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Verified and potential pathogens of predatory mites (Acari: Phytoseiidae)

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Abstract Several species of phytoseiid mites (Acari: Phytoseiidae), including species of the genera *Amblyseius*, *Galendromus*, *Metaseiulus*, *Neoseiulus*, *Phytoseiulus* and *Typhlodromus*, are currently reared for biological control of various crop pests and/or as model organisms for the study of predator–prey interactions. Pathogen-free phytoseiid mites are important to obtain high efficacy in biological pest control and to get reliable data in mite research, as pathogens may affect the performance of their host or alter their reproduction and behaviour. Potential and verified pathogens have been reported for phytoseiid mites during the past 25 years. The present review provides an overview, including potential pathogens with unknown host effects (17 reports), endosymbiotic *Wolbachia* (seven reports), other bacteria (including *Cardinium* and *Spiroplasma*) (four reports), cases of unidentified diseases (three reports) and cases of verified pathogens (six reports). From the latter group four reports refer to Microsporidia, one to a fungus and one to a bacterium. Only five entities have been studied in detail, including *Wolbachia* infecting seven predatory mite species, other endosymbiotic bacteria infecting *Metaseiulus* (*Galendromus*, *Typhlodromus*) *occidentalis* (Nesbitt), the bacterium *Acaricomes phytoseiuli* infecting *Phytoseiulus persimilis* Athias-Henriot, the microsporidium *Microsporidium phytoseiuli* infecting *P. persimilis* and the microsporidium *Oligosporidium occidentale* infecting *M. occidentale*. In four cases (*Wolbachia*, *A. phytoseiuli*, *M. phytoseiuli* and *O. occidentale*) an infection may be connected with fitness costs of the host. Moreover, infection is not always readily visible as no obvious gross symptoms are present. Monitoring of these entities on a routine and continuous basis should therefore get more attention, especially in commercial mass-production. Special attention should be paid to field-collected mites before introduction into the laboratory or mass rearing, and to mites that are exchanged among rearing facilities. However, at present general pathogen monitoring is not yet practical as effects of many entities are unknown. More research effort is needed concerning verified and potential pathogens of commercially reared arthropods and those used as model organisms in research.

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Introduction

Several species of phytoseiid mites, including species of the genera *Amblyseius*, *Galen-dromus*, *Metaseiulus*, *Neoseiulus*, *Phytoseiulus* and *Typhlodromus*, are currently reared for biological control of pests, including spider mites (*Tetranychus* spp.) and thrips (*Thrips tabaci* Lindeman and *Frankliniella occidentalis* Pergande) in protected crops, outdoor vegetables, fruit and other horticultural crops (van Lenteren 2003a, b). Phytoseiid predatory mites include specialists such as *Phytoseiulus persimilis* Athias-Henriot, which attack spider mites (*Tetranychus* spp.), selective predators such as *Neoseiulus (Amblyseius) californicus* (McGregor) and generalists such as *Neoseiulus (Amblyseius) cucumeris* (Oudemans), that prey on microarthropods but can reproduce on a pollen diet and utilise plant exudates, honeydew and fungi as food supplements (McMurtry and Croft 1997). Among the 30 species that, by the beginning of this century, are being produced in commercial insectaries on a large scale are four phytoseiid species (van Lenteren 2003a, b).

The success of biological control programmes is, among other factors, dependent on the health of the beneficials that are used. In several cases reports of poor performance in mass-reared phytoseiid mites have raised questions regarding their quality and efficacy in biological control (Steiner 1993a, b; Steiner and Bjørnson 1996; Bjørnson et al. 2000; Raworth and Bjørnson 2002; Blümel and Hausdorf 2002) and have stimulated research in mite pathology (Poinar and Poinar 1998; van der Geest et al. 2000; Bjørnson and Schütte 2003). Moreover, phytoseiid mites are used in several research groups for the study of predator–prey interactions and foraging behaviour (Yao and Chant 1990; Margolies et al. 1997; Dicke et al. 1998; Zemek and Nachman 1999; Janssen 1999; Schausberger and Croft 2000; Maeda et al. 2001; Skirvin and Fenlon 2003a, b). Pathogens may also alter the behaviour of their host (Horton and Moore 1993), thereby influencing outcomes of behavioural research. Hence, care should be taken to maintain healthy laboratory stocks.

Verified and potential pathogens have been reported in phytoseiid mites collected from the field (Furtado et al. 1996), from those currently mass-produced for biological pest control (Beerling and van der Geest 1991a, b; Bjørnson and Keddie 2000; Gols et al. 2007) and from laboratory populations (Hess and Hoy 1982; Becnel et al. 2002; Schütte et al. 2008b; Pukall et al. 2006; Gols et al. 2007). For the latter two cases it could not be determined whether the entities originated from field-collected natural enemies or arose in mass-rearing systems as a result of intense and continuous rearing under laboratory conditions. Mass-reared host populations may be more susceptible to diseases than field populations, as genetic variation is lower and immune responses may be compromised by stress factors including sub-optimal climatic conditions, starvation and overcrowding (Lighthart et al. 1988; Sikorowski and Lawrence 1994). Moreover, in mass-production of arthropods climatic conditions may be better suited for pathogens and horizontal pathogen transmission may be more effective than in natural situations (Sikorowski and Lawrence 1994). These factors may thus enhance disease incidence and the development of novel diseases and/or virulent pathotypes in mass-reared populations. The following review of verified and potential pathogens in phytoseiid mites includes cases with unknown host effects, cases of infection with endosymbiotic bacteria, cases of unidentified diseases and cases of identified diseases, with known pathologies and transmission modes.

Viruses

General characteristics of viruses in insects and mites

Viruses may be defined as biological macromolecules that have the ability to multiply within living cells. They are reported from mites and virtually every insect order and are the smallest of all entomopathogens. These pathogens, comprised of genomic RNA or DNA bound to a protein coat (capsid), are considered the simplest entities capable of replication (Boucias and Pendland 1998). Viral diseases are one of the most widely investigated infections in insects (Tanada and Kaya 1993). Some viruses are occluded at random in proteinaceous occlusion bodies that can be detected under the light microscope, whereas most non-occluded viruses can be detected only with the aid of the electron microscope (Lacey 1997).

In general, infection occurs after viruses have been ingested, but transmission may occur via the host egg (=transovarially), through natural body openings (for example spiracles) or through wounds (Tanada and Kaya 1993). Diagnostic features considered as general characteristics of viral infection in insects include: coloration (white, yellow, light blue, iridescent blue, green, purple or orange) of the gut, the fat body or the entire body, blackening of the body after death, weakening of the outer skin leading to rupturing and release of liquefied body contents (Evans and Shapiro 1997). Infected individuals may show reduced feeding, poor reproduction performance, extended development, extremely extended longevity, body paralysis or lethal sensitivity to CO₂ (Evans and Shapiro 1997). Behavioural changes of insects infected by viruses include: changes in level of activity (wandering behaviour) and changes of microhabitat preference, such as elevation seeking behaviour (=“tree-top” diseases), movement to exposed locations and diurnal behaviour of nocturnal insects (Horton and Moore 1993).

