

## 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

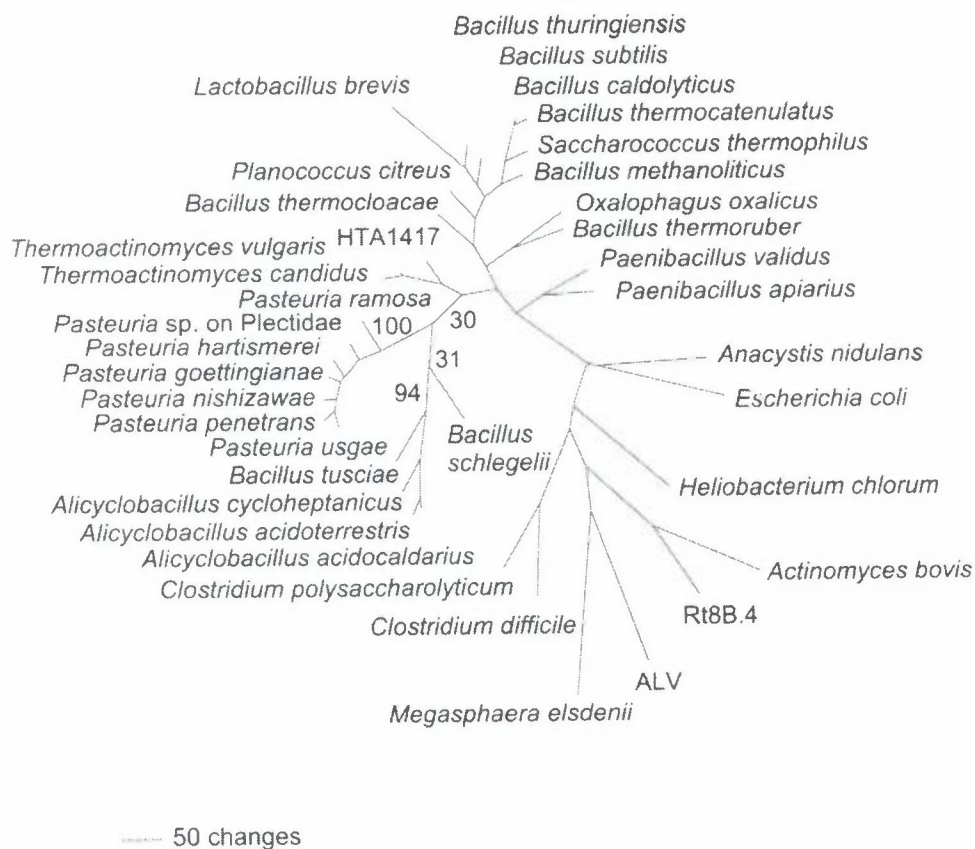


Figure 1. Phylogenetic position of *Pasteuria* spp. inferred from maximum parsimony analysis of 16S rRNA gene sequences. The accession numbers of the *Pasteuria* sequences used were as follows: *P. goettingiana*, AF1515699; *P. hartismerei*, AJ878853; *P. nishizawae*, AF134868; *P. penetrans*, AF077672; *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).

