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Review

Diseases of mites

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Abstract. An overview is given of studies on diseases of mites. Knowledge of diseases of mites is still fragmentary but in recent years more attention has been paid to acaropathogens, often because of the economic importance of many mite species. Most research on mite pathogens concerns studies on fungal pathogens of eriophyoids and spider mites especially. These fungi often play an important role in the regulation of natural mite populations and are sometimes able to decimate populations of phytophagous mites. Studies are being conducted to develop some of these fungi as commercial acaricides.

Virus diseases are known in only a few mites, namely, the citrus red mite and the European red mite. In both cases, non-occluded viruses play an important role in the regulation of mite populations in citrus and peach orchards, respectively, but application of these viruses as biological control agents does not seem feasible. A putative iridovirus has been observed in association with *Varroa* mites in moribund honeybee colonies. The virus is probably also pathogenic for honeybees and may be transmitted to them through this parasitic mite.

Few bacteria have been reported as pathogens of the Acari but in recent years research has been concentrated on intracellular organisms such as *Wolbachia* that may cause distorted sex ratios in offspring and incompatibility between populations. The role of these organisms in natural populations of spider mites is in particular discussed. The effect of *Bacillus thuringiensis* on mites is also treated in this review, although its mode of action in arthropods is mainly due to the presence of toxins and it is, therefore, not considered to be a pathogen in the true sense of the word.

Microsporidia have been observed in several mite species especially in oribatid mites, although other groups of mites may also be affected. In recent years, Microsporidia infections in Phytoseiidae have received considerable attention, as they are often found in mass rearings of beneficial arthropods. They affect the efficacy of these predators as biological control agent of insect and mite pests. Microsporidia do not seem to have potential for biological control of mites.

Key words: Acari, mite pathogens, *Hirsutella*, *Neozygites*, *Wolbachia*, Microsporidia, acaropathogenic fungi

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Introduction

Invertebrate pathology experienced a rapid development in the second half of the twentieth century. In particular, diseases of insects have been the subject of comprehensive studies. This interest can be attributed largely to the importance that many of these insects have for agriculture. Several insect pathogens are promising candidates for the biological control of pests; others are undesirable as they may confer considerable economic losses in cultures of beneficial insects (natural enemies, honeybees and other pollinators, silkworms, etc.).

Diseases in Acari have received much less attention. The relatively small size of mites makes disease diagnosis difficult. Mites, however, can often be reared easily in large quantities, allowing for detailed epizootiological studies. Few pathogens are known from mites, despite the large number of species. The number of eriophyoids is estimated at 2800 species (Amrine and Stasny, 1994) and Bolland *et al*. (1998) list 1190 species of Tetranychidae. Other groups of mites also comprise numerous review.

Reviews have been published on pathogens of mites and ticks by Lipa (1971), of spider mites by Van der Geest (1985) and of eriophyoids by McCoy (1996). Recently, Poinar and Poinar (1998) published a review on parasites and pathogens of mites, which did not refer to recent studies on mite pathogens with interesting results. We feel that these studies warrant the publication of the present manuscript. Pathogens of ticks will not be covered in this review. For diseases of ticks the reader is referred to Samish and Řeháček (1999).

Phytophagous mites feed on plant cells by inserting their piercing mouth parts into the plant tissue. It would therefore seem likely that in the case of extra-cellular pathogens, mites only suffer from fungal diseases, as these organisms are able to enter the host through the cuticle and are not dependent on the oral route for infection. This hypothesis seems to hold for eriophyoids (Lipa, 1971; McCoy, 1996), but other phytophagous mites such as spider mites and also predatory mites can be infected by pathogens from other groups of micro-organisms (Van der Geest, 1985; Beerling and Van der Geest, 1991a, b; Reed, 1981).

Diseases Caused by Fungi

Entomophthorales

General characteristics

Members of the order Entomophthorales (Division Zygomycetes) are mainly pathogens of insects and other arthropods; some may be parasitic on

desmids or fern prothalli, and some are saprophytic on plant debris (cf. Moore-Landecker, 1996). Many of the zoo-pathogenic fungi in this order belong to the family Entomophthoraceae. They are known to infect many species of insects, such as flies and aphids, but also mites, in particular spider mites. Fungi of this group are able to cause epizootics that often decimate arthropod populations.

The taxonomy of the Entomophthorales has long been confused, but recent revisions have clarified nomenclature (Humber, 1989). A well-known genus of Entomophthorales is *Entomophthora* that has now been split into several new genera of which *Neozygites* is regularly found in spider mites. The nuclear structure and the behaviour of the nucleus in *Neozygites* sp. during mitosis are different from that in other Entomophthorales (Butt and Heath, 1988; Butt and Humber, 1989). For this reason, *Neozygites* has been placed in a new family, the Neozygitaceae (Ben-Ze'ev *et al*., 1987). This family, however, is not recognised by all taxonomists (Bałazy, 1993). In this review, we will use the family, genus and species names proposed by Humber (1989).

Many entomophthoralean fungi possess a restricted host spectrum and are obligatory pathogens, which means that they can only grow on living hosts. Insects and mites infected by these fungi are usually not killed before all available nutrients have been utilised, in contrast to hosts killed by Deuteromycetes where mycotoxins often cause host death prior to complete colonisation of the body. The complete utilisation of the entire host body of the live host by the fungus seems to be consistent with the obligate nature of this group of fungi (Hajek, 1997).