Viruses of phytoseiid mites

Six reports exist on unidentified viruses of phytoseiid mites (Table 1). In all cases virus-like particles were detected in electron microscopic studies, but host effects have not been studied. Unidentified, non-occluded virus-like particles were observed in the yolk of developing eggs inside *N. cucumeris* females (Bjørnson et al. 1997). Also gravid *P. persimilis* females carried unidentified, non-occluded virus-like particles in the yolk of developing eggs (Steiner 1993a; Bjørnson et al. 1997).

Table 1 Viruses recorded in phytoseiid mites

Pathogen	Phytoseiid host/origin ^a	Symptoms	References
Non-occluded virus	<i>Neoseiulus cucumeris/c</i>	Unknown	Bjørnson et al. (1997)
Non-occluded virus	<i>Phytoseiulus persimilis/c</i>	Unknown	Steiner (1993a), Bjørnson et al. (1997)
Virus-like particles	<i>Phytoseiulus persimilis/l</i>	Unknown	Šut'áková and Rüttgen (1978)
Virus-like particles (type 1)	<i>Metaseiulus occidentalis/l</i>	Unknown	Poinar and Poinar (1998)
Virus-like particles (type 2)	<i>Metaseiulus occidentalis/l</i>	Known	Poinar and Poinar (1998)
Virus-like particles (type 3)	<i>Metaseiulus occidentalis/l</i>	Known	Poinar and Poinar (1998)

^a Origin: c, commercial population; l, laboratory population

Phytoseiulus persimilis infected with *Rickettsiella phytoseiuli* contained non-occluded virus-like particles, which both were abundant and visible in the dorsal part of the body, immediately below the cuticle (Šut'áková and Rüttgen 1978). The authors report an interaction of both entities: viruses were only present in the cytoplasm of cells infected with *R. phytoseiuli* and morphological and structural changes were induced in *R. phytoseiuli* when the host was also carrying the virus-like particles (Šut'áková and Rüttgen 1978).

Three separate types of non-occluded icosahedral virus-like particles were detected in ultrastructural micrographs of *M. occidentalis*. The predatory mites originated from populations showing the following disease symptoms: adult female predators had a lower egg production, reduced longevity, died suddenly and had a paralyzed appearance after death (Poinar and Poinar 1998). The authors clearly state that particles located in the epithelial cells (diameter = 47 nm, electron dense core 35 nm) were not associated with any particular disease symptom. These particles were similar to particles found in epithelial cells of healthy as well as diseased prey mites *Tetranychus urticae* Koch (Poinar and Poinar 1998). A second type of particles (diameter = 38 nm, electron dense core 30 nm) was present in the gut cells. These particles were found in large numbers in the midgut nuclei and as free virions in the cytoplasm of the gut cells and the midgut lumen (Poinar and Poinar 1998). The third type of particles (diameter = 45 nm, electron dense core 35 nm) was only present in the gut tissue. The authors do not give any detailed information whether the latter two types of viruses were only found in predatory mites showing disease symptoms. They also did not perform experiments to show whether these viruses are the primary source of infection or rather secondary invaders. However they suggest that viruses may be important disease agents in mites and that they may be present as latent as well as overt infections (Poinar and Poinar 1998).

Bacteria

General characteristics of bacteria in insects and mites

Bacteria are unicellular prokaryotes, their genetic information being contained within a single, double-stranded DNA molecule and small self-replicating DNA molecules termed plasmids or prophages (Boucias and Pendland 1998). Many bacteria are opportunistic pathogens that may exist in nature as saprophytes and may become pathogenic if conditions are favourable. Others are more fastidious and can grow only in the appropriate host (Boucias and Pendland 1998).

Bacterial pathogens invade their hosts mostly through the mouth and digestive tract. Less often, they are transmitted through the egg, trachea or wounds in the integument (Tanada and Kaya 1993). Upon invasion, bacterial pathogens may develop as intracellular pathogens (Rickettsiaceae) or extracellular pathogens (many opportunistic bacteria). Bacterial infections may be classified as (1) bacteremia, when bacteria multiply in the hemolymph of the host without producing toxins; (2) septicaemia, when bacteria multiply in the hemocoel and may produce toxins and kill the host; or (3) toxemia, when bacteria stay confined to the gut lumen where they produce toxins (Tanada and Kaya 1993).

Diagnostic features considered as general characteristics of bacterial infection include: distinct colour changes (white, red, amber, black or brown), reduced feeding, stopping of feeding, excretion of diarrhoea-like feces, vomiting, weakening of the outer skin, degeneration of internal tissues, cadavers becoming black, odiferous, shrivelled, dry and hard (Tanada and Kaya 1993; Lacey 1997).

The vast majority of research on bacterial insect pathogens over the past 30 years has focused on the toxin-producing *Bacillus* species (Boucias and Pendland 1998). However, studies on the effects of β -exotoxin from *Bacillus thuringiensis* on phytoseiid mites are not included in the present review as they do not represent a pathogen in the true sense of the word (for a review see van der Geest et al. 2000). Only very little work has been done on other bacterial pathogens. This is mainly due to the fact that bacteria isolated from insects that have been described as opportunistic pathogens belong to genera containing species that may infect plants and vertebrates, which makes them less interesting for the development as microbial control agents (Boucias and Pendland 1998). Several entomopathogenic species have been identified in the genus *Serratia* including *S. marcescens*. Various entomopathogenic strains of *S. marcescens* are characterised by the production of enzymes and exocellular toxins. However, it is still unclear whether this pathogen is able to actively invade its host. In many cases diseases have been associated with poor sanitation and crowded rearing conditions (Boucias and Pendland 1998).

Bacteria belonging to the family Rickettsiaceae are obligately intracellular and multiply in eukaryotic cells. Entomopathogens of this group belong to the genera *Rickettsia*, *Rickettsiella* and *Wolbachia* (Boucias and Pendland 1998). Members of the genus *Rickettsiella* are common pathogens, whereas those of the genus *Wolbachia* are seldom pathogenic in the true sense but have evolved various means to manipulate their hosts in order to enhance their own transmission (see Stouthamer et al. 1999).

The genus *Rickettsiella* is comprised of a heterogeneous group of bacteria, all members being highly fastidious arthropod pathogens. A lack of homology has been demonstrated for certain members of this genus, suggesting the eventual revision of this group (Boucias and Pendland 1998). *Rickettsiella* have developmental cycles involving the production of various cell phenotypes. The infectious particle is a small, dense rod or disc-shaped cell. All species are transmitted by feeding or through wounds. Many *Rickettsiella* undergo extensive replication in the fat body following ingestion and penetration of the alimentary tract. At present relatively few species associated to insects have been found (Boucias and Pendland 1998). Rickettsial infections may induce prominent behavioural changes in the host, including elevation-seeking behaviour and changes in temperature preference (Horton and Moore 1993).

Wolbachia are common cytoplasmic symbionts of insects, crustaceans, mites and filarial nematodes (see Stouthamer et al. 1999). They are rarely pathogenic but may manipulate the host biology by inducing parthenogenesis (whereby infected females exclusively produce daughters), feminisation (whereby infected genetic males reproduce as females), male-killing (whereby infected male embryos die, while female embryos develop into infected females), cytoplasmic incompatibility (unidirectional in its simplest form: whereby the crossing of an uninfected female and an infected male may result in embryo mortality), or by enhancing host fecundity (Stouthamer et al. 1999).

