

Review article

Bacterial endosymbionts of plant-parasitic nematodes

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Abstract

Several groups of bacteria have been reported as endosymbionts of various orders of nematodes including the filarial nematodes (*Brugia malayi*, *Wuchereria bancrofti* and *Onchocerca volvulus* (Spirurida)), the entomopathogenic nematodes (*Steinernema* spp., and *Heterorhabditis* spp. (Rhabditida)), and plant-parasitic nematodes (Dorylaimida and Tylenchida). This paper reviews the research on the symbiotic associations of bacteria with plant-parasitic nematodes and the implication for biological control of these nematodes. Emphasis is given to *Pasteuria* spp. (Firmicutes), the best characterized endosymbiont of plant-parasitic nematodes with demonstrated potential for use as biological control agents. *Candidatus Paenicardinium endonii* (Bacteroidetes), a recently described endosymbiont of the soybean cyst nematode, *Heterodera glycines* also is discussed.

Keywords: Bacteria, '*Candidatus Paenicardinium endonii*', '*Candidatus Xiphinematobacter* spp.', endosymbionts, *Pasteuria* spp., plant-parasitic nematodes, symbiosis

1. Introduction

Nematode-bacterium symbioses have been well documented over the last few decades, especially the symbioses involving bacteria of the genus *Wolbachia* and the filarial nematodes *Brugia malayi*, *Wuchereria bancrofti*, and *Onchocerca volvulus* (Fenn and Blaxter, 2004; Taylor, 2003; Saint André et al., 2002). Symbiotic associations involving bacteria of the genera *Xenorhabdus* and *Photorhabdus* and entomopathogenic nematodes of the genera *Steinernema* and *Heterorhabditis* have also been well studied (Ciche et al., 2006; Kaya, 1993, 2006; Sicard et al., 2004). In comparison, bacterial symbioses with plant-parasitic nematodes have received much less attention, with the exception of *Pasteuria* spp. However, the occurrence of bacterial endosymbionts in association with plant-parasitic nematodes has raised a great deal of interest due to the extent of crop damage caused by this group of nematodes, which are responsible for an estimated \$100 billion in annual crop loss worldwide (Koenning et al., 1999; Sasser and Freckman, 1987).

The potential of using bacterial endosymbionts of plant-parasitic nematodes as biological control agents is important in the context of increased awareness of environmental and human health concerns that have severely restricted the use of chemical nematicides, and in some cases the incriminated chemicals have simply been removed from the market. Nematode-antagonistic microbes, including bacterial endosymbionts, have potential usefulness in integrated pest management practices to control plant-parasitic nematodes (Meyer, 2003).

In this paper, we review the scant literature on the symbiotic associations of bacteria with plant-parasitic nematodes and the prospects of using these endosymbionts for the biological control of their host nematodes. We emphasize *Pasteuria* spp. (Firmicutes) and *Candidatus Paenicardinium endonii* (Bacteroidetes), a recently described endosymbiont of the soybean cyst nematode, *Heterodera glycines* (Noel and Atibalentja, 2006). We followed Margulis and Fester (1991) in our use of the term 'symbiosis' simply referring to the 'living together' in a very close association between two different organisms, regardless of the benefits, if any, derived by either (enslavement or parasitism) or both (mutualism) partners.

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Likewise, we use the term 'endosymbiont' in its broader sense to refer to the smaller of the two partners that exists during the whole or part of its life, intracellularly or not, within the body of the host.

2. Major Bacterial Endosymbionts of Plant-Parasitic Nematodes

Pasteuria spp.

Members of the genus *Pasteuria* are gram-positive, mycelial, and endospore-forming bacteria parasitic on invertebrate hosts (Sayre, 1993; Sayre and Starr, 1989). Since their discovery by Metchnikoff in 1888, the taxonomy of *Pasteuria* spp. has been marred with errors and confusion (Sayre and Starr, 1989), but the consensus now is that these bacteria form a distinct line of descent closely related to the *Alicyclobacillaceae* (Fig. 1) (Anderson et al., 1999; Atibalentja et al., 2000; Ebert et al., 1996; Preston et al., 2003). *Pasteuria* spp. are probably the best characterized endosymbionts of plant-parasitic nematodes against which they have shown a great potential as biological control agents (Atibalentja et al., 1998; Bhattacharya and Swarup, 1988; Brown et al., 1985; Chen et al., 1996, 1997b; Giblin-Davis, 1990; Gowen et al., 1998; Kariuki and Dickson, 2007; Noel et al., 2007; Weibelzahl-Fulton et al., 1996).