*Heterodera* 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

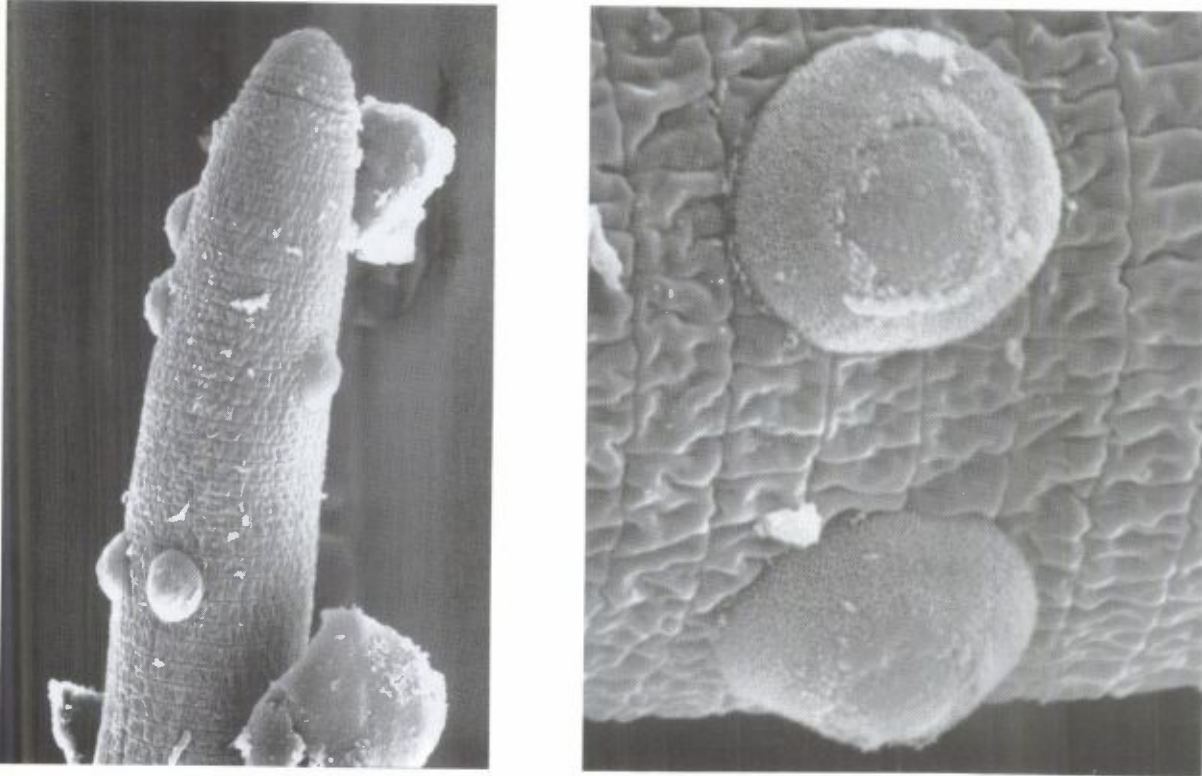


Figure 2. Scanning electron micrographs showing the attachment of endospores of *Pasteuria nishizawae* on the anterior of a second-stage juvenile of the soybean cyst nematode, *Heterodera glycines*. The picture on the right is a higher magnification of two of the endospores on the left picture. Adapted 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  $\mu\text{m}$  in diameter and from 1.8 to 3  $\mu\text{m}$  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*.

### REFERENCES

- Anderson, J.M., Preston, J.F., Dickson, D.W., Hewlett, T.E., Williams, N.H., and Maruniak, J.E. 1999. Phylogenetic analysis of *Pasteuria penetrans* by 16S rDNA gene cloning and sequencing. *Journal of Nematology* **31**: 319–325.
- Atibalentja, N., Jakstys, B.P., and Noel, G.R. 2004. Life cycle, ultrastructure, and host specificity of the North American isolate of *Pasteuria* that parasitizes the soybean cyst nematode, *Heterodera glycines*. *Journal of Nematology* **36**: 171–180.
- Atibalentja, N., Noel, G.R., and Domier, L.L. 2000. Phylogenetic position of the North American isolate of *Pasteuria* that parasitizes the soybean nematode, *Heterodera glycines*, as inferred from 16S rDNA sequence analysis. *International Journal of Systematic and Evolutionary Microbiology* **50**: 605–613.
- Atibalentja, N., Noel, G.R., Liao, T.F., and Gertner, G.Z. 1998. Population changes in *Heterodera glycines* and its bacterial parasite *Pasteuria* sp. in naturally infested soil. *Journal of Nematology* **30**: 81–92.
- Bhattacharya, D. and Swarup, G. 1988. *Pasteuria penetrans*, a pathogen of the genus *Heterodera*, its effect on nematode biology and control. *Indian Journal of Nematology* **18**: 61–70.
- Bishop, A.H. and Ellar, D.J. 1991. Attempts to culture *Pasteuria penetrans* *in vitro*. *Biocontrol Science and Technology* **1**: 101–114.