Wolbachia may be present in various tissues but are predominately present in gonadal tissue (Stouthamer et al. 1999). The symbionts are transmitted vertically through the egg. Therefore, infected mothers give rise to infected offspring. Phylogenetic studies of *Wolbachia* indicate that horizontal transmission must have taken place rather frequently. An intraspecific horizontal transfer of *Wolbachia* has recently been reported (Huigens et al. 2000). Because culturing of *Wolbachia* outside hosts has been successful in only one case, molecular techniques such as the polymerase chain reaction (PCR) are used in detecting *Wolbachia* infections (Stouthamer et al. 1993).

Recently a novel lineage of intracellular bacteria has been shown to be associated with several reproductive disorders, including (1) parthenogenesis in a number of parasitoid

wasps in the genus *Encarsia* (Zchori-Fein et al. 2001, 2004), (2) feminization in several *Brevipalpus* mite species (Weeks et al. 2001; Groot and Breeuwer 2006), and (3) cytoplasmic incompatibility in *Encarsia pergandiella* Howard (Hunter et al. 2003). Phylogenetic analysis of the 16S rRNA gene placed this bacterium in the *Bacteroidetes* group (= *Cytophaga-Flexibacter-Bacteroides* or CFB group). This bacterium has been called the *Encarsia* bacterium (Zchori-Fein et al. 2001), the CFB-BP (Weeks and Breeuwer 2003), and the *Cytophaga*-like organism (CLO) (Hunter et al. 2003; Weeks et al. 2003; Weeks and Stouthamer 2004). Recently it has been suggested to classify this symbiont from *Encarsia* as “*Candidatus Cardinium hertigii*” (Zchori-Fein et al. 2004). A large screening study has shown that the bacterium is prevalent among arthropods, and that double infection with *Wolbachia* may occur (Weeks et al. 2003).

Members of the bacterial genus *Spiroplasma* have also been shown to interfere with reproduction in their arthropod hosts. They are referred to as sex ratio organisms or SRO's and they cause the total elimination of the male progeny in several species. The genus *Spiroplasma* is very diverse, containing species that may infect plants, insects and vertebrates (Boucias and Pendland 1998). Several species are well known insect pathogens whereas others are known as SRO's and for others no effects have been recorded (Boucias and Pendland 1998).

Bacteria of phytoseiid mites

The majority of the identified bacteria recorded in phytoseiid mites are intracellular bacteria of the genera *Rickettsiella*, *Wolbachia*, *Cardinium* and *Spiroplasma* (Table 2). *Wolbachia* seem to be widespread among phytoseiid mites, as they are found by several authors in numerous populations of seven phytoseiid species.

Rickettsiella phytoseiuli

Intracellular, rickettsia-like entities named *Rickettsiella phytoseiuli* have been observed during microscopic studies of *P. persimilis* (see for a review Šut'áková 1994). Predators originated from a laboratory population of the Ukraine (Šut'áková and Rüttgen 1978) and did not show developmental abnormalities, morphological changes or increased mortality. However, all investigated mites contained polymorphous entities that were considered to represent six different stages of the reproduction cycle: dense, intermediate, bacterial, giant, crystal-forming and small dark particles (Šut'áková and Rüttgen 1978). In adult mites, infection was detected in all organs except the nervous tissue, whereas larvae and nymphs and prey spider mites (*T. urticae*) were never infected with *R. phytoseiuli* (Šut'áková 1988, 1991). A *P. persimilis* population from Slovakia exhibited the same infection, whereas a population from the Armenian Republic did not. However, other apparently symbiotic microorganisms were present in the ovaries of predators from the latter population (Šut'áková and Arutunyan 1990). *Rickettsiella phytoseiuli* isolated from *P. persimilis* could be cultivated in adult female *Dermacentor reticulatus* Fabricius ticks, where it formed all six known developmental stages (Šut'áková and Reháček 1989). Pathological effects were never recorded, though some individuals carried the microbes in high densities (Šut'áková 1991).

Endosymbiotic bacteria including *Wolbachia*, *Cardinium* and *Spiroplasma*

By using molecular methods (PCR with *Wolbachia*-specific primers), *Wolbachia* endosymbionts were detected in eight of nine laboratory populations of *M. occidentalis* and in four

Table 2 Bacteria recorded in phytoseiid mites

Pathogen	Phytoseiid host/origin ^a	Symptoms	References
<i>Rickettsiella phytoseiuli</i>	<i>Phytoseiulus persimilis</i> /l	Unknown	Šut'áková and Rüttgen (1978)
<i>Wolbachia</i>	<i>Galendromus annectens</i> /?	Unknown	Weeks et al. (2003)
	<i>Phytoseiulus longipes</i> /?	Unknown	Weeks et al. (2003)
	<i>Metaseiulus occidentalis</i> /l	Known ^b	Johanowicz and Hoy (1996), Breeuwer and Jacobs (1996), Weeks et al. (2003)
	<i>Neoseiulus barkeri</i> /f	Unknown	Breeuwer and Jacobs (1996)
	<i>Neoseiulus bibens</i> /l	Unknown	Breeuwer and Jacobs (1996)
	<i>Phytoseiulus persimilis</i> /c	Unknown	Steiner (1993b), Breeuwer and Jacobs (1996), Bjørnson et al. (1997), Weeks et al. (2003)
	<i>Proprioseiopsis lenis</i> /l	Unknown	Corpuz-Raros (2005)
<i>Cardinium</i>	<i>Metaseiulus occidentalis</i> /l, f	Known ^b	Weeks et al. (2003), Weeks and Stouthamer (2004), Hoy and Jeyaparakash (2005)
	<i>Euseius finlandicus</i> /f	Unknown	Enigl and Schausberger (2007)
<i>Spiroplasma</i>	<i>Neoseiulus californicus</i> /l	Unknown	Enigl and Schausberger (2007)
<i>Bacteroidetes</i> & <i>Enterobacter</i>	<i>Metaseiulus occidentalis</i> /l, f	Unknown	Hoy and Jeyaparakash (2005)
<i>Acaricomus phytoseiuli</i>	<i>Phytoseiulus persimilis</i> /l, c	Known ^b	Schütte (2006), Schütte et al. (1995, 1996, 1998, 2006a, b, 2008a, b), Dicke et al. (2000), Pukall et al. (2006), Gols et al. (2007)
Unidentified bacteria	<i>Metaseiulus occidentalis</i> /l	Known	Hess and Hoy (1982)
	<i>Phytoseiulus persimilis</i> /c	Unknown	Steiner (1993b), cited in Schütte et al. (2005)
	<i>Neoseiulus cucumeris</i> /?	Unknown	Cited in Schütte et al. (2005)
	<i>Neoseiulus barkeri</i> /?	Unknown	Cited in Schütte et al. (2005)

^a Origin: c, commercial population; l, laboratory population; f, field population; ?, unknown

^b Symptom induction established by experiments

laboratory populations of *T. urticae* that served as food for *M. occidentalis* (Johanowicz and Hoy 1996). In *M. occidentalis*, *Wolbachia* caused non-reciprocal reproductive incompatibilities between infected males and uninfected females. Uninfected females crossed with infected males produced few eggs and no female progeny. Many of the produced eggs were shrivelled (Johanowicz and Hoy 1998b). The mechanisms by which *Wolbachia* cause reproductive incompatibilities in *M. occidentalis* are unknown. *Wolbachia* infection seems to be associated with fitness costs as the number of female progeny was lower in infected control crosses than in uninfected control crosses. These fitness costs may have prevented the rapid spread of *Wolbachia* in three laboratory populations of *M. occidentalis* (Johanowicz and Hoy 1999). *Wolbachia* were eliminated from *M. occidentalis* when the predators were reared at an elevated temperature (33°C) (Johanowicz and Hoy 1998a, b).

