when they were attached to the body wall of *Meloidogyne* spp. J2 (Fig. 1). The ultrastructure and morphology of the endo-

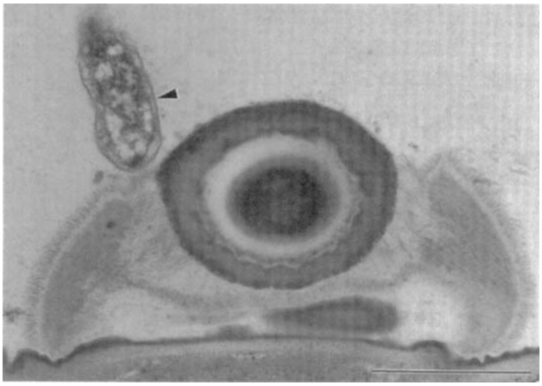

FIG. 1. A gram-negative bacterium (arrowhead) attached to a *Pasteuria penetrans* endospore that is attached to the body wall of a second-stage juvenile of *Meloidogyne arenaria*. Scale bar = 1 μm.

spores remained intact with the presence of the bacterium, which indicates that the latter may not have been an endospore parasite. The bacterium *Ensifer adhaerens* was reported to prey on endospores of *Bacillus subtilis* (Casida, 1982). Because of the similarity in endospore properties between *B. subtilis* and *P. penetrans*, it is likely that *P. penetrans* also has similar predators. More research should be directed to this area for understanding the fate of endospores in soil.

PASTEURIA PENETRANS AS A BIOLOGICAL CONTROL AGENT

Biological control potential: Pasteuria penetrans is a very promising biological control agent against root-knot nematodes. The role of *P. penetrans* in suppressing plant-parasitic nematodes has been tested on many crops, mostly in greenhouse pot tests (Table 3). *Pasteuria penetrans* suppressed *Meloidogyne* spp. on brinjal, chickpea, cucumber, eggplant, grape, hairy vetch, kiwi, mung, okra, peanut, pepper, rye, soybean, tobacco, tomato, and wheat (Table 3). Some isolates of *Pasteuria* spp. have been reported to suppress *Belonolaimus longicaudatus* on bermudagrass (Giblin-Davis, 1990), *H. avenae* and *H. zeae* on unspecified crops (Bhattacharya and Swarup, 1988), *H. cajani* on cowpea (Singh and Dhawan, 1994), *H. elachista* on rice (Nishizawa, 1987), and *Xiphinema diversicaudatum* on peach (Ciancio, 1995b).

Cross-generic suppression of nematodes also has been observed (Bhattacharya and Swarup, 1988; Mankau and Prasad, 1972). *Pasteuria penetrans* simultaneously reduced population densities of *Pratylenchus scribneri* and root galls induced by *M. javanica* and *M. incognita* in tomato (Mankau and Prasad, 1972). An Indian isolate of *P. penetrans* parasitized both *Heterodera* spp. and *M. incognita* (Bhattacharya and Swarup, 1988). Endospores of *P. penetrans* were mass-produced on *M. incognita*, and when endospores were incorporated into soil, number of cysts of *H. avenae* on wheat roots was reduced.

A successful example of the biological control potential of *P. penetrans* for management of root-knot nematodes on peanut was reported recently (Chen, 1996; Chen et al., 1996). Endospores of *P. penetrans* were incorporated into field microplots in year 1 at 0, 1,000, 3,000, 10,000, or 100,000 endospores/g of soil. Root galls and pod galls were significantly reduced at 100,000 endospores/g of soil in the first year. In year 2, root galls and pod galls were reduced at 10,000 and 100,000 endospores/g of soil. Pod yields increased 58% and 94% at 10,000 and 100,000 endospores/g of soil, respectively (Chen et al., 1996). In year 3, root galls and pod galls were nil at 100,000 endospores/g of soil, and were reduced at 1,000, 3,000, and 10,000 endospores/g of soil. Pod yields were increased 180%, 291%, 221%, and 272% at 1,000, 3,000, 10,000, and 100,000 endospores/g of soil, respectively (Chen et al., unpubl.). Population densities of J2 in soil at harvest also were significantly reduced at 10,000 and 100,000 endospores/g of soil in the third year. Apparently, the establishment and amplification of *P. penetrans* in the field microplots played an important role in the increased suppression of root-knot nematodes over the 3-year period. Oostendorp et al. (1991) also reported that amplification of *P. penetrans* to suppressive levels took 3 years.

Isolates of *Pasteuria* spp. failed to suppress populations of *Meloidogyne* spp. on sugarcane (Spaull, 1984), *Helicotylenchus lobus* on turfgrass (Ciancio et al., 1992), and *Tylenchulus semipenetrans* on citrus (Ciancio

TABLE 3. Summary of completed experimental work that used *Pasteuria* spp. as biological control agents for plant-parasitic nematodes.

Nematode, host	Results	Reference
Belonolaimus longicaudatus, bermudagrass	Soil infested with *Pasteuria* ap. endospores was not suppressive to *B. longicaudatus* on bermudagrass in the first 6 months, but caused a significant decrease in nematode populations after 1 year in a greenhouse study.	Giblin-Davis, 1990
Helicotylenchus lobus, turfgrass	No correlation found between nematode density and the percentage of nematodes with endospores in a soil infested with *Pasteuria* sp. Delayed increase in parasitism observed.	Ciancio et al., 1992
Heterodera avenae and *H. zeae*, unspecified crops	Direct mixing of endospore-infested soil was effective for suppression of cyst nematodes.	Bhattacharya and Swarup, 1988
Heterodera cajani, cowpea	*Pasteuria penetrans* reduced root penetration of J2, and numbers of cysts and J2 in soil were reduced by 87% and 99%, respectively, at a level of >40 endospores/J2.	Singh and Dhawan, 1994
Heterodera elachista, rice	*Pasteuria* sp. suppressed the nematode population after 4 years of exponential increases of the nematode population in a reclaimed area.	Nishizawa, 1987
Meloidogyne spp., tomato	*Pasteuria penetrans* reduced J2 mobility in soil.	Mankau and Prasad, 1977
Meloidogyne spp., tomato	*Meloidogyne* spp. population infested with *P. penetrans* approached extinction in 4 to 5 generations in the pot culture.	Mankau, 1980
Meloidogyne spp., tomato	The application of *P. penetrans* endospores resulted in significant control of root-knot nematodes.	Channer and Gowen, 1988
Meloidogyne spp., brinjal and mung	*Pasteuria penetrans* and *Paecilomyces lilacinus* applied individually or in combination enhanced shoot and root weight and length in brinjal, and reduced root-gall indices on brinjal and mung.	Zaki and Maqbool, 1990
Meloidogyne spp., sugarcane	Observations in sugarcane fields in South Africa revealed that more females were infected by *P. penetrans* in coarse soils than in fine-textured soils; populations of *Meloidogyne* spp. were generally greater in fields infested with *P. penetrans* than in noninfested fields, and data collected from one field showed that the level of parasitism was greater at higher densities of the host.	Spaull, 1984
Meloidogyne acronea, tomato	*Pasteuria* sp. infection of juvenile stages, males, and females resulted in almost complete destruction of nematode populations in a greenhouse.	Page and Bridge, 1985
Meloidogyne arenaria, tomato	A soil infested with *P. penetrans* and suppressive to *M. arenaria* on peanut was tested in a greenhouse; reductions of root penetration by J2, root galling, and nematode reproduction were observed.	Minton and Sayre, 1989
M. arenaria, peanut, rye, and vetch	Three years after the initial inoculation of endospore-encumbered J2 in different cropping systems, peanut yield increased in plots treated with *P. penetrans*.	Oostendorp et al., 1991
M. arenaria, peanut	The incorporation of *P. penetrans* endospores into microplots reduced root galls and pod galls, and increased pod and foliage yields. The suppression of root-knot nematodes required 10,000 endospores/g of soil.	Chen et al., 1996
M. arenaria, peanut	Numbers of eggs per root system, J2 per 100 cm^3 soil at harvest, root galls, and pod galls decreased with increasing *P. penetrans* infestation levels.	Chen et al., 1997c
Meloidogyne graminicola, tomato	*Pasteuria penetrans* reduced root galls and increased the root biomass.	Duponnois et al., 1997