Zygomycetes are characterised by their sexual reproduction, the so-called zygospore formation. This spore is formed by the fusion of two gametangia that develop into a zygote and subsequently into a thick-walled zygospore, or resting spore (Figure 1). Other types of resting spores are chlamydospores, thick-walled, nonsexual spores originating from transformed hyphal cells, and azygospores. The latter may arise from the parthenogenetic development of hyphal bodies (short segments of mycelium, see below), by budding of chlamydospores or are formed at the tips of hyphae that arise from chlamydospores or hyphal bodies. Resting spores aid the fungus in surviving unfavourable conditions.

More common is the formation of asexual spores. These so-called sporangiospores, are nonmotile and are formed within a sac-like structure, the sporangiole. Under nearly saturated conditions, these primary spores are discharged with force from the sporangiophore, the structure on which the spores are being formed. These forcibly discharged spores are also named ballistospores, but most mycologists call these spores primary conidia and this

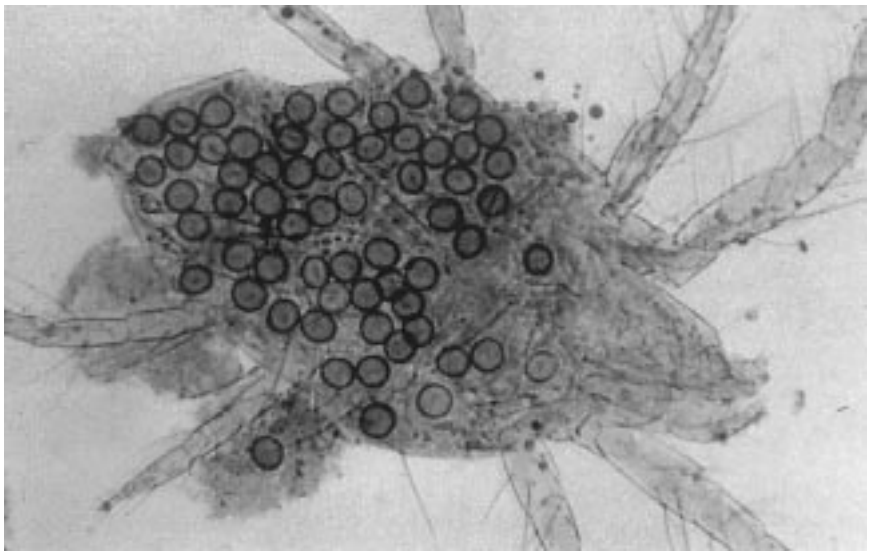

Figure 1. Resting spores of *Neozygites floridana* in the two-spotted spider mite *Tetranychus urticae.* Published with permission of Siegfried Keller.

term will be used in this review onwards. The conidia are often sticky due to the presence of a mucous substance on the outside that causes the spores to attach to a substrate when released from the fungus body. For details on the formation and structure of the spores and the process of discharge the reader is referred to Latgé *et al.* (1989).

Entomophthorales usually penetrate their host through the cuticle by means of a germ tube that is formed by the conidium. Secondary and even tertiary conidia (often similar in shape as the primary conidia, but smaller in size) may be formed when the germ tube has not penetrated into a suitable host or landed on non-host substrate, and this process should therefore be considered as simple resporulation. In some species, capilliconidia are formed from primary conidia at the tip of slender capillary tubes. These are secondary conidia, but they have a shape different from primary conidia. Capilliconidia are considered the infective propagules of entomophthoralean fungi infecting spider mites. After ingress, mycelium is formed that later fragments into a number of short segments, the hyphal bodies. Hyphal bodies serve as propagative units by budding and by undergoing fission. A schematic representation of the life cycle is shown in Figure 2. In addition, rhizoids may be formed by the fungus: hyphae, often branched, that extend from the infected arthropod and adhere to the substrate. In this way, the infected host remains fixed to the substrate, also after death. Under favourable conditions (high relative humidity) conidia are formed on conidiophores that extend

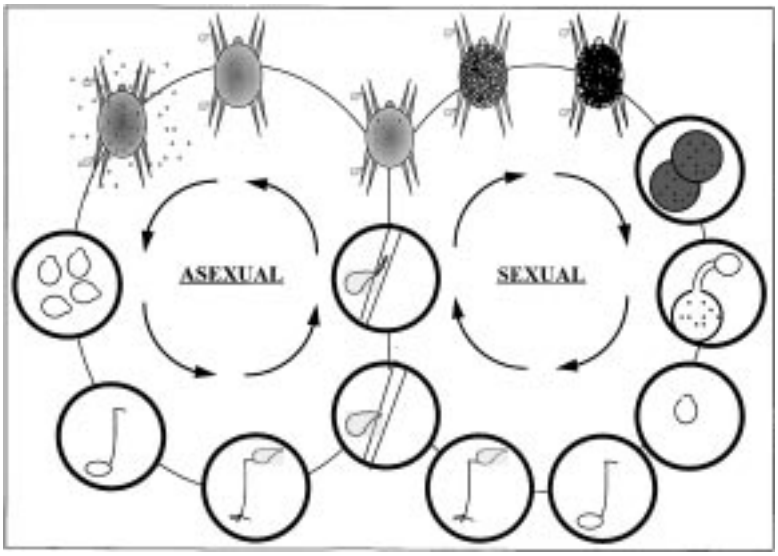

Figure 2. Schematic representation of the asexual and sexual life cycles of *Neozygites floridana* in the cassava green mite *Mononychellus tanajoa*. Hyphal bodies within a live infected mite (top centre) can either follow the asexual cycle or the sexual cycle. In the first case, the mite dies and mummifies (top), and then sporulates to form primary conidia (left). These germinate to form capilliconidia (bottom) which infect new hosts (centre). In the sexual cycle, resting spores are formed and the host dies (top). These spores germinate after a period of dormancy to produce germ conidia (right) which germinate to form germ capilliconidia (bottom) which infect new hosts (centre). From S.L. Elliot (1998).

through the cuticle of the dead host. Conidia are discharged with force from the conidiophores and form a halo around the dead host. The conidia may be picked up by a new, uninfected host.