Moreover, Breeuwer and Jacobs (1996) detected *Wolbachia* in a population of *M. occidentalis* from the USA, in a commercial population of *P. persimilis* from the

Netherlands, in a population of *Neoseiulus (Amblyseius) barkeri* Hughes collected in the Netherlands and a population of *Neoseiulus (Amblyseius) bibens* Blommers from Madagascar. *Wolbachia*-infection has also been found in *Galendromus annectens* (De Leon) and *Phytoseiulus longipes* Evans (Weeks et al. 2003) and in a laboratory stock of *Proprioseiopsis (Amblyseius) lenis* (Corpuz-Raros & Rimando) from the Philippines (Corpuz-Raros 2005). The effects of *Wolbachia* on the species other than *M. occidentalis* have not yet been investigated, but it is likely that *Wolbachia* are associated with non-reciprocal reproductive incompatibilities (for a discussion, see Breeuwer and Jacobs 1996). Rickettsia-like particles, belonging to the genus *Wolbachia* were also reported by Steiner (1993b); Bjørnson et al. (1997). The latter author detected with molecular methods that *Wolbachia* was present in commercial *P. persimilis* populations from seven sources. It even has been suggested that the intracellular bacteria of *P. persimilis* named *Rickettsiella phytoseiuli* (Šut'áková and Rüttgen 1978) and the rickettsia-like microorganisms observed in *M. occidentalis* (Hess and Hoy 1982) may in fact be *Wolbachia* (for a discussion see van der Geest et al. 2000).

However, recently Enigl et al. (2005) screened several strains of *P. persimilis* (seven strains obtained from Europe, Africa and the USA and alcohol samples of 10 other strains) for the occurrence of *Wolbachia* and no sample tested positive. They therefore suggested that infection of *P. persimilis* with *Wolbachia* seems to be rare and of minor importance (Enigl et al. 2005). During this study *T. urticae* used as food for the different strains of *P. persimilis* was infected with *Wolbachia*. The authors prevented false positive results from undigested prey by starving *P. persimilis* or feeding them *Wolbachia*-free *T. urticae* before the PCR tests. After a period of 16 h at 25°C and 48 h at 20°C *Wolbachia* was no longer detected in the predators (Enigl et al. 2005). Moreover, the same authors could not detect *Wolbachia* in six other phytoseiid species, including *N. cucumeris*, *N. barkeri*, *Euseius finlandicus* (Oudemans), *Kampimodromus aberrans* (Oudemans), *N. californicus* and *Typhlodromus pyri* Scheuten (Enigl and Schausberger 2007).

In a large-scale survey of arthropod hosts infection with the endosymbiotic bacterium *Candidatus Cardinium hertigii* was detected by sensitive hemi-nested PCR in *M. occidentalis* (Weeks et al. 2003). Test results were negative for *P. persimilis*, *Phytoseiulus macropilis* (Banks), *Neoseiulus (Amblyseius) fallacis* (Garman), *M. longipes*, *Galendromus helveolus* (Chant) and *G. annectens*. Interestingly *M. occidentalis* showed double infection of *Wolbachia* and *Cardinium*. In another study Weeks and Stouthamer (2004) reported that three inbred lines of *M. occidentalis* showed a clear and significant increase in fecundity associated with infection by *Cardinium*. Fecundity advantage of infected females versus non-infected females was approximately 1.6 times over a 6-day oviposition period. As the endosymbiont described by Hess and Hoy (1982) has recently been identified as *Cardinium* (Weeks and Breeuwer 2003) and as *M. occidentalis* may harbour both *Wolbachia* and *Cardinium* at the same time, the authors suggest that the results of the studies of Johanicz and Hoy (1998a) on cytoplasmic incompatibility in *M. occidentalis* may have been influenced by the presence of *Cardinium* (Weeks et al. 2003). In a molecular screening, using a high-fidelity PCR protocol (allowing the detection of as few as 100 copies of *Wolbachia* DNA, Jeyaprakash and Hoy 2004), several bacterial species were detected in *M. occidentalis* after the clones were sequenced: one each was closely related to species in the genera *Enterobacter*, *Wolbachia* and *Cardinium*, and one was related to an unnamed microorganism in the phylum *Bacteroidetes* (Hoy and Jeyaprakash 2005). PCR tests with newly designed primers for the sequences of the detected bacteria were positive for several laboratory and field-collected *M. occidentalis* populations suggesting that all bacteria are important in the biology of this phytoseiid species (Hoy and Jeyaprakash 2005).

In a recent survey Enigl and Schausberger (2007) screened several predatory mite species with a PCR technique for infection with *Cardinium* and *Spiroplasma*. *Cardinium* was detected in two populations of *E. finlandicus*. Test results were negative for *N. cucumeris*, *N. barkeri*, *K. aberrans*, *N. californicus* and *T. pyri*. *Spiroplasma* was found in *N. californicus*. Test results were negative for *N. cucumeris*, *N. barkeri*, *E. finlandicus*, *K. aberrans* and *T. pyri*. However, it is not very probable that *Spiroplasma* is a pathogen or SRO in this case, as in an earlier study *Spiroplasma* did not have any effect on the number of eggs produced and the percentage of female offspring of *N. californicus* (Zchori-Fein et al., unpublished data, cited in Enigl and Schausberger 2007).

Acaricomes phytoseiuli

Lighthart et al. (1988) were the first to show susceptibility of a predatory mite to a bacterial pathogen. The authors tested the effect of several stress factors on the susceptibility of *M. occidentalis* to the weak bacterial pathogen *Serratia marcescens*. A high pre-inoculation temperature pulse under relatively uncrowded conditions was most effective in enhancing susceptibility, higher mortality being the only disease symptom. Remarkably, starvation did not have such an effect. However, the bacterial isolate did not originate from mites.

Thus, the only well documented case of a bacterial disease in phytoseiid mites represents the infection of *P. persimilis* with *Acaricomes phytoseiuli* (Schütte 2006; Schütte et al. 1995, 1996, 1998, 2006a, b, 2008a, b; Dicke et al. 2000; Pukall et al. 2006; Gols et al. 2007). During the early 1990s the first conspicuous disease symptom that became obvious was a behavioural change (Schütte et al. 1995; Dicke et al. 2000). An important behavioural characteristic of healthy adult female *P. persimilis* is their attraction to plant odours, currently called “herbivore-induced plant volatiles” (HIPV), which are released in response to feeding damage by their prey *T. urticae* (Sabelis and van de Baan 1983; Dicke and Sabelis 1988). Since 1983 this behavioural response has been reported in numerous laboratories (see reviews by Dicke et al. 1998, Sabelis et al., 1999) and it has been shown that it plays an important role in successful host location in the field (Zemek and Nachman 1999; Janssen 1999). However, since mid 1992 a laboratory population of *P. persimilis* showed a lower degree of attraction to herbivore-induced plant volatiles than in the first part of 1992 and the previous year. This so-called non-responding (=NR) population originated from the normally responding population from a Dutch natural enemy producer and had been reared in the laboratory for many years prior to 1992. The behavioural change occurred suddenly and was of a permanent nature. Moreover at the beginning of 1994 the same behavioural change occurred in a population of *P. persimilis* from a commercial source (Dicke et al. 2000). A similar phenomenon had occurred earlier in two other species of phytoseiid mites reared at the same laboratory. Between July 1985 and November 1987 the attraction to herbivore-induced plant volatiles fluctuated widely in three laboratory populations of *Amblyseius potentillae* (Garman) (= *Amblyseius andersoni* (Chant)) and one laboratory population of *T. pyri* (Dicke et al. 1991). Several possible causes for this variation were investigated, but no definite conclusions could be drawn (Dicke et al. 1991).