TABLE 3. *Continued*

Nematode, host	Results	Reference
Meloidogyne incognita, tobacco, soybean, and hairy vetch	Yield increases were observed in field plots treated with *P. penetrans* endospores.	Brown et al., 1985
M. incognita, tomato	Root penetration of J2 was inhibited by *P. penetrans* in laboratory and greenhouse tests.	Brown and Smart, 1985
M. incognita, tomato, tobacco, soybean, hairy vetch, and pepper	*M. incognita* was controlled more effectively and yields of host plants were greater when *Paecilomyces lilacinus* and *P. penetrans* were applied together in field microplots than when either was applied alone.	Dube and Smart, 1987
M. incognita, M. javanica, and *Meloidogyne* sp., tomato	Soil from a vineyard was able to suppress egg masses produced on tomato in pot tests; suppressiveness was removed by autoclaving the soil.	Bird and Brisbane, 1988
M. incognita, tomato	Tomato root invasive by J2 was reduced by 86% when J2 with ≥15 endospores attached were added to soil; numbers of second-generation nematodes were reduced by 82% to 93% when J2 with 1 to 15 endospores were added to soil.	Davies et al., 1988b
M. incognita, tomato	*Pasteuria penetrans* reduced root invasion by J2 and resulted in the improved growth of tomato.	De Channer, 1989
M. incognita, tomato, eggplant, and wheat	The inoculation of endospore-encumbered J2 in one crop and reincorporation of the *P. penetrans*-infested roots after successive crops were successful and resulted in fewer galls and egg masses on the host plant.	Ahmed, 1990
M. incognita, tomato	*Pasteuria penetrans* reduced root penetration by J2, gall formation, and nematode reproduction.	Sekhar and Gill, 1990
M. incognita, tomato	Egg masses were reduced by 66% in pots treated with 9,000 endospores/g of soil	Ahmed and Gowen, 1991
M. incognita, tomato	*Pasteuria penetrans* reduced the motility of J2 and the number of females that developed in roots.	Davies et al., 1991
M. incognita, tomato	Application of *P. penetrans* and carbofuran, individually or in combination, reduced gall formation and improved growth of tomato in a pot experiment.	Sekhar and Gill, 1991
M. incognita, okra	*Paecilomyces lilacinus, Talaromyces flavus,* and *Bacillus subtilis,* used individually or in combination with *P. penetrans,* increased the length and weight of shoots and reduced root-gall indices.	Zaki and Maqbool, 1991
M. incognita, tomato	*Verticillium chlamydosporium* and *P. penetrans* in combination tended to complement each other, reducing the population density in pots by 92% at the second harvest.	De Leij et al., 1992
M. incognita, tomato	In three greenhouse experiments, *P. penetrans* reduced root-gall indices, numbers of J2 in soil, and egg mass numbers on roots.	Vargas et al., 1992
M. incognita, M. arenaria, and *M. hapla,* kiwi	In a kiwi orchard, the number of females per gram of roots showed seasonal fluctuations and was positively correlated to the percentage of females with *P. penetrans;* parasitized females also were correlated to percentage of J2 with endospores.	Verdejo-Lucas, 1992
M. incognita, cherry tomato	Numbers of J2 in soil and root-gall indices were reduced with incorporation of *P. penetrans* endospores to soil.	Kasumimoto et al., 1993
M. incognita, tomato	A mixture of *M. incognita* and *P. penetrans* endospores resulted in suppression of root galls (81%) and nematode reproduction (97%).	Adiko and Gowen, 1994
M. incognita, tomato	*Pasteuria penetrans* applied 2.5 cm deep in soil was more effective than when applied at the soil surface and at 5 cm deep.	Ahmed et al., 1994

TABLE 3. *Continued*

Nematode, host	Results	Reference
M. incognita and *M. javanica,* tomato and cucumber	*Pasteuria penetrans* applied alone and with oxamyl reduced root galling, egg production, and juvenile population densities.	Gowen and Tzortzakakis, 1994
M. incognita and *M. javanica,* tomato and cucumber	Root galling and egg masses on tomato were reduced in plots treated with *P. penetrans* and oxamyl; the efficacy of the parasite was enhanced by oxamyl applications; root galling, number of egg masses, and J2 in soil were reduced after growing cucumber for 10 weeks in treatments with *P. penetrans,* oxamyl, and solarization; the efficacy of *P. penetrans* was enhanced with oxamyl application and probably in solarized soil.	Tzortzakakis and Gowen, 1994
M. incognita and *M. javanica,* tobacco	In a nematode-suppressive soil in Florida, *P. penetrans* reduced numbers of root galls, egg masses, and eggs of *M. incognita* and *M. javanica.*	Weibelzahl-Fulton et al., 1996
Meloidogyne javanica, M. incognita, and *Pratylenchus scribneri,* tomato	*Pasteuria penetrans* reduced root galls and suppressed *P. scribneri* populations in soil and in roots.	Mankau and Prasad, 1972
M. javanica, tomato and grape	Root galls and the soil J2 at harvest were reduced by *P. penetrans* when tomato root material containing endospores was incorporated into nematode-infested soil. Numbers of J2 penetrating roots decreased with increasing endospore concentration and distance that J2 moved in soil; in pot experiments with grapes, there were fewer J2 in vineyard soil infested with *P. penetrans* than without *P. penetrans.*	Stirling, 1984
M. javanica, tomato	In greenhouse pot trials, treatment of *M. javanica*-infested soil with *P. penetrans* endospores as well as aldicarb or carbofuran reduced galling by a factor of 10.	Brown and Nordmeyer, 1985
M. javanica, tomato	Application of *P. penetrans* in combination with nematicides improved plant growth and reduced root galling.	Maheswari et al., 1987
M. javanica, tomato	*Pasteuria penetrans* reduced the multiplication of the nematode and increased the weight of shoots and roots.	Jaya Raj and Mani, 1988
M. javanica, tomato	*Pasteuria penetrans* and *Paecilomyces lilacinus* applied individually enhanced plant growth; combined application of the two organisms was more effective and increased dry weight of the shoot and lowered soil J2 populations.	Maheswari and Mani, 1988
M. javanica, tomato	*Pasteuria penetrans* as well as four types of oil cakes reduced nematode infection and improved plant growth, and the combined treatments increased their effectiveness.	Maheswari et al., 1988
M. javanica, grape	Oxamyl and phenamiphos reduced abundance of J2 and rate of *P. penetrans* infection for periods of ≤2 months; soil solarization increased rate of *P. penetrans* infection for at least 10 months but did not reduce abundance of *M. javanica.*	Walker and Wachtel, 1989
M. javanica, tomato	*Pasteuria penetrans* suppressed galling and egg masses and increased the shoot weight.	Daudi et al., 1990
M. javanica, tomato	*Pasteuria penetrans* and oxamyl alone, or in combination, inhibited the production of egg masses.	Daudi and Gowen, 1992
M. javanica, chickpea	*Pasteuria penetrans* reduced root galling by 81% and 58% in two greenhouse tests.	Sharma, 1992
M. javanica, brinjal and mung	Application of *P. penetrans* and *P. lilacinus* alone, and in combination, increased yields and reduced root-gall indices.	Zaki and Maqbool, 1992b