Natural entomophthoralean infections in spider mites

Table 1 summarises data on mite pathogens with their respective hosts. The first record of a *Neozygites* species infecting spider mites was made by Fisher (1951) who observed adult mortality ranging from 32–95% in populations of the citrus red mite, *Panonychus citri*. The fungus was found throughout the Florida peninsula and was especially prevalent during late summer and early autumn. *Neozygites* was subsequently noted in populations of several other species of spider mites. Weiser and Muma (1966) described *N. floridana* as a pathogen of the Texas citrus mite, *Eotetranychus banksi*, while Weiser (1968) described *N. tetranychi* on the two-spotted spider mite, *Tetranychus urticae* (= *althaeae*) from a fruit orchard in Southern Bohemia, Czech Republic. The fungus caused epizootics in late fall, killing approximately 80–85% of the mites. It appears to be very close to *N. floridana*; the roughness of the surface

Table 1. An overview of pathogens of mites

Pathogen	Mite host	Mite taxon	Reference
Bacteria			
β-exotoxin *Bacillus thuringiensis*	*Panonychus citri*	Tetranychidae	Hall *et al.* (1971)
	Metaseiulus occidentalis	Phytoseiidae	Chapman and Hoy (1991)
	Phytoseiulus persimilis	Phytoseiidae	Guo *et al.* (1991)
	Tetranychus pacificus	Tetranychidae	Hoy and Ouyang (1987)
	Tetranychus urticae	Tetranychidae	Royalty *et al.* (1990), Guo *et al.* (1991)
Bacillus thuringiensis var. *israelensis*	*Dermatophagoides pteronyssinus*	Pyroglyphidae	Saleh *et al.* (1991)
Bacillus sphaericus	*Dermatophagoides pteronyssinus*	Pyroglyphidae	Saleh *et al.* (1991)
Rickettsia sp.	*Metaseiulus occidentalis*	Phytoseiidae	Hess and Hoy (1982)
	Vatacarus ipoides	Trombiculidae	Thomas and Poinar (1973)
Rickettsiella phytoseiuli	*Phytoseiulus persimilis*	Phytoseiidae	Šut'áková, 1988
Wolbachia	*Bryobia* sp.	Tetranychidae	A. Weeks (pers. comm.)
	Eutetranychus orientalis	Tetranychidae	Breeuwer and Jacobs (1996)
	Oligonychus biharensis	Tetranychidae	Breeuwer and Jacobs (1996)
	Tetranychus yusti	Tetranychidae	Breeuwer and Jacobs (1996)
	Tetranychus kanzawai	Tetranychidae	Breeuwer and Jacobs (1996), Gotoh and Gomi (1966)
	Tetranychus neocaledonicus	Tetranychidae	Breeuwer and Jacobs (1996)
	Tetranychus turkestani	Tetranychidae	Breeuwer and Jacobs (1996)
	Tetranychus quercivorus	Tetranychidae	Gotoh *et al.* (1995b)

Table 1. (*Continued*)

Pathogen	Mite host	Mite taxon	Reference
	Tetranychus urticae	Tetranychidae	Breeuwer and Jacobs (1996), Tsagkarakou *et al.* (1996)
	Metaseiulus occidentals	Phytoseiidae	Johanowicz and Hoy (1966), Breeuwer and Jacobs (1996)
	Neoseiulus barkeri	Phytoseiidae	Breeuwer and Jacobs (1996)
	Neoseiulus bibens	Phytoseiidae	Breeuwer and Jacobs (1996)
	Phytoseiulus persimilis	Phytoseiidae	Steiner (1993), Breeuwer and Jacobs (1996)
Serratia marcescens	*Metaseiulus occidentalis*	Phytoseiidae	Lighthart *et al.* (1988)
Fungi			
Zygomycetes			
Entomophthoralean species	*Arctoseius* sp.	Arctoseiinae	Bałazy and Wisniewski (1989)
	Macrocheles peregrinus	Macrochelidae	Milner (1985)
	Pergamasus crassipes	Parasitidae	Milner (1985)
Erynia phalangicidae	*Pergamasus* sp.	Parasitidae	Bałazy and Wisniewski (1984)
Neozygites sp.	*Euseius citrifolius*	Phytoseiidae	Furtado *et al*. (1996)
Neozygites acaridis	*Halotydeus destructor*	Penthaleidae	James (1994)
	Penthaleus major	Penthaleidae	James (1994)
Neozygites floridana	*Bryobia* sp.	Tetranychidae	Miętkiewski *et al.* (1993)
	Eotetranychus banksi	Tetranychidae	Weiser and Muma (1966)
	Mononychellus tanajoa	Tetranychidae	Delalibera *et al*. (1992)

Table 1. (*Continued*)