As several experiments on the behavioural change in *P. persimilis* indicated that it was most probably caused by an infectious agent (Schütte et al., unpublished; Dicke et al. 2000), follow-up studies aimed at verifying this hypothesis. A crucial first step towards verification of this hypothesis was evidence of the infectious character of the behavioural change. Mated female *P. persimilis* that had been exposed to dead conspecifics of the NR-population and their products showed a lower degree of attraction and a higher

mortality than predators that had been exposed to the products of live conspecifics of the NR-population (Schütte et al. 1998). In a diseased population early dying individuals are likely candidates to carry and release pathogens and common routes of disease transmission consist of pathogen release prior to or after death and cannibalism on dead conspecifics (Andreadis 1987).

In a comparative study other characteristics of the NR-population were investigated in order to describe a distinct disease syndrome, designated the 'non-responding (=NR) syndrome' (Schütte et al. 2006a). The following set of symptoms was described for adult females from the NR-population: (1) size change by shrinkage to dorso-ventrally flattened form, (2) reduced fecundity caused by oviposition stop after shrinkage, (3) high mortality several days after shrinkage, (4) presence of excretory crystals in the legs, (5) low predation and/or feeding rate, (6) low excretion rate, (7) low degree of attraction to prey-induced plant volatiles, (8) short choice time during behavioural test, (9) early dispersal from prey-patches (Schütte et al. 1995, 2006a). Interestingly there are several publications in which remarkable peculiarities of *P. persimilis* have been stated, that are similar to the NR-syndrome among which (1) poor performance in terms of fecundity and survival (Steiner 1993a, b; Steiner and Bjørnson 1996; Raworth and Bjørnson 2002; Blümel and Hausdorf 2002); (2) poor performance in terms of life span (De Courcy Williams et al. 2004a); (3) size change by shrinkage to dorso-ventrally flattened form (Bjørnson et al. 2000); (4) remarkable effect of rearing condition on olfactory response (Maeda et al. 2000); (5) remarkable differences in dispersal behaviour (van de Vrie and Price 1997; Skirvin and Fenlon 2003a); (6) unusual results concerning the predation rate (Skirvin and Fenlon 2003b). However, most of these studies did not consider or test the possibility of pathogen infection (for a detailed discussion see Schütte 2006).

Several routes of transmission were investigated for six of the nine symptoms of the NR-syndrome. There was no evidence for (1) vertical transmission, i.e. transmission from parent to offspring directly via the egg, (2) interspecific horizontal transmission between the prey *T. urticae* and adult female *P. persimilis*, (3) horizontal transmission via body fluids, i.e. from squashed female predators to female *P. persimilis* (Schütte et al. 2006b). Instead there was clear evidence for horizontal transmission between and among generations via feces and debris released by diseased adult female *P. persimilis* (Schütte et al. 2006b). After contact with feces and debris deposited by diseased females during only 1 day, the majority of healthy female *P. persimilis* (65%) became dorso-ventrally flattened after only 3 days. From eggs laid by diseased mothers a minority of the offspring became dorso-ventrally flattened (17%) when adult. This was only the case, when the eggs were left on the place where the mother had laid them (Schütte et al. 2006b).

With knowledge about the main reservoir of the infectious agent it could be determined to which group the pathogen in question belongs (Schütte et al. 2008a). A reliable bioassay for testing the infectiousness of predator feces and debris fractions was developed, by keeping healthy adult female predators during a period of 3 days on prey-infested bean leaves, which had previously been sprayed with an aqueous suspension of feces and debris. After exposure six of the nine symptoms as listed above were assessed. A vast majority of healthy female *P. persimilis* (88–100%) became dorso-ventrally flattened after contact with a feces and debris suspension collected from symptomatic females. This effect vanished totally when the suspension was treated with the antibiotic tetracycline. Moreover did the bacterial fraction of feces and debris suspension collected from symptomatic predators induce the NR-syndrome whereas the viral fraction of the same suspension did not (Schütte et al. 2008a). These findings proved that bacteria are involved in the induction of the NR-syndrome.

Numerous bacterial isolates from mated female predators from the NR-population and their feces and debris were tested for their effects on healthy adult female *P. persimilis* (Schütte et al., unpublished data). The final aim, namely satisfying the Koch's postulates of pathogenicity was achieved with only one isolate, representing a new bacterial species in a new genus, described as *Acaricomex phytoseiuli* (Pukall et al. 2006). The NR-syndrome was clearly induced in those predators that had been exposed to the bacterial inoculum (=treatment predators), whereas predators exposed to water (=control predators) did not show the NR-syndrome. Moreover, *A. phytoseiuli* was never isolated from control predators whereas it could be re-isolated from 60% of the treatment predators and from feces of 41% of treatment predators (Schütte et al. 2008b). Light and electron microscopic studies of predators exposed to *A. phytoseiuli* revealed striking bacterial accumulations in the lumen of the alimentary tract together with extreme degeneration of its epithelium. In addition, bacterial foci also occurred in the fat body. These phenomena were not observed in control predators that had been exposed to sterile water (Schütte et al. 2008b). Thus *A. phytoseiuli* may infect the predatory mite *P. persimilis* and induce the occurrence of the NR-syndrome in adult female *P. persimilis*.

Acaricomex phytoseiuli is a gram-positive, rod-shaped, none-spore-forming bacterium. Comparative analysis of the 16S rDNA sequence revealed that the strain was a new member of the family of the Micrococcaceae. Nearest phylogenetic neighbours were determined as *Renibacterium salmoninarum* (94.0%), *Arthrobacter globiformis* (94.8%) and *Arthrobacter ruscicus* (94.6%) (Pukall et al. 2006). It appears that the new genus *Acaricomex* is closely related to the genus *Arthrobacter*. Recently a specific and reliable PCR-test has been developed for the detection of *A. phytoseiuli* (Gols et al. 2007). In two validation tests healthy female *P. persimilis* were previously infected with *A. phytoseiuli*. In one test 36% of the predators had become symptomatic and 38% of the predators tested positive; in the second test 70% of the predators had become symptomatic and 61% of the predators tested positive. Moreover a significant negative correlation was found between the proportion of predators being attracted to herbivore induced plant volatiles and the proportion of PCR-positive samples (Gols et al. 2007). By using this molecular detection method it was demonstrated that *A. phytoseiuli* is rather widespread among European populations of *P. persimilis*. All but one of the seven European populations of *P. persimilis* tested were *A. phytoseiuli*-positive, whereas two populations from outside Europe turned out to be negative. The prey mite *T. urticae* and other commercially used predatory mite species including *A. andersoni* (= *A. potentillae*), *N. cucumeris*, *Iphiseius* (*Amblyseius*) *degenerans* (Berlese), *N. californicus*, *Hypoaspis aculeifer* Canestrini and *Hypoaspis miles* Berlese, were not infected (Gols et al. 2007). It can thus be concluded, that *A. phytoseiuli* is currently infecting several populations of commercial and laboratory populations of *P. persimilis*, and that it has detrimental effects on them. Screening of populations on a regular basis for an infection with *A. phytoseiuli* should therefore be executed, as in this case a reliable detection method has been developed. Possible methods of curing infected populations consist of antibiotic treatment (Schütte et al. 2008a) and washing of eggs with bleach (Schütte et al. 2006b).