TABLE 3. *Continued*

Nematode, host	Results	Reference
M. javanica, okra	Application of root materials containing endospores of *P. penetrans* into a nematode-infested soil reduced root-knot nematode infection and increased lengths and fresh weights of plant shoots and roots.	Zaki and Maqbool, 1992a
M. javanica, tomato	In a factorial experiment, results suggested a density-dependent relationship between *P. penetrans* and *M. javanica* on tomato.	Ciancio and Bourijate, 1995
Xiphinema diversicaudatum, peach	Parasitism of *X. diversicaudatum* by *Pasteuria* sp. was density-dependent.	Ciancio, 1995b

and Roccuzzo, 1992). A survey in sugarcane fields in South Africa revealed that population densities of *Meloidogyne* spp. were generally higher in fields infested with *P. penetrans* and that the level of nematode parasitism was greater at higher nematode densities (Spaull, 1984). On turfgrass, there was no correlation between the population density of *Helicotylenchus lobus* and the percentage of nematodes with endospores (Ciancio et al., 1992). However, an increase in parasitism was observed 2 months after a 10-fold nematode population growth (Ciancio et al., 1992).

Mode of action: Pasteuria penetrans reduced the number of J2 penetrating roots (Brown and Smart, 1985; Davies et al., 1988a, 1988b; Sekhar and Gill, 1990), number of females in roots (Davies et al., 1991), female fecundity (Bird, 1986; Bird and Brisbane, 1988), number of J2 in soil (Chen et al., 1997c; Davies et al., 1988a, 1988b), and number of eggs on roots (Ahmed and Gowen, 1991; Bird and Brisbane, 1988; Chen et al., 1997c; Weibelzahl-Fulton et al., 1996). Movement and mobility of J2 were reduced and their ability to locate host roots was affected when J2 were encumbered with endospores (Davies et al., 1991; Mankau and Prasad, 1977).

FUTURE PROSPECTS

The lack of efficient technology for the large-scale production of *P. penetrans* is a major impediment to the marketing of this organism as a biological control agent. It is readily apparent that mass cultivation depends on fully understanding the nutrient requirements of *P. penetrans.* A medium similar in nature to the chemical composition of the pseudocoelomic fluid of nematodes may be required to provide adequate nutrients for development of *Pasteuria* spp. However, only the pseudocoelomic fluid of large, animal-parasitic nematodes has been even partially characterized, and there are no known reports of a *Pasteuria* or *Pasteuria*-like organism parasitizing these nematodes. Consequently, models of the chemical composition and physical environment of the pseudocoelomic fluid of plant-parasitic nematodes are crucial for comparing the biological and physiological differences between plant-parasitic and animal-parasitic nematodes. The clues for rearing *Pasteuria* spp. may be revealed once the chemical composition and physical makeup of the pseudocoelomic fluid of plant-parasitic nematodes is understood.

With the abundant distribution of *P. penetrans* in soil (Dickson et al., 1994; Hewlett et al., 1994; Sayre and Starr, 1988; Sturhan, 1988), it may be possible to amplify the soil endospore densities to levels that provide biological control of nematodes (Stirling, 1991). Currently, we are investigating the effects of root-knot nematode tolerant and susceptible crops on amplification efficiency of *P. penetrans* under a continuous monoculture system. Unfortunately, technology for the quantification of endospores in soil is not yet available, thus limiting our understanding of the ecology of endospores in soil.

Cross-generic parasitism of *Pasteuria* spp. has been observed (Bhattacharya and Swarup, 1988; Mankau, 1975a; Mankau and Prasad, 1972; Oostendorp et al., 1990; Pan et al., 1993; Sharma and Davies, 1996), but there have been few investigations using alternative hosts to culture *P. penetrans.* Relatively low-cost cultivation of some nematodes on media has been developed (Friedman, 1990). If such systems could be transferred to the cultivation of *P. penetrans,* it might be possible to produce large quantities of endospores for field application.

Protein lectins, ligands, and collagen that appear to be involved in the attachment of endospores to the nematode cuticle require further qualitative and quantitative analyses (Davies, 1994; Davies et al., 1992; Persidis et al., 1991). Recent evidence indicated that a hydrophobic interaction originating from fibronectin on the nematode cuticle was involved in endospore attachment (Davies et al., 1996). It is likely that such information would facilitate our understanding of the nature of attachment and help elucidate the mechanism of host preference.

LITERATURE CITED

Abrantes, I. M. O., and N. Vovlas. 1988. A note on parasitism of the phytonematodes *Meloidogyne* sp. and *Heterodera fici* by *Pasteuria penetrans.* Canadian Journal of Zoology 66:2852–2854.

Adiko, A., and S. R. Gowen. 1994. Comparison of two inoculation methods of root-knot nematodes for the assessment of the biocontrol potential of *Pasteuria penetrans.* Afro-Asian Journal of Nematology 4:32–34.

Afolabi, P., K. G. Davies, and P. S. O'Shea. 1995. The electrostatic nature of the spore of *Pasteuria penetrans,* the bacterial parasite of root-knot nematodes. Journal of Applied Bacteriology 79:244–249.

Ahmed, R. 1990. Studies on the efficacy of *Pasteuria penetrans* for the biological control of *Meloidogyne* species. Ph.D. dissertation, University of Reading, Reading, UK.

Ahmed, R., M. K. Abbas, M. A. Khan, M. Inam ul Haq, N. Javed, and S. T. Sahi. 1994. Evaluation of different methods of application of *Pasteuria penetrans* for the biocontrol of root-knot of tomato (*Meloidogyne incognita*). Pakistan Journal of Nematology 12:155–160.

Ahmed, R., and S. R. Gowen. 1991. Studies on the infection of *Meloidogyne* spp. with isolates of *Pasteuria penetrans.* Nematologia Mediterranea 19:229–233.

Allen, W. A. 1941. *Aphelenchoides megadorus,* a new species of Tylenchoidea (Nematoda). Proceedings of the Helminthological Society of Washington 8:21–23.