Pathogen	Mite host	Mite taxon	Reference
	Oligonychus gossypii	Tetranychidae	Yaninek *et al*. (1996)
	Oligonychus pratensis	Tetranychidae	Dick *et al.* (1992), Dick and Buschman (1995)
	Panonychus citri	Tetranychidae	Fisher (1951)
	Tetranychus ludeni	Tetranychidae	Rameseshiah (1971)
	Tetranychus tumidus	Tetranychidae	Saba (1971)
	Tetranychus urticae	Tetranychidae	Smith and Furr (1975), Carner (1976)
Tarichium acaricolum	*Pergamasus* sp.	Parasitidae	Bałazy and Wisniewski (1984)
Tarichium obtusoangulatum	*Uropoda minima*	Uropodidae	Bałazy and Wisniewski (1984)
Tarichium pusillum	*Pergamasus* sp.	Parasitidae	Bałazy and Wisniewski (1984)
Tarichium sphaericum	*Trachyuropoda coccinea*	Trachyuropodidae	Bałazy and Wisniewski (1984)
Tarichium subglobosum	*Pergamasus* sp.	Parasitidae	Bałazy and Wisniewski (1984)
	Uropoda minima.	Uropodidae	Bałazy and Wisniewski (1984)
Tarichium svalbardense	*Pergamasus* sp.	Parasitidae	Bałazy and Wisniewski (1984)
Tarichium tenuisculpturatum	*Pergamasus* sp.	Parasitidae	Bałazy and Wisniewski (1984)
Tarichium uropodinis	*Trachyuropoda coccinea*	Trachyuropodidae	Bałazy and Wisniewski (1982)
Undescribed Entomophthoralean fungus	*Tetranychus desertorum*	Tetranychidae	Walter (1999)
Deuteromycetes			
Aspergillus flavus	*Dinothrombium giganteum*	Trombidiidae	Sanassi and Oliver (1971)
	Trombidium gigas	Trombidiidae	Sanassi and Armirthavalli (1970)

Table 1. (*Continued*)

Pathogen	Mite host	Mite taxon	Reference
Beauveria bassiana	*Polyphagotarsonemus latus*	Tarsonemidae	Peña *et al.* (1996)
Cephalosporium diversiphialidum	*Tetranychus urticae*	Tetranychidae	Bałazy (1973)
Cladosporium cladosporioides	*Eotetranychus* sp.	Tetranychidae	Humber (1992)
Hirsutella brownorum	Mites in soil		Humber (1992)
Hirsutella gregis	*Abacarus hystrix*	Eriophyoidea	Minter *et al.* (1983)
Hirsutella haptospora	*Uropodina* sp.	Uropodoidea	Humber (1992)
Hirsutella kirchneri	*Abacarus hystrix*	Eriophyoidea	Minter *et al.* (1983)
	Eutetranychus orientalis	Tetranychidae	Sztejnberg *et al*. (1997)
	Hemisarcoptes coccophagus	Hemisarcoptidae	Sztejnberg *et al*. (1997)
	Panonychus citri	Tetranychidae	Sztejnberg *et al*. (1997)
	Phyllocoptruta oleivora	Eriophyoidea	Cabrera and Dominguez (1987a), Sztejnberg *et al*. (1997)
	Tetranychus cinnabarinus	Tetranychidae	Sztejnberg *et al*. (1997)
Hirsutella necatrix	*Abacarus hystrix*	Eriophyoidea	Minter *et al.* (1983)
	Tetranychus cinnabarinus	Tetranychidae	Sztejnberg *et al*. (1997)
Hirsutella nodulosa	*Aceria guerreronis*	Eriophyoidea	Cabrera and Dominguez (1987b)
	Phyllocoptruta oleivora	Eriophyoidea	Cabrera and Dominguez (1987a)
	Polyphagotarsonemus latus	Tarsonemidae	Peña *et al*. (1996)
Hirsutella rosrata	*Dendrolaelaps tetraspinosus*	Digamasellidae	Bałazy and Wisniewski (1989)
	Proctolaelaps sp.	Ascidae	Bałazy and Wisniewski (1989)
Hirsutella thompsonii	*Abacarus hystrix*	Eriophyoidea	Lewis *et al.* (1981)
	Acalitus vaccinii	Eriophyoidea	Baker and Neunzig (1968)

Table 1. (*Continued*)

Pathogen	Mite host	Mite taxon	Reference
	Aceria sp.	Eriophyoidea	McCoy and Selhime (1977)
	Aceria guerreronis	Eriophyoidea	Humber (1992)
	Aceria sheldonii	Eriophyoidea	McCoy (1996), Sosa Gomez and Moscardi (1991)
	Calacarus heveae	Eriophyoidea	Tanzini *et al.* (2000)
	Colomerus novahebridensis	Eriophyoidea	Hall *et al.* (1980)
	Dolichotetranychus floridanus	Tenuipalpidae	Humber (1992)
	Eutetranychus banksi	Tetranychidae	McCoy and Selhime (1974)
	Eutetranychus sexmaculatus	Tetranychidae	McCoy and Selhime (1974)
	Mononychellus tanajoa	Tetranychidae	Yaninek *et al.* (1996)
	Panonychus citri	Tetranychidae	McCoy and Selhime (1974)
	Phyllocoptruta oleivora	Eriophyoidea	Fisher (1950)
	Polyphagotarsonemus latus	Tarsonemidae	Peña *et al*. (1996)
	Retracus elaeis	Eriophyoidea	Urueta (1980)
	Rhynacus sp.	Eriophyoidea	Cabrera *et al.* (1987)
	Tetranychus cinnabarinus	Tetranychidae	Cehrnin *et al*. (1997)
	Tetranychus ilicis	Tetranychidae	Gardner *et al.* (1982)
	Tetranychus urticae	Tetranychidae	Gardner *et al.* (1982)
	Trachyuropoda coccinea	Trachyuropodidae	Bałazy and Wisniewski (1982)
	Vasates destructor	Eriophyoidea	McCoy (1996)
Hirsutella tydeicola	*Lorryia formosa*	Tydeidae	Cabrera (see Samson and McCoy, 1982)