Apart from *P. ramosa*, the type species, parasitic on water fleas of the family *Daphnidae* (Ebert et al., 1996; Metchnikoff, 1888), all other known *Pasteuria* are parasites of nematodes. The *Pasteuria* endosymbionts of nematodes comprise both validly and provisionally described species. The validly described species include *P. penetrans* on root-knot nematodes, *Meloidogyne* spp. (Sayre and Starr, 1985; Starr and Sayre, 1988), *P. thornei* on root-lesion nematodes, *Pratylenchus* spp. (Starr and Sayre, 1988), and *P. nishizawae* on cyst nematodes of the genera *Heterodera* and *Globodera* (Noel et al., 2005; Sayre et al., 1991a,b). The nematode-infecting *Pasteuria* with provisional species designation include 'Candidatus *Pasteuria usgae*' on *Belonolaimus longicaudatus* (Giblin-Davis et al., 2003), 'Candidatus *Pasteuria goettingiana*' on the pea cyst nematode, *H. goettingiana* (GenBank accession number AF515699; Sturhan et al., 1994), and 'Candidatus *Pasteuria hartismerei*' on nematode pathogens of birch (GenBank accession number AJ878853). Several other undescribed *Pasteuria* isolates also have been reported on plant-parasitic nematodes including *Hoplolaimus galeatus* (Giblin-Davis et al., 1990), *H. avenae* (Davies et al., 1990), *H. cajani* (Sharma and Davies, 1996), *Tylenchulus semipenetrans* (Fattah et al., 1989; Kaplan, 1994; Sorribas et al., 2000), and *Tylenchorhynchus cylindricus* (Galeano et al., 2003). Indeed, nematode parasitism by *Pasteuria* seems ubiquitous. The most recent records of nematode hosts of

Pasteuria list more than 300 taxa, many of them plant-parasites, distributed worldwide (Chen and Dickson, 1998).

Infection by *Pasteuria* is initiated when the dormant endospores attach to the cuticle of susceptible nematodes in the soil (Fig. 2). Attachment of *Pasteuria* endospores is very host specific to the extent where some isolates of the bacterium would not only attach to a particular nematode species but also to specific populations of the same nematode species (Davies et al., 1988; Stirling, 1985). Host specificity has been shown to be mediated by complex interactions between epitopes on the surface of the endospore and receptors on the nematode cuticle (Davies et al., 1992, 1994; Persidis et al., 1991; Spiegel et al., 1996). At least one of the endospores attached to the nematode cuticle must germinate for a successful infection to take place. During germination, the endospore differentiates a germ tube that penetrates into the body of the nematode and grows initially as dichotomously branching hyphae (Atibalentja et al., 2004). Vegetative growth is followed by the production of primary microcolonies, which subsequently fragment and proliferate throughout the pseudocoelom. Ultimately, the body cavity of the nematode is filled with mature *Pasteuria* endospores. The life cycle is completed when endospores are released into the soil upon disintegration of the parasitized nematode (Atibalentja et al., 2004; Chen et al., 1997a; Davies et al., 1990; Giblin-Davis et al., 2001; Sayre et al., 1991a,b; Sturhan et al., 1994). The number of *Pasteuria* endospores released into the soil varies with the size of the nematode host, from a few hundreds in second-stage juveniles (J2) of *H. avenae* and *H. goettingiana* (Davies et al., 1990; Sturhan et al., 1994), through half a million in females of *H. glycines*, to two million in females of *Meloidogyne* spp. (Sayre et al., 1991b).

Depending on the life stage of the nematode host in which *Pasteuria* completes its life cycle, at least four different variants of the bacterium life cycle have been observed. In the first type exhibited by *P. thornei* on root-lesion nematodes, *Pratylenchus* spp., and by 'Candidatus *Pasteuria usgae*' on *Belonolaimus longicaudatus*, the bacterium is able to develop in all the stages of the host nematode (Giblin-Davis et al., 2003; Starr and Sayre, 1988). In the second type observed on 'Candidatus *Pasteuria goettingiana*', parasite of the pea cyst nematode, *H. goettingiana*, and on the *Pasteuria* isolate that infects the oat cyst nematode, *H. avenae*, the bacterium develops only in J2 of the host nematode (GenBank accession number AF515699; Davies et al., 1990; Sturhan et al., 1994). The third type of life cycle occurs on the *Pasteuria* isolate that infects the citrus nematode, *Tylenchulus semipenetrans*. In this host *Pasteuria* develops in J2 and males, but not in females (Fattah et al., 1989; Sorribas et al., 2000). In the fourth type of life cycle shown by *P. penetrans* on root-knot nematodes, *Meloidogyne* spp., and by *P. nishizawae* on cyst nematodes of the genera