Atibalentja, N., and G. R. Noel. 1997. Life cycle and host specificity of *Pasteuria* sp. parasitizing *Heterodera glycines.* Journal of Nematology 29:568 (Abstr.).

Barooti, S. 1989. Distribution of *Pasteuria penetrans,* a parasite of nematodes in Iran. Iranian Journal of Plant Pathology 25:9–10.

Berkeley, R. C. W., and N. Ali. 1994. Classification and identification of endospore-forming bacteria. Pp. 1–8 *in* G. W. Gould, A. D. Russell, and D. E. S. Stewart-Tull, eds. Fundamental and applied aspects of bacterial spores. Oxford, UK: Blackwell Scientific Publications.

Bhattacharya, D., and G. Swarup. 1988. *Pasteuria penetrans,* a pathogen of the genus *Heterodera,* its effect on nematode biology and control. Indian Journal of Nematology 18:61–70.

Bird, A. F. 1986. The influence of the actinomycete, *Pasteuria penetrans,* on the host-parasite relationship of the plant-parasitic nematode, *Meloidogyne javanica.* Parasitology 93:571–580.

Bird, A. F., I. Bonig, and A. Bacic. 1989. Factors affecting the adhesion of micro-organisms to the surfaces of plant-parasitic nematodes. Parasitology 98:155–164.

Bird, A. F., and P. G. Brisbane. 1988. The influence of *Pasteuria penetrans* in field soils on the reproduction of root-knot nematodes. Revue de Nématologie 11:75–81.

Bird, A. F., P. G. Brisbane, S. G. McClure, and R. W. L. Kimber. 1990. Studies on the properties of the spores of some populations of *Pasteuria penetrans.* Journal of Invertebrate Pathology 55:169–178.

Bishop, A. H., and D. J. Ellar. 1991. Attempts to culture *Pasteuria penetrans* in vitro. Biocontrol Science and Technology 1:101–114.

Brown, S. M., J. L. Kepner, and G. C. Smart, Jr. 1985. Increased crop yields following application of *Bacillus penetrans* to field plots infested with *Meloidogyne incognita.* Soil Biology and Biochemistry 17:483–486.

Brown, S. M., and D. Nordmeyer. 1985. Synergistic reduction in root galling by *Meloidogyne javanica* with *Pasteuria penetrans* and nematicides. Revue de Nématologie 8:285–286.

Brown, S. M., and G. C. Smart, Jr. 1984. Attachment of *Bacillus penetrans* to *Meloidogyne incognita.* Nematropica 14:171–172.

Brown, S. M., and G. C. Smart, Jr. 1985. Root penetration by *Meloidogyne incognita* juveniles infected with *Bacillus penetrans.* Journal of Nematology 17:123–126.

Bull, A. T., M. Goodfellow, and J. H. Slater. 1992. Biodiversity as a source of innovation in biotechnology. Annual Reviews of Microbiology 46:219–252.

Casida, L. E., Jr. 1982. *Ensifer adhaerens* gen. nov., sp. nov.: A bacterial predator of bacteria in soil. International Journal of Systematic Bacteriology 32:339–345.

Channer, A. G., and S. R. Gowen. 1988. Preliminary studies on the potential of *Pasteuria penetrans* to control *Meloidogyne* species. Proceedings of Brighton Crop Protection Conference, Pests and Diseases. Brighton, UK: The British Crop Protection Council.

Chen, S. Y., J. Charnecki, J. F. Preston, D. W. Dickson, and J. D. Rice. 1997a. Antibodies from chicken eggs as probes for antigens from *Pasteuria penetrans* endospores. Journal of Nematology 29:268–275.

Chen, Z. X. 1996. Biological control potential of *Pasteuria penetrans.* Ph.D. dissertation, University of Florida, Gainesville, FL.

Chen, Z. X., and D. W. Dickson. 1997a. Minimal developmental temperature of *Pasteuria penetrans.* Supplement to the Journal of Nematology 29:635–644.

Chen, Z. X., and D. W. Dickson. 1997b. Effects of ammonium nitrate and time of harvest on mass production of *Pasteuria penetrans.* Nematropica 27:51–58.

Chen, Z. X., D. W. Dickson, L. G. Freitas, and J. F. Preston. 1997b. Ultrastructure, morphology and sporogenesis of *Pasteuria penetrans.* Phytopathology 87:273–283.

Chen, Z. X., D. W. Dickson, R. McSorley, D. J. Mitchell, and T. E. Hewlett. 1996. Suppression of *Meloidogyne arenaria* race 1 by soil application of endospores of *Pasteuria penetrans.* Journal of Nematology 28: 159–168.

Chen, Z. X., D. W. Dickson, D. J. Mitchell, R. McSorley, and T. E. Hewlett. 1997c. Suppression mechanisms of *Meloidogyne arenaria* race 1 by *Pasteuria penetrans.* Journal of Nematology 29:1–8.

Ciancio, A. 1995a. Phenotypic adaptations in *Pasteuria* spp. nematode parasites. Journal of Nematology 27: 328–338.

Ciancio, A. 1995b. Density-dependent parasitism of *Xiphinema diversicaudatum* by *Pasteuria penetrans* in a naturally infested field. Phytopathology 85:144–149.

Ciancio, A., R. Bonsignore, N. Vovlas, and F. Lamberti. 1994. Host records and spore morphometrics of *Pasteuria penetrans* group parasites of nematodes. Journal of Invertebrate Pathology 63:260–267.

Ciancio, A., and M. Bourijate. 1995. Relationship between *Pasteuria penetrans* infection levels and density of *Meloidogyne javanica.* Nematologia Mediterranea 23:43–49.

Ciancio, A., and R. Mankau. 1989a. The occurrence of *Pasteuria penetrans*-like parasites in several Cephalobidae species. Journal of Nematology 21:556 (Abstr.).

Ciancio, A., and R. Mankau. 1989b. Note on *Pasteuria* sp. parasitic in longidorid nematodes. Nematropica 19: 105–109.

Ciancio, A., R. Mankau, and M. Mundo Ocampo. 1992. Parasitism of *Helicotylenchus lobus* by *Pasteuria penetrans* in naturally infested soil. Journal of Nematology 24:29–35.

Ciancio, A., and G. Roccuzzo. 1992. Observations on a *Pasteuria* sp. parasitic in *Tylenchulus semipenetrans.* Nematologica 38:403–404 (Abstr.).

Cobb, N. A. 1906. Fungus maladies of the sugar cane, with notes on associated insects and nematodes. 2nd ed. Honolulu: Hawaiian Sugar Planters Association.

Cobb, N. A. 1916. Notes on filter-bed nematodes. Journal of Parasitology 2:198.

Daudi, A. T., A. G. Channer, R. Ahmed, and S. R. Gowen. 1990. *Pasteuria penetrans* as a biocontrol agent of *Meloidogyne javanica* in the field in Malawi and in microplots in Pakistan. Proceedings of Brighton Crop Protection Conference, Pests and Diseases. Brighton, UK: British Crop Protection Council.

Daudi, A. T., and S. R. Gowen. 1992. The potential for managing root-knot nematodes by use of *Pasteuria penetrans* and oxamyl. Nematologia Mediterranea 20: 241–244.