Table 1. (*Continued*)

Pathogen	Mite host	Mite taxon	Reference
	Tydeus californicus	Tydeidae	Cabrera (see Samson and McCoy, 1982)
	Tydeus gloveri	Tydeidae	Samson and McCoy (1982)
Paecilomyces eriophytis	*Aceria hippocastani*	Eriophyoidea	Leatherdale (1965)
	Aceria vaccinii	Eriophyoidea	Baker and Neunzig (1968)
	Cecidophyopsis ribis	Eriophyoidea	Leatherdale (1965)
	Eriophyes padi	Eriophyoidea	Leatherdale (1965)
	Panonychus ulmi	Tetranychidae	Leatherdale (1965)
	Phytoptus avellanae	Eriophyoidea	Leatherdale (1965)
	Polyphagotarsonemus latus	Tarsonemidae	Peña *et al*. (1996)
	Vasates spondiasi	Eriophyoidea	see McCoy (1996)
Paecilomyces terricola	*Tetranychus urticae*	Tetranychidae	Kenneth (1971)
Sporothrix schenckii	*Aculus fockeui*	Eriophyoidea	Schliesske (1992)
Tolypocladium inflatum	Mites in soil	Oribatidae	Humber (1992)
Tolypocladium niveum	*Mycobates* sp.	Mycobatidae	Humber (1992)
Verticillium lecanii	*Abacarus hystrix*	Eriophyoidea	Lewis *et al.* (1981)
	Tetranychus urticae	Tetranychidae	Gams (1971)
	Mites in soil	Oribatidae	Humber (1992)
Laboulbeniales			
Rickia sp.	*Lobogynium* sp.	Diplogyniidae	see Poinar and Poinar (1990)
Unknown species	*Hirstionyssus* sp.	Dermanyssidae	Steinhaus and Marsh (1962)

Table 1. (*Continued*)

Pathogen	Mite host	Mite taxon	Reference
Protozoa			
Apicomplexa			
Acarogregarina corolla	*Scutovertex minutus*	Scutoverticidae	Erhardová (1955)
Asterophora caloglyphi	*Caloglyphus moniezi*	Acaridae	Geus (1969)
Erhardovina bisphaera	*Damaeus clavipes*	Damaeidae	Purrini and Ormieres (1981)
	Damaeus onustus	Damaeidae	Purrini and Ormieres (1981)
	Eupelops hirtus	Eupelopidae	Purrini and Ormieres (1981)
Erhardovina carabodesi	*Carabodes coriaceus*	Carabodidae	Purrini and Ormieres (1981)
Erhardovina euzeti	*Euzetes seminulum*	Euzetidae	Lipa (1982)
Erhardovina fuscozetesi	*Fuscozetes setosus*	Ceratozetidae	Purrini *et al.* (1979)
Erhardovina fuscozetis	*Euzetes globulus*	Euzetidae	Purrini and Ormieres (1981)
Erhardovina oribatarum	Mite		see Lipa (1971)
Erhardovina phtiracari[1]	*Phthiracarus globosus*	Phthiracaroidea	Purrini and Ormieres (1981)
	Phthiracarus piger	Phthiracaroidea	Purrini and Ormieres (1981)
Erhardovina platynothri	*Platynothrus peltifer*	Nothroidea	Purrini and Ormieres (1981)
Erhardovina postneri	*Hermannia gibba*	Hermannioidea	Purrini *et al.* (1979)
Erhardovina scutovertexi	*Scutovertex minutus*	Scutoverticidae	Erhardová (1955)
Erhardovina sp.	*Limnochares aquatica*	Hydrachnellae	Issi and Lipa (1968)
Gregarina sp.	*Eupelops subuliger*	Eupelopidae	Purrini *et al.* (1979)
	Eupelops torulosus	Eupelopidae	Purrini *et al.* (1979)
	Rhysotritia ardua	Phthiracaroidea	Purrini *et al.* (1979)
Erhardovina sp.?	*Damaeus geniculatus*	Damaeidaesee	Lipa (1971)

Table 1. (*Continued*)