Unidentified bacteria

Hess and Hoy (1982) observed two different pathological manifestations in several laboratory populations of *M. occidentalis*. (1) Some adult females were plump and had a cream-coloured to pink rectal "plug" that extruded from their posterior end and occasionally caused mites to become glued to the substrate. The rectal plug was associated with

motor dysfunction, reduced oviposition and eventually death, and was most common in older females. Immatures and males rarely had rectal plugs. (2) Mites became very pale and so thin that they became translucent. Females failed to oviposit, immatures exhibited high mortality and colonies died out. According to the authors both pathologies were associated with overcrowding (Hess and Hoy 1982). The authors described two morphologically distinct unidentified micro-organisms in symptomatic and non-symptomatic *M. occidentalis*. Whether these forms represent one or two species was not established. One form (which they called type A) was exclusively intracellular. This type was present in all mites in varying numbers and in all tissues examined, except ovarian and nervous tissues. According to the authors this micro-organism did not appear to be detrimental. The second rickettsia-like form (type B) occurred both intra- and extracellularly. This type was present in two-thirds of symptomatic and asymptomatic mites. In some cases it completely dominated the internal organs and the hemocoel and was associated with the rectal plug. Thin and pale mites also contained predominantly the second type, but tissues of these mites appeared more damaged, perhaps accounting for their lucidity. When present in moderate numbers, these micro-organisms were observed in the hemocoel, the Malpighian tubules and within the ovarian tissue, which may suggest transovarial transmission (Hess and Hoy 1982). The authors did not determine whether the increase of the second bacterial type was the primary cause of the disease or a secondary effect. Later it has been suggested that the rickettsia-like microorganisms (type B) may in fact be *Wolbachia* (for a discussion see van der Geest et al. 2000) and that the endosymbiont (type A) is likely to be *Cardinium* (Weeks and Breeuwer 2003).

In a microscopic study of the digestive tract of *P. persimilis*, bacteria-like entities detected in the gut lumen were thought to have entered the digestive tract during feeding (Arutunyan 1985). However, these bacteria bear a marked similarity to birefringent dumbbell-shaped crystals that are frequently observed in the Malpighian tubules, the digestive tract and rectum of phytoseiid mites (Steiner 1993b; Schütte et al. 1995; Di Palma 1996; Bjørnson et al. 1997, 2000; R. G. Kleespies, pers. comm.).

Bacterial micro-organisms other than rickettsia have been recorded for dead and moribund *P. persimilis* (Steiner 1993b). However, the author stated that these bacteria are secondary opportunistic invaders rather than a primary infection source. Moreover unidentified bacteria were reported in microscopic investigations of several diseased mite populations of *P. persimilis*, *N. cucumeris* and *N. barkeri* (cited in Schütte et al. 2005).

Protozoa

General characteristics of protozoa in insects and mites

All protozoa recorded for phytoseiid mites belong to the phylum Microspora. Microsporidia are small, spore-forming protozoa. However, recent molecular studies indicate that they are related to fungi, which may in part explain the sensitivity of microsporidia to selected anti-fungal drugs (Boucias and Pendland 1998). Microsporidia infect a wide range of hosts from all major animal phyla, fish and arthropods being their most common hosts (Tanada and Kaya 1993). They are obligate intracellular parasites that lack typical mitochondria, a classical Golgi apparatus, centrioles and peroxisomes (Boucias and Pendland 1998). Many species cause severe and acute infections in insects, but some produce only inapparent and chronic infections, that nonetheless may play an important role in host regulation (Tanada and Kaya 1993).

The microsporidia have a complex biology that may involve two obligate hosts, vertical or horizontal transmission and/or multiple cell-types (Boucias and Pendland 1998). The life cycle consists of two phases, the vegetative phase and the sporulation phase, which results in the production of transmissible spores. In most cases the spore-to-spore cycle takes place in one cell (Tanada and Kaya 1993). Microsporidia may invade the host tissues when spores are ingested, when the pathogen is transmitted from parent to progeny, or occasionally through wounds in the integument (Tanada and Kaya 1993). Microsporidian spores are structurally unique and contain a characteristic tube-like polar filament through which an infective stage (sporoplasm) is injected into an adjacent host cell. This starts the infective cycle of the pathogen.

Diagnostic features considered as general characteristics of microsporidian infection are variable and may include: retardation of development and growth, reduced activity, abnormal coloration, diapause alterations, reduction of longevity and reproductive performance (Boucias and Pendland 1998). Microsporidia-infected insects may also exhibit behavioural changes including changes in temperature preference (Horton and Moore 1993).

Protozoa of phytoseiid mites

Microsporidia seem to be rather common among phytoseiid mites. Microsporidiosis has been observed in four phytoseiid species of varying origin (Table 3).

Oligosporidium occidentale

A new microsporidian pathogen has recently been isolated from a laboratory population of *M. occidentale* (Becnel et al. 2002). Immature stages and mature spores were found in the cytoplasm of ceacal cells, lyrate organ cells, ganglia, epithelial cells, muscle, ovary and mature eggs (Becnel et al. 2002). Microsporidia were never detected in the spider mite (*T. urticae*) prey of *M. occidentale* (Olsen and Hoy 2002). Two classes of uninucleate spores were produced, differing primarily in the length of the polar filaments and the presence of a large posterior vacuole in one spore type (Becnel et al. 2002). The authors suspect that spores with long filaments are involved in horizontal disease transmission, which may take place by cannibalism of infected eggs (Olsen and Hoy 2002), whereas

Table 3 Protozoa recorded in phytoseiid mites

Pathogen	Phytoseiid host/origin ^a	Symptoms	References
<i>Microsporidium phytoseiuli</i>	<i>Phytoseiulus persimilis</i> /c	Known ^b	Bjørnson et al. (1996)
<i>Oligosporidium occidentale</i>	<i>Metaseiulus occidentale</i> /l	Known ^b	Becnel et al. (2002)
<i>Nosema steinhausi</i>	<i>Neoseiulus cucumeris</i> /c	Unknown	Huger (1988)
	<i>Neoseiulus barkeri</i> /c	Unknown	Huger (1988)
Unidentified microsporidia	<i>Neoseiulus barkeri</i> /c	Known	Beerling and van der Geest (1991a, b)
	<i>Neoseiulus cucumeris</i> /c	Known	Beerling and van der Geest (1991a, b)
	<i>Phytoseiulus persimilis</i> /c	Unknown	Bjørnson and Keddie (2000)
	<i>Phytoseiulus persimilis</i> /c	Unknown	Bjørnson and Keddie (2000)

^a Origin: c, commercial population; l, laboratory population

^b Symptom induction established by experiments

spores with the short polar filament may play a role in autoinfection and vertical transovarial transmission, that is highly efficient (99% infected offspring is produced by infected parents) (Olsen and Hoy 2002).