Davies, K. G. 1994. In vitro recognition of a 190-kDa putative attachment receptor from the cuticle of *Meloidogyne javanica* by *Pasteuria penetrans* spore extract. Biocontrol Science and Technology 4:367–374.

Davies, K. G., P. Afolabi, and P. O'Shea. 1996. Adhesion of *Pasteuria penetrans* to the cuticle of root-knot nematodes (*Meloidogyne* spp.) inhibited by fibronectin: A study of electrostatic and hydrophobic interactions. Parasitology 112:553–559.

Davies, K. G., and C. Danks. 1993. Carbohydrate/protein interactions between the cuticle of infective juveniles of *Meloidogyne incognita* and spores of the obligate hyperparasite *Pasteuria penetrans.* Nematologica 39: 53–64.

Davies, K. G., C. A. Flynn, and B. R. Kerry. 1988a. The life cycle and pathology of the root-knot nematode parasite *Pasteuria penetrans.* Proceedings of Brighton Crop Protection Conference, Pests and Diseases. Brighton, UK: British Crop Protection Council.

Davies, K. G., C. A. Flynn, V. Laird, and B. R. Kerry. 1990. The life-cycle, population dynamics, and host specificity of a parasite of *Heterodera avenae,* similar to *Pasteuria penetrans.* Revue de Nématologie 13:303–309.

Davies, K. G., B. R. Kerry, and C. A. Flynn. 1988b. Observations on the pathogenicity of *Pasteuria penetrans,* a parasite of root-knot nematodes. Annals of Applied Biology 112:491–501.

Davies, K. G., V. Laird, and B. R. Kerry. 1991. The motility, development and infection of *Meloidogyne incognita* encumbered with spores of the obligate hyperparasite *Pasteuria penetrans.* Revue de Nématologie 14: 611–618.

Davies, K. G., and M. Redden. 1997. Diversity and partial characterization of putative virulence determinants in *Pasteuria penetrans,* the hyperparasitic bacterium of root-knot nematodes (*Meloidogyne* spp.). Journal of Applied Microbiology 83:227–235.

Davies, K. G., M. Redden, and T. K. Pearson. 1994. Endospore heterogeneity in *Pasteuria penetrans* related to adhesion to plant-parasitic nematodes. Letters in Applied Microbiology 19:370–373.

Davies, K. G., M. P. Robinson, and V. Laird. 1992. Proteins involved in the attachment of a hyperparasite. *Pasteuria penetrans,* to its plant-parasitic nematode host, *Meloidogyne incognita.* Journal of Invertebrate Pathology 59:18–23.

De Channer, A. G. 1989. The potential of *Pasteuria penetrans* for the biological control of *Meloidogyne* species. Ph.D. dissertation, University of Reading, Reading, UK.

De Leij, F. A. A. M., K. G. Davies, and B. R. Kerry. 1992. The use of *Verticillium chlamydosporium* Goddard and *Pasteuria penetrans* (Thorne) Sayre & Starr alone and in combination to control *Meloidogyne incognita* on tomato plants. Fundamental and Applied Nematology 15:235–242.

Dickson, D. W., M. Oostendorp, R. Giblin-Davis, and D. J. Mitchell. 1994. Control of plant-parasitic nematodes by biological antagonists. Pp. 575–601 *in* D. Rosen, F. D. Bennett, and J. L. Capinera, eds. Pest management in the subtropics. Biological control—a Florida perspective. Andover, UK: Intercept.

Dube, B., and G. C. Smart, Jr. 1987. Biological control of *Meloidogyne incognita* by *Paecilomyces lilacinus* and *Pasteuria penetrans.* Journal of Nematology 19:222–227.

Duponnois, R., C. Netscher, and T. Mateille. 1997. Effect of the rhizosphere microflora on *Pasteuria penetrans* parasitizing *Meloidogyne graminicola.* Nematologia Mediterranea 25:99–103.

Dutky, E. M., and R. M. Sayre. 1978. Some factors affecting infection of nematodes by the bacterial spore parasite *Bacillus penetrans.* Journal of Nematology 10: 285 (Abstr.).

Ebert, D., P. Rainey, T. M. Embley, and D. Scholz. 1996. Development, life cycle, ultrastructure and phylogenetic position of *Pasteuria ramosa* Metchnikoff 1888: Rediscovery of an obligate endoparasite of *Daphnia magna* Straus. Philosophical Transactions of the Royal Society of London Series B—Biological Sciences 351: 1689–1701.

Elekcioglu, I. H. 1995. Occurrence of *Pasteuria* bacteria as parasites of plant-parasitic nematodes in the east Mediterranean region of Turkey. Nematologia Mediterranea 23:213–215.

Español, M., S. Verdejo-Lucas, K. G. Davies, and B. R. Kerry. 1997. Compatibility between *Pasteuria penetrans* isolates and *Meloidogyne* populations from Spain. Biocontrol Science and Technology 7:219–230.

Fattah, F. A., H. M. Saleh, and H. M. Aboud. 1989. Parasitism of the citrus nematode, *Tylenchulus semipenetrans,* by *Pasteuria penetrans* in Iraq. Journal of Nematology 21:431–433.

Freitas, L. G. 1997. The effects of soil solarization, organic amendment, and fumigant nematicides on *Pasteuria penetrans* and its infectivity of *Meloidogyne arenaria* race 1 in tomato. Ph.D. dissertation, University of Florida, Gainesville, FL.

Freitas, L. G., D. J. Mitchell, and D. W. Dickson. 1997. Temperature effects on attachment of *P. penetrans* endospores to *Meloidogyne arenaria* race 1. Journal of Nematology 29:547–555.

Friedman, M. J. 1990. Commercial production and development. Pp. 153–172 *in* R. Gaugler and H. K. Kaya, eds. Entomopathogenic nematodes in biological control. Boca Raton, FL: CRC Press.

Gerhardt, P., and R. E. Marquis. 1989. Spore thermoresistance mechanisms. Pp. 43–63 *in* I. Smith, R. Slepecky, and P. Setlow, eds. Regulation of procaryotic development. Washington, DC: American Society of Microbiology.

Giannakou, I. O., B. Pembroke, S. R. Gowen, and K. G. Davies. 1997. Effects of long-term storage and above-normal temperatures on spore adhesion of *Pasteuria penetrans* and infection of the root-knot nematode *Meloidogyne javanica.* Nematologica 43:185–192.

Giblin-Davis, R. M. 1990. Potential for biological control of phytoparasitic nematodes in bermudagrass turf with isolates of the *Pasteuria penetrans* group. Proceedings of the Florida State Horticultural Society 103:349–351.

Giblin-Davis, R. M., L. L. McDaniel, and F. G. Bilz. 1990. Isolates of the *Pasteuria penetrans* group from phytoparasitic nematodes in bermudagrass turf. Journal of Nematology 22:750–762.

Giblin-Davis, R. M., D. Williams, T. E. Hewlett, and D. W. Dickson. 1995. Development and host attachment studies using *Pasteuria* from *Belonolaimus longicaudatus* from Florida. Journal of Nematology 27:500 (Abstr.).

Goodfellow, M., and A. G. O'Donnell. 1993. Handbook of new bacterial systematics. London: Academic Press.