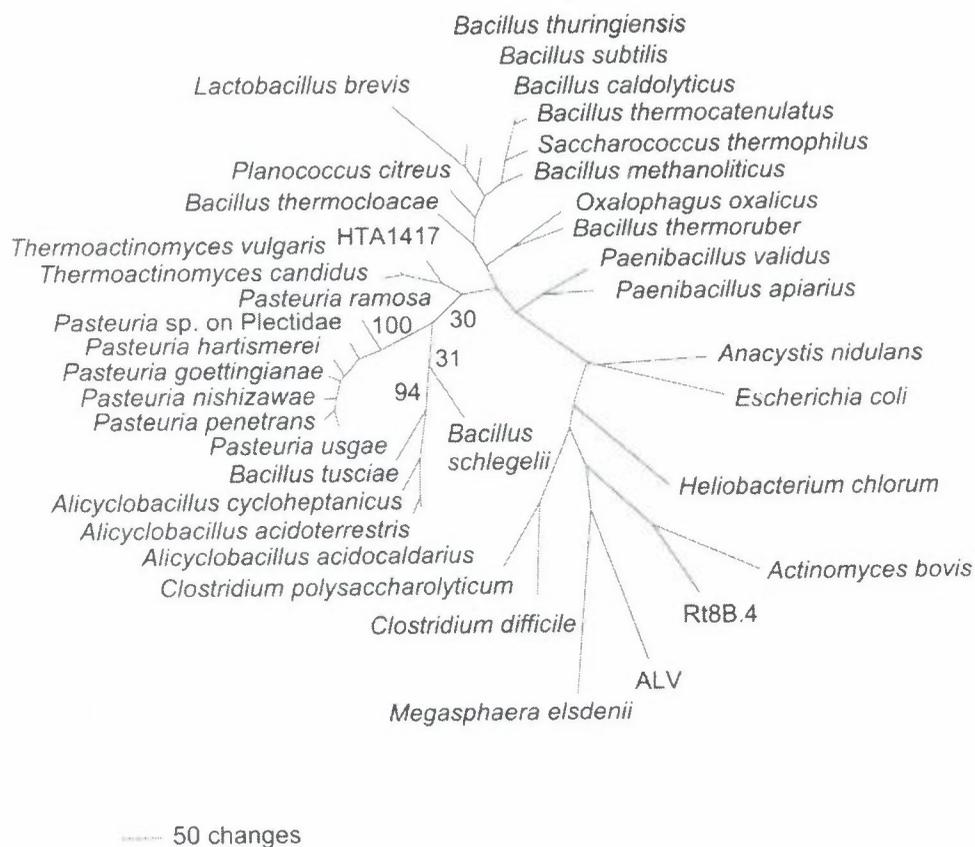


Figure 1. Phylogenetic position of *Pasteuria* spp. inferred from maximum parsimony analysis of 16S rRNA gene sequences. The accession numbers of the *Pasteuria* sequences used were as follows: *P. goettingiana*, AF1515699; *P. hartismerei*, AJ878853; *P. nishizawae*, AF134868; *P. penetrans*, AF077672; *Pasteuria* sp. parasitic on nematodes of the family Plectidae, AY652776; *P. ramosa*, DEU34688; and *P. usgae*, AF254387. The accession numbers for the other sequences were the same as in Atibalentja et al. (2000). *Anacystis nidulans* (Cyanobacteria) and *Escherichia coli* (Proteobacteria) were used as outgroup taxa. Bootstrap proportions (10,000 replications) are shown, wherever possible, for nodes that are relevant for *Pasteuria* spp. The figures not shown are 98, 96, 53, 87, and 93, respectively, for branches leading to *Pasteuria* sp. on Plectidae, *P. hartismerei*, *P. goettingiana*, *P. nishizawae*, and *P. penetrans*. Bootstrap support was 100% for each of the branches leading to *A. cycloheptanicus* and *A. acidoterrestris*. The alignment of the 16S rRNA gene sequences was performed with CLUSTAL X (Thompson et al., 1997) and phylogenetic analyses were conducted with PAUP* 4.0b10 (Swofford, 2003).