Pathogen	Mite host	Mite taxon	Reference
Erhardovina sp.?	*Damaeus oblongus*	Damaeidaesee	Lipa (1971)
Gurleya sokolovii	*Limnochares aquatica*	Hydrachnellae	Issi and Lipa (1968)
Unidentified gregarine	*Tyrophagus putrescentiae*	Acaridae	Steiner (1993)
Adelina acarinae	*Nothrus silvestris*	Nothroidea	Purrini (1984)
Microspora			
Intexta acarivora	*Tyrophagus putrescentiae*	Tyroglyphidae	Larsson *et al.* (1997)
Microsporidium phytoseiuli	*Phytoseiulus persimilis*	Phytoseiidae	Bjørnson *et al.* (1996)
Microsporidium sp.	*Amblyseius barkeri*	Phytoseiidae	Beerling and Van der Geest (1991a,b)
	Neoseiulus cucumeris	Phytoseiidae	Beerling and Van der Geest (1991a,b)
Napamichum aequifolium	*Limnochares aquatica*	Hydrachnellae	Larsson (1990)
Nosema acari	*Damaeus onustus*	Damaeidae	Purrini and Weiser (1981)
	Damaeus clavipes	Damaeidae	Purrini and Weiser (1981)
Nosema euzeti	*Euzetes seminulum*	Euzetidae	Lipa (1982)
Nosema führeri	*Phthiracarus globosus*	Phthiracaroidea	Purrini and Weiser (1981)
Nosema helminthorum	*Ceratoppia* sp.	Liacaroidea	Moniez (1887)
	Ceratoppia bipilis	Liacaroidea	Dissanaike (1958)
	Xenillus tegeocranus	Liacaroidea	Dissanaike (1958)
Nosema hermanniae	*Hermannia gibba*	Hermannioidea	Purrini *et al.* (1979)
Nosema ptyctimae	*Rhysotritia ardua*	Phthiracaroidea	Purrini and Bäumler (1976)
Nosema sperchoni	*Sperchon* sp.	Sperchontidae	Lipa (1962)
Nosema steganacari	*Steganacarus striculus*	Phthiracaroidea	Purrini and Weiser (1981)
Nosema steinhausi	*Tyrophagus putrescentiae*	Tyroglyphidae	Weiser (1956)

Table 1. (*Continued*)

Pathogen	Mite host	Mite taxon	Reference
Pleistophora cephei	*Cepheus dentatus*	Cepheoidea	Purrini and Weiser (1981)
Pleistophora dindali	*Carabodes coriaceus*	Carabodidae	Purrini and Weiser (1981)
Pleistophora platynothri	*Platynothrus peltifer*	Nothroidea	Purrini and Weiser (1981)
Pleistophora oribatei	*Carabodes femoralis*	Carabodidae	Purrini and Weiser (1981)
	Damaeus clavipes	Damaeidae	Purrini and Weiser (1981)
	Microtritia minima	Euphthiracaroidea	Purrini and Weiser (1981)
	Phthiracarus piger	Phthiracaroidea	Purrini and Weiser (1981)
	Phthiracarus sp.	Phthiracaroidea	Purrini and Weiser (1981)
	Physotritia duplicata	Phthiracaroidea	Purrini and Weiser (1981)
Thelohania microtritiae	*Microtritia minima*	Euphthiracaroidea	Purrini and Weiser (1981)
Viruses			
Non-occluded virus	*Panonychus citri*	Tetranychidae	Muma (1955), Reed and Hall (1972)
Non-occluded virus	*Panonychus ulmi*	Tetranychidae	Putman and Herne (1966)
Non-occluded virus	*Neoseiulus cucumeris*	Phytoseiidae	Steiner (1993)
Non-occluded virus	*Phytoseiulus persimilis*	Phytoseiidae	Bjørnson *et al*. (1997)
Non-occluded virus	*Varroa jacobsoni*	Varroidae	Kleespies *et al*. (2000)
Iridovirus	*Varroa jacobsoni*	Varroidae	Camazine and Liu (1998)
Picornavirus	*Acarapis woodi*	Tarsonemidae	Liu (1991)

[1]This species was described by Purrini and Ormieres (1981) from the hosts *Phthiracarus globosus* and *P. piger*. The genus and family names of these mites were misspelled by the authors (*Phtiracarus*, resp. Phtiracaridae). The species name of *Erhardovina phtiracari* was also misspelled; this spelling has been used in the revision by Levine (1988).

of the capilliconidia as opposed to the smooth surface of the capilliconidia in *N. floridana* is probably an artefact resulting from preparation techniques (Bałazy, 1993).

Neozygites floridana has subsequently been observed on several species of spider mites on various agricultural crops. For example, it was reported on *T. tumidus* on cotton (Saba, 1971), on *T. evansi* on tomato in Brazil (Humber *et al*., 1981), on *T. ludeni* on bean in India (Rameseshiah, 1971) on *Oligonychus hondoensis* on cedar in Japan (Nemoto and Aoki, 1975), on *T. urticae* on field corn in North Carolina, USA (Brandenburg and Kennedy, 1982) and on the cassava green mite, *Mononychellus tanajoa*, in Venezuela (Agudela-Silva, 1986) and in Brazil (Delalibera *et al*., 1992). Some of these reports concern only observations without details on the effect that the fungus may cause to spider mite populations. However, some studies are detailed epidemiological studies, such as the study of Saba (1971) on *T. tumidus* in cotton and the work on the cassava green mite (see below). *Neozygites* has also been reported on *T. urticae* and *Bryobia* sp. on various wild plants in Poland by Miętkiewski *et al.* (1993). The fungus was especially present during autumn and late summer; infection rates were high with disease prevalence of sometimes 60–80%.

Keller and Wuest (1983) observed infections of *T. urticae* on bean by *N. adjarica* in Switzerland. Isolates of *N. adjarica* and fresh material collected from North Carolina were compared with the type specimen of *N. floridana*, and it was concluded that these fungi are identical and that *N. floridana* should be used as the valid name (Keller, 1991). Keller (1991) also compared the morphology of the cassava green mite isolates with type material and decided that these fungi should also be named *N. floridana*. It is very possible that all *Neozygites* isolates from spider mites belong to *N. floridana*, as assumed by Keller (1997). However, there are differences between the isolates: e.g. *N. floridana* isolated from the cassava green mite has a very restricted host spectrum and is hardly infectious for other spider mite species such as *T. urticae* and *T. bastosi* (De Moraes and Delalibera, 1992). In addition, size of the conidia of different isolates may differ. For example, *Neozygites* from two-spotted spider mites near Londrina, Paraná, Brazil has larger primary conidia than *Neozygites* from cassava green mite in Bahia (Sosa-Gómez *et al.*, 1996). Molecular techniques may provide helpful to distinguish isolates and to gain information about the relatedness of different strains.