Gowen, S. R., and E. Tzortzakakis. 1994. Biological control of *Meloidogyne* spp. with *Pasteuria penetrans.* Bulletin OEPP 24:495–500.

Hatz, B., and D. W. Dickson. 1992. Effect of temperature on attachment, development, and interactions of *Pasteuria penetrans* on *Meloidogyne arenaria.* Journal of Nematology 24:512–521.

Hewlett, T. E., R. Cox, D. W. Dickson, and R. A. Dunn. 1994. Occurrence of *Pasteuria* spp. in Florida. Journal of Nematology 26:616–619.

Hewlett, T. E., and D. W. Dickson. 1994. Endospore attachment specificity of *Pasteuria penetrans* from a peanut field in Florida. Journal of Nematology 26:103–104 (Abstr.).

Hirsh, P. 1972. Re-evaluation of *Pasteuria ramosa,* Metchnikoff 1888, a bacterium pathogenic for *Daphnia* species. International Journal of Systematic Bacteriology 22:112–116.

Inserra, R. N., M. Oostendorp, and D. W. Dickson. 1992. *Pasteuria* sp. parasitizing *Trophonema okamotoi* in Florida. Journal of Nematology 24:36–39.

Jaya Raj, M. A., and A. Mani. 1988. Biocontrol of *Meloidogyne javanica* with the bacterial spore parasite *Pasteuria penetrans.* International Nematology Network Newsletter 5:3–4.

Judicial Commission of the International Committee on Systematic Bacteriology. 1986. Rejection of the type strain of *Pasteuria ramosa* (ATCC 27377) and conservation of the species *Pasteuria ramosa* Metchnikoff 1888 on the basis of the type descriptive material (Opinion 61). International Journal of Systematic Bacteriology 36: 119.

Kaplan, D. T. 1994. Partial characterization of a *Pasteuria* sp. attacking the citrus nematode, *Tylenchulus semipenetrans,* in Florida. Fundamental and Applied Nematology 17:509–512.

Kasumimoto T., R. Ikeda, and H. Kawada. 1993. Dose response of *Meloidogyne incognita*-infected cherry tomatoes to application of *Pasteuria penetrans.* Japanese Journal of Nematology 23:10–18.

Ko, M. P., E. C. Bernard, D. P. Schmitt, and B. S. Sipes. 1995. Occurrence of *Pasteuria*-like organisms on selected plant-parasitic nematodes of pineapple in the Hawaiian Islands. Journal of Nematology 27:395–408.

Lapage, S. P., P. H. A. Sneath, E. J. Lessel, V. B. D. Skerman, H. P. R. Seeliger, and W. A. Clark. 1975. International code of nomenclature of bacteria: Published for the International Association of Microbiological Societies. Washington, DC: American Society for Microbiology.

Lin, X. M., and Q. Q. Chen. 1992. Studies on the disease of root-knot nematodes of crops and a discovery of pathogenic bacteria (*Bacillus penetrans*) of nematodes in Fujian. Wuyi Science Journal 9:261–268.

Maafi, Z. T. 1993. *Pasteuria* sp. as a parasite of citrus nematode (*Tylenchulus semipenetrans*) in the north of Iran. Iranian Journal of Plant Pathology 29:39.

Maheswari, T. U., and A. Mani. 1988. Combined efficacy of *Pasteuria penetrans* and *Paecilomyces lilacinus* on the biocontrol of *Meloidogyne javanica* on tomato. International Nematology Network Newsletter 5:10–11.

Maheswari, T. U., A. Mani, and P. K. Rao. 1987. Combined efficacy of the bacterial spore parasite, *Pasteuria penetrans* (Thorne, 1940), and nematicides in the control of *Meloidogyne javanica* on tomato. Journal of Biological Control 1:53–57.

Maheswari, T. U., A. Mani, and P. K. Rao. 1988. Efficacy of the bacterial spore parasite, *Pasteuria penetrans,* and oil cakes in the control of *Meloidogyne javanica* on tomato. Journal of Biological Control 2:34–36.

Mani, A. 1988. Studies on the bacterial parasite *Pasteuria penetrans:* I. Spore viability after storage. II. Culture on citrus nematode *Tylenchulus semipenetrans.* International Nematology Network Newsletter 5:24–25.

Mankau, R. 1975a. *Bacillus penetrans* n. comb. causing a virulent disease of plant-parasitic nematodes. Journal of Invertebrate Pathology 26:333–339.

Mankau, R. 1975b. Prokaryote affinities of *Duboscqia penetrans,* Thorne. Journal of Protozoology 21:31–34.

Mankau, R. 1980. Biological control of *Meloidogyne* populations by *Bacillus penetrans* in West Africa. Journal of Nematology 12:230 (Abstr.).

Mankau, R., and J. L. Imbriani. 1975. The life cycle of an endoparasite in some tylenchid nematodes. Nematologica 21:89–94.

Mankau, R., J. L. Imbriani, and A. H. Bell. 1976. SEM observations on nematode cuticle penetration of *Bacillus penetrans.* Journal of Nematology 8:179–181.

Mankau, R., and N. Prasad. 1972. Possibilities and problems in the use of a sporozoan endoparasite for biological control of plant-parasitic nematodes. Nematropica 2:7–8.

Mankau, R., and N. Prasad. 1977. Infectivity of *Bacillus penetrans* in plant-parasitic nematodes. Journal of Nematology 9:40–45.

Maqbool, M. A., and M. J. Zaki. 1990. Occurrence of *Pasteuria penetrans* on mature females of *Meloidogyne javanica* and *M. incognita* root-knot nematodes in Pakistan. Pakistan Journal of Nematology 8:13–15.

Mateille, T., R. Duponnois, and M. T. Diop. 1995. Influence of abiotic soil factors and the host plant on the infection of photoparasitic nematodes of the genus *Meloidogyne* by the actinomycete parasitoid *Pasteuria penetrans.* Agronomie 15:581–591.

Metchnikoff, E. 1888. *Pasteuria ramosa,* un représentant des bactéries à division longitudinale. Annales de l'Institut Pasteur 2:165–170.

Micoletzky, H. 1925. Die freilebenden Susswasser und Moornematoden Danemarks. Copenhagen: Host and Son.

Migula, W. 1900. System der Bakterien. Jena, Germany: Gustav Fisher.

Minton, N. A., and R. M. Sayre. 1989. Suppressive influence of *Pasteuria penetrans* in Georgia soil on reproduction of *Meloidogyne arenaria.* Journal of Nematology 21:574–575 (Abstr.).

Nilsson, M., and I. Renberg. 1990. Viable endospores of *Thermoactinomyces vulgaris* in lake sediments as indicators of agricultural history. Application and Environmental Microbiology 56:2025–2028.

Nishizawa, T. 1987. A decline phenomenon in a population of upland cyst nematode, *Heterodera elachista,* caused by bacterial parasite, *Pasteuria penetrans.* Journal of Nematology 19:546 (Abstr.).

Noel, G. R., and B. A. Stanger. 1994. First report of *Pasteuria* sp. attacking *Heterodera glycines* in North America. Supplement to the Journal of Nematology 26: 612–615.

Oostendorp, M., D. W. Dickson, and D. J. Mitchell. 1990. Host range and ecology of isolates of *Pasteuria* spp. from the southeastern United States. Journal of Nematology 22:525–531.