Hetrodera and *Globodera*, *Pasteuria* develops only in females (Noel et al., 2005; Starr and Sayre, 1988; Sayre et al., 1991a,b). This type of life cycle is, by far, the most interesting from the biological control standpoint, considering the hundreds of eggs that would have been produced had the nematode not been parasitized by *Pasteuria*, and the millions of endospores released into the soil by parasitized females of *Meloidogynidae* and *Heteroderidae*. Therefore, it only makes sense that these sedentary endoparasites are precisely the ones on which the potential of *Pasteuria* spp. as biological control agents has been the most established (Atibalentja et al., 1998; Brown et al., 1985; Chen et al., 1996, 1997b; Gowen et al., 1998; Kariuki and Dickson, 2007; Noel et al., 2007; Weibelzahl-

Fulton et al., 1996). On soybean cyst nematode, for example, microplot studies have shown that *Pasteuria* reduced *H. glycines* populations to equilibrium densities below the damage threshold (Atibalentja et al., 1998). This finding has been confirmed by the results of a long-term field study during which *Pasteuria* was successfully transferred from the microplots to the field (Noel et al., 2007).

Unfortunately, in spite of numerous studies demonstrating the efficacy of *Pasteuria* spp. as biological control agents of plant-parasitic nematodes, large-scale exploitation of this parasite has been stalled by the lack of suitable techniques of mass-production (Bishop and Ellar, 1991; Williams et al., 1989). Although some success was

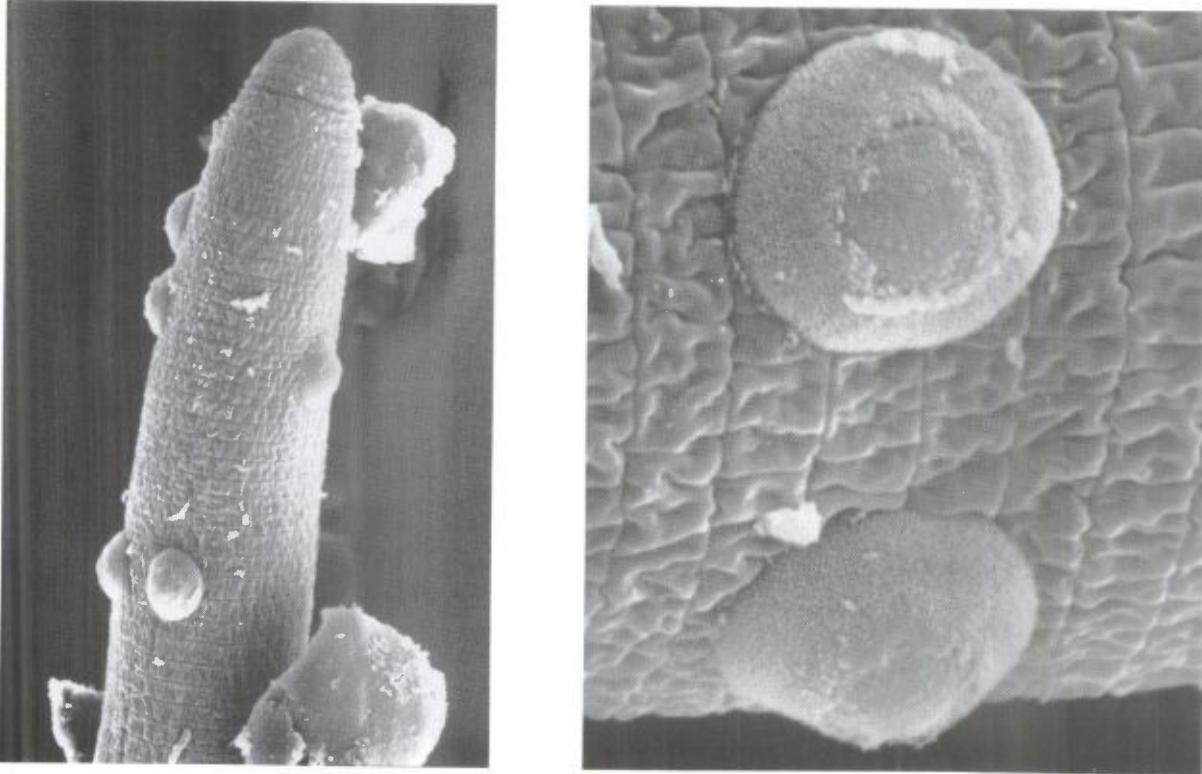


Figure 2. Scanning electron micrographs showing the attachment of endospores of *Pasteuria nishizawae* on the anterior of a second-stage juvenile of the soybean cyst nematode, *Heterodera glycines*. The picture on the right is a higher magnification of two of the endospores on the left picture. Adapted from Noel and Stanger (1994).

reported a few years ago toward *in vitro* cultivation of *P. penetrans* (Hewlett et al., 2002), the details of the technique remain proprietary information that might not be available to the public in a foreseeable future.