Effect of Neozygites sp. *on natural spider mite populations*

The role that entomophthoraceous fungi play in the regulation of natural populations of spider mites has been analysed by several authors and reviewed by Van der Geest (1985). Saba (1971) observed *Neozygites* infections

in *T. tumidus* in cotton fields in the humid subtropical part of Florida. He observed a reduction of a field infestation of 220 mites per cotton leaf down to < 1 spider mite per leaf during a period of warm humid weather with heavy rainfall. The reduction was mainly caused by the fungus. Smith and Furr (1975) made similar observations in the delta of the Mississippi: they showed that *Neozygites* is the main factor limiting late-season population increases of *T. urticae* on cotton. Carner (1976) found *Neozygites* in *T. urticae* throughout the states Georgia, South Carolina and Alabama, USA, and considered it an important factor in regulating spider mite populations in cotton throughout most of the southeastern United States, although *T. turkestani* is not affected (Carner and Canerday, 1968, 1970). Several other crops have been monitored with respect to the incidence of fungus disease in spider mite infestations: Smitley *et al.* (1986b) studied the role of *N. floridana* in population decline of the two-spotted spider mite in field corn in North Carolina. The relative importance of disease in spider mites was dependent on climatic conditions and varied from year to year. Moist weather conditions induced epizootics of *N. floridana* before corn plants became heavily infested with spider mites. However, under dry weather conditions, spider mite populations expanded unchecked until plants became heavily infested. Early dispersal of mites was then the factor causing population decline.

Periods of hot dry weather in the midwestern United States in the 1980s resulted in very high spider mite infestations in soybean (Klubertanz *et al.*, 1991). When hot and dry conditions intensified in 1983, over 600,000 acres of soybean were chemically treated for spider mite control. In subsequent years only localised mite infestations were found which lead to early economically important spider mite infestations during a period of drought of 1988. The outbreak was unique as spider mite populations became damaging early in the season and continued to increase in intensity during most of the summer. In an experimental set up where direct rainfall was excluded, Klubertanz *et al.* (1991) studied population dynamics of the spider mites and possible causes for the observed decline in population density. In 1987, 33% of the mites in the upper canopy were infected with a fungal pathogen within 28 days after infestation. One week later, hyphal bodies were found in 100% of the mites. The results clearly indicated that *Neozygites* epizootics might develop without rainfall, when the ambient conditions are conducive to fungal sporulation. The following year was characterised by drought and the weather was more variable than in the previous year. Although the first infected mite was found 2 weeks after infestation, no infected mites were observed in the subsequent sampling dates. Significant infection rates were noted 33 days after infestation. Prior to this date, three days with high relative humidity made conditions conducive for sporulation. Approximately 7.8% of

the mites sampled late in 1988 contained thick-walled resting spores. This is an indication that the fungus does not need live hosts to overwinter. The formation of these environmentally more resistant spores seems to be more related with late season epizootics in temperate climate where conidia cannot successfully overwinter. In other localities, for example North Carolina, the fungus overwinters as hyphae in partly active mites in forages or along field margins (Brandenburg and Kennedy, 1981).

The Banks grass mite, *Oligonychus pratensis*, and the two-spotted spider mite *T. urticae* can be decimated in the Western Great Plains of the United States by the occurrence of disease caused by *Neozygites* (Dick *et al.*, 1992; Dick and Buschman, 1995). The Banks grass mite is a pest on field corn and grain sorghum, often causing economic damage to these crops. The fungus was investigated by Dick *et al.* (1992) and identified as *Neozygites adjarica*, although Keller (1991) considers this species a synonym of *N. floridana*. Fungal epizootics in *O. pratensis* usually followed periods of 8–10 h of ambient relative humidity above 80% (Dick and Buschman, 1995). It was not clear whether the fungus was the main cause of death, as predators, acaricides and corn maturity were also factors that may have contributed to mite mortality.

Treatments with fungicide may affect the incidence of fungus disease in populations of spider mites. Brandenburg and Kennedy (1983) observed a lower proportion of spider mites infected by *N. floridana* in lima bean when benomyl was applied. This fungicide did not affect sporulation of the fungus but seemed to affect conidial germination and growth of the fungus negatively.

Immature stages of *T. urticae* are more susceptible to *N. floridana* than adult mites and female adults are more susceptible to infection than adult males (Susilo *et al*., 1994). A probable cause could be the thinner cuticle of the immature mites, making these more vulnerable to fungus infection. The authors suggested that the lower susceptibility of the males is caused by a stronger cuticle of this sex compared to that of females. Males have to compete in combat with other males which may have resulted in a tougher cuticle. In addition, females have a more elastic opisthosomal cuticle, needed for ovarial development and oviposition. The authors speculate that this cuticle might be thinner, or different in chemical composition. Infection by entomogenous fungi results from direct penetration of the fungus through the host cuticle by a combination of enzymatic and mechanical processes. Successful infections by fungi depend largely upon the effectiveness of various antifungal substances in the host cuticle. Differential susceptibility of different stages and sexes of mites can be attributed in part to the presence or absence of antifungal substances. This finding contrasts with those of a study by Elliot (1998) on an epizootic of *N. floridana* in *M. tanajoa* in Brazil. Here, many

fewer capilliconidia of the fungus were found on field-collected juveniles than on adult females and the vast majority of killed mycosed mites were adult females. Elliot (1998) postulated that the limited movement of the juveniles relative to adults makes them much less likely to pick up capilliconidia from the leaf surface. Whether or not this is correct, this differential ecological or behavioural susceptibility must have a large influence on the progress of an epizootic through the host population.