Oostendorp, M., D. W. Dickson, and D. J. Mitchell. 1991. Population development of *Pasteuria penetrans* on *Meloidogyne arenaria.* Journal of Nematology 23:58–64.

Orui, Y. 1997. Effect of spore sonication on attachment and host-attachment range of *P. penetrans* to the root-knot nematode. Applied Entomology and Zoology 32:101–107.

Page, S. L. J., and J. Bridge. 1985. Observations on *Pasteuria penetrans* as a parasite of *Meloidogyne acronea.* Nematologica 31:238–240.

Pan, C., J. Lin, Z. Ni, and S. Wang. 1993. Study on the pathogenic bacteria parasitizing root-knot nematodes discovered in China and their application to biological control. Acta Microbiologica Sinica 33:313–316.

Persidis, A., J. G. Lay, T. Manousis, A. H. Bishop, and D. J. Ellar. 1991. Characterisation of potential adhesins of the bacterium *Pasteuria penetrans,* and of putative receptors on the cuticle of *Meloidogyne incognita,* a nematode host. Journal of Cell Science 100:613–622.

Previc, E. P., and R. J. Cox. 1992. Production of endospores from *Pasteuria* by culturing with explanted tissues from nematodes. U.S. Patent Number 5,094,954. U.S. Patent Office, U.S. Dept. of Commerce, Washington, D.C.

Reise, R. W., K. L. Hackett, R. M. Sayre, and R. N. Huettel. 1988. Factors affecting cultivation of three isolates of *Pasteuria* spp. Journal of Nematology 20:657 (Abstr.).

Roccuzzo, G., and A. Ciancio. 1991. Notes on nematodes found in irrigation water in southern Italy. Nematologia Mediterranea 19:105–108.

Sayre, R. M. 1993. *Pasteuria,* Metchnikoff, 1888. Pp. 101–111 *in* A. L. Sonenshein, J. A. Hoch, and R. Losick, eds. *Bacillus subtilis* and other gram-positive bacteria: Biochemistry, physiology, and molecular genetics. Washington, DC: American Society for Microbiology.

Sayre, R. M., J. R. Adams, and W. P. Wergin. 1979. Bacterial parasite of a cladoceran: Morphology, development in vivo, and taxonomic relationships with *Pasteuria ramosa* Metchnikoff 1888. International Journal of Systematic Bacteriology 29:252–262.

Sayre, R. M., and M. P. Starr. 1985. *Pasteuria penetrans* (ex Thorne, 1940) nom. rev., comb. n., sp. n., a mycelial and endospore-forming bacterium parasitic in plant-parasitic nematodes. Proceedings of the Helminthological Society of Washington 52:149–165.

Sayre, R. M., and M. P. Starr. 1988. Bacterial diseases and antagonisms of nematodes. Pp. 69–101 *in* G. O. Poinar, Jr., and H.-B. Jansson, eds. Diseases of nematodes. Boca Raton, FL: CRC Press.

Sayre, R. M., and M. P. Starr. 1989. Genus *Pasteuria* Metchnikoff, 1888. Pp. 2601–2615 *in* S. T. Williams, M. E. Sharpe, and J. G. Holt, eds. Bergey's manual of systematic bacteriology. Baltimore, MD: Williams and Wilkins.

Sayre, R. M., and W. P. Wergin. 1977a. Morphological comparison of the bacterial spore parasite of *Meloidogyne* sp. to *Pasteuria ramosa,* a bacteria parasite in water fleas. Journal of Nematology 9:283–284 (Abstr.).

Sayre, R. M., and W. P. Wergin. 1977b. Bacterial parasite of a plant nematode: Morphology and ultrastructure. Journal of Bacteriology 129:1091–1101.

Sayre, R. M., W. P. Wergin, and R. E. Davies. 1977. Occurrence in *Moina rectirostris* (Cladocera: Daphnidae) of a parasite morphologically similar to *Pasteuria ramosa* (Metchnikoff, 1888). Canadian Journal of Microbiology 23:1573–1579.

Sekhar, N. S., and J. S. Gill. 1990. Penetration and multiplication of *Meloidogyne incognita* as influenced by *Pasteuria penetrans.* Indian Journal of Nematology 20: 213–218.

Sekhar, N. S., and J. S. Gill. 1991. Efficacy of *Pasteuria penetrans* alone and in combination with carbofuran in controlling *Meloidogyne incognita.* Indian Journal of Nematology 21:61–65.

Serracin, M., A. C. Schuerger, D. W. Dickson, and D. P. Weingartner. 1997. Temperature-dependent development of *Pasteuria penetrans* in *Meloidogyne arenaria.* Journal of Nematology. 29:228–238.

Serracin, M., A. C. Schuerger, D. W. Dickson, D. P. Weingartner, and T. E. Hewlett. 1994. An alternative method for culturing *Pasteuria penetrans.* Journal of Nematology 26:565 (Abstr).

Setlow, P. 1994. Mechanisms which contribute to the long-term survival of spores of *Bacillus* species. Pp. 49–60 *in* G. W. Gould, A. D. Russell, and D. E. S. Stewart-Tull, eds. Fundamental and applied aspects of bacterial spores. Oxford, UK: Blackwell Scientific Publications.

Sharma, R., and S. B. Sharma. 1989. Sticky swarm disease of *Heterodera cajani* and *Meloidogyne javanica* caused by *Pasteuria penetrans.* International Pigeonpea Newsletter 10:26–27.

Sharma, R. D. 1992. Biocontrol efficiency of *Pasteuria penetrans* against *Meloidogyne javanica.* Ciencia Biologica, Ecologia e Systematica 12:43–47.

Sharma, S. B., and K. G. Davies. 1996. Characterization of *Pasteuria* isolated from *Heterodera cajani* using morphology, pathology, and serology of endospores. Systematic and Applied Microbiology 19:106–112.

Sharma, R. D., and G. R. Stirling. 1991. In vivo mass production systems for *Pasteuria penetrans.* Nematologica 37:483–484.

Siddiqi, M. R. 1991. *Tanzanius coffeae* gen. n., sp. n., and *Zygradua rector* gen. n., sp. n. (Nematoda; Tylenchida) from Africa. Afro-Asian Journal of Nematology 1:101–107.

Singh, B., and S. C. Dhawan. 1990. A new bacterial strain of *Pasteuria penetrans,* its host range and effect of temperature on spore attachment to second-stage juveniles of pigeon-pea cyst nematode, *Heterodera cajani.* Indian Journal of Nematology 20:161–166.

Singh, B., and S. C. Dhawan. 1994. Effect of *Pasteuria penetrans* on the penetration and multiplication of *Heterodera cajani* in *Vigna unguiculata* roots. Nematologia Mediterranea 22:159–161.

Skerman, V. B. D., V. McGowan, and P. H. A. Sneath. 1980. Approved lists of bacterial names. International Journal of Systematic Bacteriology 30:225–420.

Spaull, V. W. 1981. *Bacillus penetrans* in South African plant-parasitic nematodes. Nematologica 27:244–245.