- Brown, S.M., Kepner, J.L., and Smart, Jr., G.C. 1985. Increased crop yields following application of *Bacillus penetrans* to field plots infested with *Meloidogyne incognita*. *Soil Biology and Biochemistry* **17**: 483–486.
- Chen, Z.X. and Dickson, D.W. 1998. Review of *Pasteuria penetrans*: biology, ecology, and biological control potential. *Journal of Nematology* **30**: 313–340.
- Chen, Z.X., Dickson, D.W., Freitas, L.G., and Preston, J.F. 1997a. Ultrastructure, morphology, and sporogenesis of *Pasteuria penetrans*. *Phytopathology* **87**: 273–283.
- Chen, Z.X., Dickson, D.W., McSorley, R., Mitchell, D.J., and Hewlett, T.E. 1996. Suppression of *Meloidogyne arenaria* race 1 by soil application of endospores of *Pasteuria penetrans*. *Journal of Nematology* **28**: 159–168.
- Chen, Z.X., Dickson, D.W., Mitchell, D.J., McSorley, R., and Hewlett, T.E. 1997b. Suppression mechanisms of *Meloidogyne arenaria* race 1 by *Pasteuria penetrans*. *Journal of Nematology* **29**: 1–8.
- Ciche, T.A., Darby, C., Ehlers, R.-U., Forst, S., and Goodrich-Blair, H. 2006. Dangerous liaisons: the symbiosis of entomopathogenic nematodes and bacteria. *Biological Control* **38**: 22–46.
- Coomans, A., Vandekerckhove, T.M., and Claeys, M. 2000. Transovarial transmission of symbionts in *Xiphinema brevicollum* (Nematoda: Longidoridae). *Nematology* **2**: 443–449.
- Davies, K.G., Flynn, C.A., Laird, V., and Kerry, B.R. 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., Kerry, B.R., Flynn, C.A. 1988. Observations on the pathogenicity of *Pasteuria penetrans*, a parasite of root-knot nematodes. *Annals of Applied Biology* **112**: 491–501.
- Davies, K.G., Redden, M., and Pearson, T.K. 1994. Endospore heterogeneity in *Pasteuria penetrans* related to adhesion to plant-parasitic nematodes. *Letters in Applied Microbiology* **19**: 370–373.