Molecular data (analysis of small subunit ribosomal DNA) indicated that this microsporidium is a new species, which is most closely related to the *Nosemal Variomorpha* clade of microsporidia, whereas developmental and morphological data suggest a placement into the genus *Unikaryon* or *Oligosporidium*. The authors discuss this conflict of morphological and molecular data and assign the new species the name *Oligosporidium occidentaleis*.

Predators infected by *O. occidentaleis* did not exhibit any external signs of infections. However, *O. occidentaleis* has clear negative effects on its host. Infected female predators had a shorter life span, a lower oviposition rate and a lower number of female offspring, as infected mites have a male-biased sex ratio (Olsen and Hoy 2002). Heat treatment was effective to cure infected populations of *M. occidentaleis* and did induce relatively low mortality (~20%). Predator colonies initiated from mites that were reared from egg to adult at 33°C showed an initial reduction in infection. However, disease incidence raised to 98% after 10 weeks. Colonies initiated from progeny of the heat-treated mites remained healthy during the observation period of 10 weeks (Olsen and Hoy 2002).

Microsporidium phytoseiuli and unidentified microsporidia in *Phytoseiulus persimilis*

Three distinct species of microsporidia have been reported from *P. persimilis* from three commercial sources. The species assigned as *Microsporidium phytoseiuli* was isolated from a European population (Bjørnson et al. 1996), one unnamed species (A) was found in a population from North America and another unnamed species (B) in a population from Israel (Bjørnson and Keddie 2000). Becnel et al. (2002) suggested that *M. phytoseiuli* may also be a member of the genus *Oligosporidium*, because of a number of biological and morphological similarities with *O. occidentaleis*.

The microsporidia of *P. persimilis* were not restricted to specific tissues and spores were found in muscle fibres, the super- and suboesophageal ganglia, ovaries, eggs, cells underlying the cuticle, and cells lining the caecal lumen and Malpighian tubules. Early development of all three microsporidia occurred in cells of the lyrate organ. The lyrate organ occupies a significant portion of the body and is thought to be involved in oogenesis or embryogenesis. Each microsporidium occupied a specific site within these cells. Infection of the lyrate organ may be necessary for the efficient vertical transmission of microsporidia in *P. persimilis* (Bjørnson et al. 1996; Bjørnson and Keddie 2000).

Microsporidium phytoseiuli was not present in the prey mites, *T. urticae*. Therefore, prey mites did not contribute to pathogen transmission among *P. persimilis* mites. Maternal-mediated vertical transmission of *M. phytoseiuli* was 100%. Males did not contribute to infection of the progeny. Horizontal transmission of *M. phytoseiuli* did not occur when uninfected adult predators were kept together with infected *P. persimilis* females or on leaves carrying solutions of microsporidian spores. Horizontal transmission was low (about 15%) when uninfected immatures were kept together with infected adult and immature mites (Bjørnson and Keddie 2001). At present little is known regarding the mechanisms of transmission.

Microsporidia-infected *P. persimilis* did not exhibit any obvious external symptoms. Therefore, routine monitoring is necessary to detect microsporidia when disease prevalence is low (Bjørnson and Keddie 1999). *P. persimilis* infected by *M. phytoseiuli* produced fewer eggs, had a reduced longevity and lower prey consumption rate than

healthy predators. Moreover, infected females produced fewer female progeny than uninfected females, as the sex ratio of offspring of infected females is male biased (Bjørnson and Keddie 1999).

Several methods to cure an infection with microsporidia were tested by Bjørnson (1998). The antimicrobial compounds albendazole, fumagillin, metronidazole and nifedipine were ineffective for control of microsporidia in *P. persimilis*, regardless of their dose. The author doubted whether the chemical compounds were able to penetrate the egg chorion. Rearing predators at 30°C did not eliminate microsporidian infections either. The Pasteur method, whereby progeny of healthy mothers is selected for the rearing, was the only effective means to eliminate microsporidia from *P. persimilis* populations (Bjørnson 1998).

Unidentified microsporidia and *Nosema steinhausi* in *Neoseiulus cucumeris* and *N. barkeri*

Unidentified microsporidia were reported in commercial mass-rearings of *N. cucumeris* and *N. barkeri* (Beerling and van der Geest 1991a, b). This was the first report of microsporidia in mass-reared predatory mites. Predators of the commercial populations showed a low reproduction rate and unsatisfactory predation capacity. Moreover, mites were sluggish and had a swollen and whitish appearance (Beerling and van der Geest 1991a). Squash preparations of symptomatic mites revealed the presence of numerous microsporidian spores and heavily infected predators released spores after death (Beerling and van der Geest 1991a). Microsporidia were also present in the prey mites but the mechanisms of pathogen transmission have not been determined for this system. Three types of microsporidian spores have been found in *N. cucumeris* and *N. barkeri* (Beerling et al. 1993), but it is unclear whether they represent one species of microsporidia with three different spore types or three distinct species. Oblong spores were detected in both predator and prey species, small and more oval spores were exclusively found in prey mites. Beerling et al. (1993) developed a monoclonal antibody ELISA as a bioassay for the detection of microsporidia in mass-reared *N. cucumeris* and *N. barkeri*. Monoclonal antibodies were produced for one spore type that was present in both predator and prey species. Further work is needed to determine the sensitivity of this test as a suitable screening method for microsporidia in mites. Interestingly, Huger (1988) detected the microsporidium *Nosema steinhausi* in diseased mass-reared populations of the same phytoseiid species (*N. cucumeris* and *N. barkeri*).

Fungi

General characteristics of fungi in insects and mites

Fungi are eukaryotic heterotrophes that obtain nutrients either from dead organic matter (saprobes) or from living organisms (parasites). Some parasitic fungi are obligate pathogens, but the majority are facultative pathogens capable of growing without their host (Tanada and Kaya 1993). Entomopathogenic fungi are characterized by their ability to attach to and penetrate host cuticle or spiracles; however, some penetrate through the gut. They replicate inside the host, usually in the hemocoel, where they compete for soluble nutrients and may release mycotoxins, which interfere with normal host development and metamorphosis and in some cases with the immune defense mechanisms (Boucias and Pendland 1998). Fungi then invade and digest tissues and cause premature death of the

Table 4 Fungi recorded in phytoseiid mites

Pathogen	Phytoseiid host/origin ^a	Symptoms	References
<i>Neozygites</i> sp.	<i>Euseius citrifolius</i> /f	Known	Furtado et al. (1996)
<i>Neozygites acaricida</i>	<i>Euseius citrifolius</i> /f	Unknown	Keller (1997)
<i>N. cf. acaridis</i>	<i>Euseius citrifolius</i> /f	Unknown	Keller (1997)
Unidentified fungi	<i>Phytoseiulus persimilis</i> ?	Unknown	Cited in Schütte et al. (2005)

^a Origin: f, field population; ?, unknown

host. Thereafter the fungus lives as a saprophyte on the cadaver, producing spores. Under unfavorable conditions resting forms are produced (Tanada and Kaya 1993). Adhesion and germination of fungal spores on the host cuticle are highly dependent on relative humidity and temperature, but light conditions and nutritional requirements are also important factors (Tanada and Kaya 1993).