Spaull, V. W. 1984. Observations on *Bacillus penetrans* infecting *Meloidogyne* in sugarcane fields in South Africa. Revue de Nématologie 7:277–282.

Spiegel, Y., M. Mor, and E. Sharon. 1996. Attachment of *Pasteuria penetrans* endospores to the surface of *Meloidogyne javanica* second-stage juveniles. Journal of Nematology 28:328–334.

Starr, M. P., and R. M. Sayre. 1988. *Pasteuria thornei* sp. nov. and *Pasteuria penetrans* sensu stricto emend., mycelial and endospore-forming bacteria parasitic, respectively, on plant-parasitic nematodes of the genera *Pratylenchus* and *Meloidogyne.* Annales de l'Institut Pasteur, Microbiologie 139:11–31.

Starr, M. P., R. M. Sayre, and J. M. Schmidt. 1983. Assignment of ATCC 27377 to *Planctomyces staleyi* sp. nov. and conservation of *Pasteuria ramosa* Metchnikoff 1888 on the basis of type descriptive material—request for an opinion. International Journal of Systematic Bacteriology 33:666–671.

Steiner, G. 1938. Opuscula miscellanea nematologica. Proceedings of the Helminthological Society of Washington 5:35–40.

Stirling, G. R. 1981. Effect of temperature on infection of *Meloidogyne javanica* by *Bacillus penetrans.* Nematologica 27:458–462.

Stirling, G. R. 1984. Biological control of *Meloidogyne javanica* with *Bacillus penetrans.* Phytopathology 74:55–60.

Stirling, G. R. 1985. Host specificity of *Pasteuria penetrans* within the genus *Meloidogyne.* Nematologica 31: 203–209.

Stirling, G. R. 1991. Biological control of plant-parasitic nematodes: Progress, problems, and prospects. Wallingford, UK: CAB International.

Stirling, G. R., R. D. Sharma, and J. Perry. 1990. Attachment of *Pasteuria penetrans* spores to the root-knot nematode *Meloidogyne javanica* in soil and its effects on infectivity. Nematologica 36:246–252.

Stirling, G. R., and M. F. Wachtel. 1980. Mass production of *Bacillus penetrans* for the biological control of root-knot nematodes. Nematologica 26:308–312.

Sturhan, D. 1988. New host and geographical records of nematode-parasitic bacteria of the *Pasteuria penetrans* group. Nematologica 34:350–356.

Sturhan, D., R. Winkelheide, R. M. Sayre, and W. P. Wergin. 1994. Light and electron microscopical studies of the life cycle and developmental stages of a *Pasteuria* isolate parasitizing the pea cyst nematode, *Heterodera goettingiana.* Fundamental and Applied Nematology 17: 29–42.

Subbotin, S. A., D. Sturhan, and A. Y. Ryss. 1994. Occurrence of nematode-parasitic bacteria of the genus *Pasteuria* in the former USSR. Russian Journal of Nematology 2:61–64.

Thorne, G. 1940. *Duboscqia penetrans* n. sp. (Sporozoa, Microsporidia, Nosematidae), a parasite of the nematode *Pratylenchus pratensis* (de Man) Filipjev. Proceedings of the Helminthological Society of Washington 7:51–53.

Tzortzakakis, E. A., and S. R. Gowen. 1994. Evaluation of *Pasteuria penetrans* alone and in combination with oxamyl, plant resistance, and solarization for control of *Meloidogyne* spp. on vegetables grown in greenhouses in Crete. Crop Protection 13:455–462.

Van Gundy, S. D. 1985. Ecology of *Meloidogyne* spp.—emphasis on environmental factors affecting survival and pathogenicity. Pp. 178–182 *in* J. N. Sasser and C. C. Carter, eds. An advanced treatise on *Meloidogyne:* Biology and control. Raleigh, NC: North Carolina State University Press.

Vargas, R., and N. Acosta. 1990. *Pasteuria penetrans:* A biological agent for the suppression of nematodes in Puerto Rico. Journal of Agriculture of the University of Puerto Rico 74:319–321.

Vargas, R., N., Acosta, A. Monllor, and C. Betancourt. 1992. Control of *Meloidogyne* spp. with *Pasteuria penetrans* (Thorne) Sayre and Starr. Journal of Agriculture of the University of Puerto Rico 76:63–70.

Verdejo, S., and B. A. Jaffee. 1988. Reproduction of *Pasteuria penetrans* in a tissue-culture system containing *Meloidogyne javanica* and *Agrobacterium rhizogenes*-transformed roots. Phytopathology 78:1284–1286.

Verdejo, S., and R. Mankau. 1986. Culture of *Pasteuria penetrans* in *Meloidogyne incognita* on oligoxenic excised tomato root culture. Journal of Nematology 18: 635 (Abstr.).

Verdejo-Lucas, S. 1992. Seasonal population fluctuations of *Meloidogyne* spp. and the *Pasteuria penetrans* group in kiwi orchards. Plant Disease 76:1275–1279.

Vovlas, N., A. Ciancio, and E. G. Vlachopoulos. 1993. *Pasteuria penetrans* parasitizing *Helicotylenchus pseudorobustus* and *Rotylenchus capensis* in Greece. Afro-Asian Journal of Nematology 3:39–42.

Walker, G. E., and M. F. Wachtel. 1989. The influence of soil solarisation and non-fumigant nematicides on infection of *Meloidogyne javanica* by *Pasteuria penetrans.* Nematologica 34:477–483.

Weibelzahl-Fulton, E., D. W. Dickson, and E. B. Whitty. 1996. Suppression of *Meloidogyne incognita* and *M. javanica* by *Pasteuria penetrans* in field soil. Journal of Nematology 28:43–49.

Williams, A. B., G. R. Stirling, A. C. Hayward, and J. Perry. 1989. Properties and attempted culture of *Pasteuria penetrans,* a bacterial parasite of root-knot nematode (*Meloidogyne javanica*). Journal of Applied Bacteriology 67:145–156.

Winkelheide, R., and D. Sturhan. 1996. Studies on host specificity of *Pasteuria* isolate from *Heterodera goettingiana.* Mitteilungen der Biologischen Bundesanstalt für Land-Forstwirtschaft 317:46–53.

Yeates, G. W. 1967. Studies on nematodes from dune sands, 1. Tylenchida. New Zealand Journal of Science 10:280–286.

Zaki, M. J., and M. A. Maqbool. 1990. Effect of *Pasteuria penetrans* and *Paecilomyces lilacinus* on the control of root-knot nematodes of brinjal and mung. Pakistan Journal of Phytopathology 2:37–42.

Zaki, M. J., and M. A. Maqbool. 1991. Combined efficacy of *Pasteuria penetrans* and other biocontrol agents on the control of root-knot nematode on okra. Pakistan Journal of Nematology 9:49–52.

Zaki, M. J., and M. A. Maqbool. 1992a. Effects of spore concentrations of *Pasteuria penetrans* on the attachment of *Meloidogyne* larvae and growth of okra plants. Pakistan Journal of Nematology 10:69–73.

Zaki, M. J., and M. A. Maqbool. 1992b. Effects of *Pasteuria penetrans* and *Paecilomyces lilacinus* on the control of root-knot nematodes on brinjal and mung. Pakistan Journal of Nematology 10:75–79.