- Davies, K.G., Robinson, M.P., and Laird, V. 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.
- Dedeine, F., Vavre, F., Fleury, F., Loppin, B., Hochberg, M.E., and Boulétreau, M. 2001. Removing symbiotic *Wolbachia* bacteria specifically inhibits oogenesis in parasitic wasp. *Proceedings of the National Academy of Science USA* **98**: 6247–6252.
- Ebert, D., Rainey, P., Embley, T.M., and Scholz, D. 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.
- Endo, B.Y. 1979. The ultrastructure and distribution of an intracellular bacterium-like microorganism in tissues of larvae of soybean cyst nematode, *Heterodera glycines*. *Journal of Ultrastructure Research* **67**: 1–14.
- Fattah, F.A., Saleh, H.M., and Aboud, H.M. 1989. Parasitism of the citrus nematode, *Tylenchulus semipenetrans*, by *Pasteuria penetrans* in Iraq. *Journal of Nematology* **21**: 431–433.
- Fenn, K. and Blaxter, M. 2004. Are filarial nematode *Wolbachia* obligate mutualist symbionts? *TRENDS in Ecology and Evolution* **19**: 163–166.
- Galeano, M., Verdejo-Lucas, S., and Ciancio, A. 2003. Morphology and ultrastructure of a *Pasteuria* form parasitic in *Tylenchorhynchus cylindricus* (Nematoda). *Journal of Invertebrate Pathology* **83**: 83–85.
- 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., McDaniel, L.L., and Biltz, F.G. 1990. Isolates of the *Pasteuria penetrans* group from phytoparasitic nematodes in bermudagrass turf. *Supplement to Journal of Nematology* **22**: 750–762.
- Giblin-Davis, R.M., Williams, D.S., Bekal, S., Dickson, D.W., Brito, J.A., Becker, J.O., and Preston, J.F. 2003. '*Candidatus Pasteuria usgae*' sp. nov., an obligate endoparasite of the phytoparasitic nematode *Belonolaimus longicaudatus*. *International Journal of Systematic and Evolutionary Microbiology* **53**: 197–200.
- Giblin-Davis, R.M., Williams, D.S., Wergin, W.P., Dickson, D.W., Hewlett, T.E., Bekal, S., and Becker, J.O. 2001. Ultrastructure and development of *Pasteuria* sp. (S-1 strain), an obligate endoparasite of *Belonolaimus longicaudatus* (Nematoda: Tylenchida). *Journal of Nematology* **33**: 227–238.
- Gowen, S.R., Tzortzakakis, E.A., and Channer, A.G. De R. 1998. Control of the root-knot nematode *Meloidogyne javanica* by the parasite *Pasteuria penetrans* as influenced by the initial nematode population densities. *Nematologica* **44**: 369–379.
- Hewlett, T.E., Gerber, J.F., Smith, K.S., and White, J.H. 2002. *In vitro* culture of *Pasteuria penetrans*. *Nematology* **4**: 152–153.
- 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.
- Kariuki, G.M. and Dickson, D.W. 2007. Transfer and development of *Pasteuria penetrans*. *Journal of Nematology* **39**: 55–61.
- Kaya, H.K. 1993. Entomogenous and entomopathogenic nematodes in biological control. In: *Plant Parasitic Nematodes in Temperate Agriculture*. Evans, K., Trudgill, D.L., and Webster, J.M., eds. CAB International, Wallingford, UK, pp. 565–591.
- Kaya, H.K. 2006. Third international symposium on entomopathogenic nematodes and symbiotic bacteria. *Biological Control* **38**: 1–3.
- Koenning, S.R., Overstreet, C., Noling, J.W., Donald, P.A., Becker, J.O., and Fortnum, B.A. 1999. Survey of crop losses in response to phytoparasitic nematodes in the United States for 1994. *Journal of Nematology* **31**: 587–618.
- Margulis, L. and Fester, R. eds. 1991. *Symbiosis as a Source of Evolutionary Innovation*. MIT Press.
- Metchnikoff, M.E. 1888. *Pasteuria ramosa*. Un représentant des bactéries à division longitudinale. *Annales de l'Institut Pasteur* **2**: 165–170.
- Meyer, S.L.F. 2003. United States Department of Agriculture – Agricultural Research Service research programs on microbes for management of plant-parasitic nematodes. *Pest Management Science* **59**: 665–670.
- Noel, G.R. and Atibalentja, N. 2006. '*Candidatus Paenicardinium endonii*', an endosymbiont of the plant-parasitic nematode *Heterodera glycines* (Nematoda: Tylenchida) affiliated to the phylum Bacteroidetes. *International Journal of Systematic and Evolutionary Microbiology* **56**: 1697–1702.
- Noel, G.R., Atibalentja, N., and Domier, L.L. 2005. Emended description of *Pasteuria nishizawae*. *International Journal of Systematic and Evolutionary Microbiology* **55**: 1681–1685.
- Noel, G.R., Bauer, S. and Atibalentja, N. 2007. Soybean cyst nematode populations suppressed by *Pasteuria nishizawae*. *Journal of Nematology* **39**: 82.
- Noel, G.R. and Stanger, B.A. 1994. First report of *Pasteuria* sp. attacking *Heterodera glycines* in North America. *Supplement to Journal of Nematology* **26**: 612–615.
- Persidis, A., Lay, J.G., Manousis, T., Bishop, A.H., and Ellar, D.J. 1991. Characterization 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**: 613–623.
- Preston, J.F., Dickson, D.W., Maruniak, J.E., Nong, G., Brito, J.A., Schmidt, L.M., and Giblin-Davis, R.M. 2003. *Pasteuria* spp.: systematics and phylogeny of these bacterial parasites of phytopathogenic nematodes. *Journal of Nematology* **35**: 198–207.
- Saint André, A.V., Blackwell, N.M., Hall, L.R., et al. 2002. The role of endosymbiotic *Wolbachia* bacteria in the pathogenesis of river blindness. *Science* **295**: 1892–1895.
- Sasser, J.N. and Freckman, D.W. 1987. A world perspective on nematology: the role of society. In: *Vistas on Nematology*. Veech, J.A. and Dickson, D.W., eds. Society of Nematologists, Hyattsville. pp. 7–14.
- Sayre, R.M. 1993. *Pasteuria*, Metchnikoff, 1888. In: *Bacillus subtilis and Other Gram-positive Bacteria: Biochemistry, Physiology, and Molecular Genetics*. Sonenshein, A.L., Hoch, J.A., and Losick, R., eds. American Society for Microbiology, Washington, DC. pp. 101–111.
- Sayre, R.M. and Starr, M.P. 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 Starr, M.P. 1989. Genus *Pasteuria* Metchnikoff 1888, 166, <sup>AL</sup> emend. Sayre and Starr 1985, 149, Starr and Sayre 1988a, 27 (Nom. Cons. Opin. 61 Jud. Comm. 1986, 119). Not *Pasteuria* in the sense of Henrici and Johnson (1935), Hirsch (1972), or Staley (1973); see Starr et al., (1983) and Judicial Commission (1986). In: *Bergey's Manual of*