Diagnostic features considered as general characteristics of fungal infection may include: blackening surfaces at sites where fungi have penetrated, coloration (white, yellow, black), reduced feeding, the presence of filamentous hyphae, the presence of characteristically coloured reproductive structures (fruiting structures, spores) on the external surface of the dead host, weakness and partial paralysis, bodies may be hard (Boucias and Pendland 1998).

In some cases, behavioural changes occur prior to death. Symptoms in insects may include restlessness, loss of coordination and body tremors, reproductive behaviour by castrated hosts and changes in microhabitat preference (Horton and Moore 1993; Boucias and Pendland 1998). The latter include elevation-seeking behaviour (fungal “summit disease”), movement to exposed locations, change in oviposition or foraging sites and change in temperature preference (Horton and Moore 1993).

Fungi in phytoseiid mites

Pathogenic fungi have been recorded for only two phytoseiid species up to now (Table 4). Field-collected *Euseius citrifolius* Denmark and Muma were heavily infected by the fungus *Neozygites* sp. (Furtado et al. 1996) and showed a high rate of mortality. Some cadavers carried near-white hyphae that produced pear-shaped conidia. However, *Neoseiulus* (*Amblyseius*) *idaeus* Denmark and Muma and *Typhlodromalus* (*Amblyseius*) *limonicus* (Garman and McGregor) were not infected by *Neozygites* sp. isolated from the cassava green mite in laboratory tests (De Moraes and Delalibera 1992). *Euseius citrifolius* collected in Brazil on two subsequent occasions contained viable resting spores and hyphal bodies of two distinct fungal species identified as *Neozygites acaricida* and *N. cf. acaridis* (Keller 1997). Moreover unidentified fungi were reported in microscopic investigations of a diseased population of *P. persimilis* (cited in Schütte et al. 2005).

Unidentified diseases

General characteristics in insects and mites

Insect diseases may be broadly categorised as either infectious or non-infectious, based on the respective presence or absence of a transmissible living organism. Diseases classified

as non-infectious may be caused by mechanical injury, adverse physical environmental factors, chemical agents, injuries made by predators and parasitoids, genetic factors, nutritional deficiencies and hormonal disruption (Tanada and Kaya 1993). Traditionally, insect pathologists have focused their research on infectious diseases that might be caused by a variety of pathogens. However, non-infectious diseases may play an important role in insect populations (Tanada and Kaya 1993). Thus, in cases of obvious detrimental symptoms where the involvement of pathogens cannot be proved, pathogens may not (yet) be detectable or other factors may cause the disease.

Unidentified diseases of phytoseiid mites

For phytoseiid mites several reports exist on poor performance, anatomical peculiarities and peculiar colorations (Tanigoshi et al. 1981; Tanigoshi 1982; Hess and Hoy 1982; Bjørnson et al. 1997, 2000). However, in these cases it was not unambiguously shown that pathogens may have been involved (Table 5).

Tanigoshi et al. (1981) observed the formation of a dark-red occlusion within the alimentary tract near the distal end of the opisthosoma for *Euseius (Amblyseius) hibisci* (Chant) of both sexes when fed exclusively on *Panonychus citri* (McGregor). Newly eclosed *E. hibisci* larvae acquired a red coloration of the gut directly after feeding and became less robust and vigorous after each moult. Complete immature mortality occurred at 32 and 35°C. Immediately after the last moult female predators became dorso-ventrally flattened, more concave in profile, lethargic, did not lay eggs and exhibited the characteristic dark-red gut occlusion prior to their death. The pigmented mass inside the mite was thought to be associated with the incomplete digestion of the prey mites, as symptoms were not observed in mites fed a diet of pollen from the ice plant, *Malephora crocea* Jacq. (Tanigoshi et al. 1981).

Birefringent, dumbbell-shaped crystals have been observed in *P. persimilis* from several sources (Bjørnson et al. 1997, 2000). Excessive crystal formation was associated with white discoloration of the opisthosoma. Discoloration may include (1) a white dorsal spot at the distal end of the opisthosoma, (2) two white stripes along the dorsal lateral sides of the body in the region of the Malpighian tubules, or (3) a combination of both forms (Bjørnson et al. 2000). Mites carrying discoloration(s) appeared lethargic and provided poor pest control (Steiner 1993b; Bjørnson et al. 1997). Rectal plugs, which were observed when symptoms were more pronounced, often disrupted normal excretion and might cause the affected individual to become stuck to the leaf surface (Bjørnson et al. 1997). The frequent occurrence of a prominent white dot in the opisthosoma of *P. persimilis* was correlated with reduced fecundity and predation rate in mites examined following shipment from commercial producers (Bjørnson et al. 2000). Crystals were observed in immature and adult *P. persimilis* (Bjørnson et al. 1997); therefore, non-excessive crystal formation is likely a normal physiological process (Bjørnson et al. 1997). An examination of *P. persimilis* from 14 commercial and academic sources revealed no correlation between the occurrence of crystals and the presence of microsporidia, rickettsia or virus-like particles in *P. persimilis*.

Table 5 Unidentified diseases recorded in phytoseiid mites

Pathogen	Phytoseiid host/origin ^a	Symptoms	References
Unidentified	<i>Euseius hibisci</i> /l	Known	Tanigoshi et al. (1981)
Unidentified	<i>Phytoseiulus persimilis</i> /c	Known	Bjørnson et al. (1997, 2000)

^a Origin: c, commercial population; l, laboratory population

(Bjørnson et al. 1997). However, in a follow-up study Bjørnson and Raworth (2003) found that the expression of white opisthosomal discolorations in *P. persimilis* does not necessarily affect predator performance and concluded that the opisthosomal discolorations are an expression of normal excretory function in *P. persimilis* related to plant nutrition (Bjørnson and Raworth 2003).

Conclusions

Several potential pathogens—pathogens in the true sense and unidentified diseases—have been reported for phytoseiid mites. However, the status and impact of many described entities on their host is unclear. Fourteen reports are descriptive with unknown host effects; three reports mention pathological manifestations without proving the final cause of the symptoms and eleven reports describe endosymbiotic bacteria. Only six reports present pathogens in the true sense of the word. From the latter group four reports refer to Microsporidia, one to a bacterium and one to a fungus. Microsporidian infections often appear not to be readily visible as no obvious external symptoms are present and female predators infected by *A. phytoseiuli* may be mistaken for unmated females. Such infections may thus remain undetected for extended periods meanwhile spreading in the case of exchange of predator populations among producers and laboratories. Screening of these pathogens on a regular basis is therefore advisable for maintenance of healthy predator populations over long periods. However, as only few pathogens in the true sense are described up to now it is too early to plead for regular general pathogen screening in phytoseiid mite mass rearings. Yet, the reports on true pathogens, often made in response to unexpected phenomena in a mass rearing, show that pathogens of beneficial mites can be an important factor hampering the quality of the mass-reared mites. The final conclusion of this review therefore is that more research on diseases of beneficial mites that are applied in biological pest control is needed.

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