'*Candidatus Paenicardinium endonii*'

Shepherd et al. (1973) were the first to report on an intracellular 'bacterium-like organism' other than *Pasteuria* spp. in adult females of two populations of cyst-forming, plant-parasitic nematodes. One population was of the potato cyst nematode, *Globodera rostochiensis*, from Bolivia, and the other of the pea cyst nematode, *H. goettingiana*, from England. Endo (1979) reported a similar intracellular bacterium-like organism in J2 of a population of the soybean cyst nematode, *H. glycines*, from Tennessee, USA. In both cases, the bacterium-like organisms were described as being rod-shaped, ranging in size from 0.3 to 0.5 μm in diameter and from 1.8 to 3 μm in length. They also contained characteristic Microfilament-Like Structures (MLSs) similar to those observed in '*Candidatus Cardinium hertigii*', an endosymbiont of *Encarsia* spp. wasps (Zchori-Fein et al., 2004).

The bacterium-like endosymbionts of cyst nematodes have subsequently been found in all life stages (J2, females, and males) of their nematode hosts in which they are present in most tissues, predominantly in reproductive tissues of both males and females (Endo, 1979; Noel and Atibalentja, 2006; Shepherd et al., 1973; Walsh et al., 1983a,b). Unlike their relatives on wasp, the endosymbionts of cyst nematodes are not known to affect host reproduction or to cause any noticeable pathological effects (Shepherd et al., 1973; Walsh et al., 1983a,b).

The bacterial endosymbiont of *H. glycines* was described recently as '*Candidatus Paenicardinium endonii*' on the basis of transmission electron microscopy observations and phylogenetic analysis of the 16S rRNA and *gyrB* genes (Noel and Atibalentja, 2006). It would be interesting to determine whether the bacteria-like endosymbionts of *G. rostochiensis* and *H. goettingiana* also are '*Candidatus Paenicardinium endonii*' or new taxa.

'*Candidatus Xiphinematobacter* spp.'

Another group of bacterial endosymbionts of plant-parasitic nematodes occur in three species of the *Xiphinema*

americanum group (Dorylaimida: Longidoridae) including *X. americanum*, *X. rivesi*, and *X. brevicollum*, all ectoparasites of vine and other fruit crops. Each of the aforementioned species of *Xiphinema* harbors its own specific intracellular bacterial symbiont belonging to a new branch within the division of the *Verrucomicrobia*. These include 'Candidatus *Xiphinematobacter americani*', 'Candidatus *Xiphinematobacter rivesi*', and 'Candidatus *Xiphinematobacter brevicolli*', respectively, for *X. americanum*, *X. rivesi*, and *X. brevicollum* (Vandekerckhove et al., 2000).

'Candidatus *Xiphinematobacter*' endosymbionts are inherited maternally and their *Xiphinema* hosts reproduce by thelytokous (mother-to-daughter) parthenogenesis, males being extremely rare (Coomans et al., 2000). It has been suggested that the verrucomicrobial organisms might be responsible for manipulating their host's sex ratio in the same way as *Wolbachia* spp. do in parasitoid wasps (Coomans et al., 2000; Dedeine et al., 2001; Stouthamer and Kazmer, 1994, Vandekerckhove et al., 2000). Fluorescent *in situ* hybridization (FISH) with *Verrucomicrobia*-specific probes has been very useful for the detection of 'Candidatus *Xiphinematobacter*' cells and the study of their behavior in their nematode hosts, from the egg to adult females and males (Vandekerckhove et al., 2002). Specifically, microscopic observations of FISH-treated specimen of *X. americanum* and *X. brevicollum* have shown that the endosymbionts in the mononuclear intrauterine egg migrate to the pole where the gut primordium is formed. Subsequently, the bacteria populate the intestinal epithelia of juveniles. However, when the fourth stage juveniles molt into adult females, the endosymbionts reshuffle themselves in order to access the vertical transmission pathway. First they concentrate around the developing ovaries to occupy the ovarian wall. Thereafter, the bacteria are enclosed in the ripening oocytes where they are transmitted to the next generation. The *Verrucomicrobia* endosymbionts also populate the male gut epithelium but not the ripe testes, hence they are not vertically transmitted through males (Vandekerckhove et al., 2002).

3. Conclusion

Bacterial endosymbionts of plant-parasitic nematodes form a relatively diverse and interesting group of organisms, some of which have shown a great potential as biological control agents. However, much research is needed before the specific interactions between these bacteria and their plant-parasitic nematode hosts are fully understood and exploited in agriculture to manage nematode pests. The major obstacle to this goal is our current inability to culture these microorganisms *in vitro*.

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