Neozygites floridana *and the cassava green mite* Mononychellus tanajoa

The introduction of the cassava green mite (CGM), *M. tanajoa*, from Latin America into Africa during the early 1970s has been the impetus for a comprehensive search for classical biological control agents, including predators and pathogens. The CGM was introduced into Uganda probably in 1971 and had dispersed across the cassava belt in Africa within 10 years after its first introduction. It threatened cassava production in vast areas over the tropical part of the African continent (Yaninek, 1988). Several attempts have been made to use exotic natural enemies from South America, in particular phytoseiid predators, to control the CGM. The finding of an entomophthoralean infection in the CGM in Venezuela (Agudelo-Silva, 1986) and later in Northeast Brazil (Delalibera *et al*., 1992; De Moraes and Delalibera, 1992) was the cause for a comprehensive study on the biological properties of this fungus (Oduor, 1995). The Latin American isolate of this fungus which was shown to be *Neozygites floridana* seem to have a very narrow host spectrum and cannot infect other tetranychid mites (de Moraes and Delalibera, 1992). It is also harder to grow *in vitro* than an isolate from *T. urticae* (Leite *et al.*, 2000). The former property makes the fungus a very promising classical biological control agent against CGM on the African continent. A detailed study on the biological properties of this fungus species was set up in order to gain information on the suitability of the fungus as a biological control agent.

In a series of reports, Oduor *et al*. (1995a, b, 1996a, b, 1997a, b) described the results of a study on the biology of the acaropathogenic fungus *N. floridana* and its effect on the CGM. Production of primary conidia is affected by ambient humidity, temperature and photoperiod: production increased between 13°C and 23°C, but no conidium production was obtained above 28°C (Oduor *et al.*, 1996a). Similar results were reported by Smitley *et al*. (1986a) in a study on the pathogenesis of *N. floridana* in the two-spotted spider mite. In addition, germination of capilliconidia of *N. floridana* on the CGM is affected by exposure time, temperature, ambient humidity and photoperiod (Oduor *et al.*, 1996a). Capilliconidia lose their infectivity after several days: a storage period of 10 days allowed only 3.5% spores to germinate. Germination was obtained at all temperatures tested (13–33°C);

even at 13°C, more than 15% of the capilliconidia germinated, indicating that the minimum temperature for germination is still lower. It was also observed that germination in the dark is significantly higher than in the light. Humidity greatly affects germination of the capilliconidia: germination at a SD (saturation deficit) of 1.2 was only 2.8%, but 60.9% at an SD of 0.

Survival of the fungus as dry hyphal bodies in mummified cassava green mites appeared to be strongly affected by storage temperature (Oduor *et al.*, 1995b). Mite cadavers, containing non-sporulating fungus, can be stored in the refrigerator over prolonged periods in well-sealed plastic tubes with cotton wool partially soaked in glycerol to ensure a low humidity. In this manner, the fungus remains viable over periods of several months to years. Survival of the fungus in mummies that were kept at 24°C could be demonstrated for a period of 6–7 months, but when stored at 4°C, fungus sporulated from 90% of the mummies liberating an average of 187 primary conidia per mummy even after a storage period of 16 months (when the experiment was terminated). Viability of the primary conidia was also greatly affected by temperature, saturation deficit and light conditions: conidia survived less than 1 h when exposed to saturation deficits of 2.0 mm Hg at any tested temperature. Lower temperatures maintained higher conidium viability than high temperatures, while light also adversely affected viability. Germination of capilliconidia was higher at lower temperatures (18°C) than at higher temperatures, while germination was also favoured by the absence of light (Oduor *et al.*, 1996b). The fungus apparently sporulates under natural conditions early in the morning before sunrise when the temperature is low and the relative humidity is high. Primary conidia can then disperse and produce capilliconidia before sunrise. These structures can then remain on the leaf surface awaiting pick-up by passing mites.

Mortality of the CGM as a result of infection by the fungus is affected by several factors: Mean LT_{50} (time for half of the infected mites to die) decreased with increasing temperatures from 3.9 days at 18°C to 2.5 days at 33°C. Light or ambient humidity did not affect the disease process inside the mites, although a high relative humidity is required for subsequent sporulation of the conidia. This confirms earlier work of Carner (1976), who studied *Neozygites* infections in *T. urticae*. Oduor *et al*. (1997a) also showed that pathogen dosage affects the pathogenicity of the fungus. All inoculum sizes tested (one, two, four, six and eight capilliconidia) were lethal to individual mites, but time to mortality was shorter when pathogen dosage was larger.

A model was developed to demonstrate the behaviour of the fungus in cassava green mite populations (Oduor *et al*., 1997b). Local populations of spider mites have in general a viscous structure, which would normally hamper the

spread of a pathogen that is transmitted by the contact of susceptible hosts with the halo of capilliconidia surrounding an infectious host. However, conditions in such populations are met when infected mites search and settle to produce capilliconidia on sites where they are surrounded by susceptible mites before becoming infectious. Based on these assumptions, the authors developed a simple, analytically tractable model that can be used to estimate the maximal capacity of the fungus to decimate local populations of the cassava green mite. It was shown that the pathogen can reduce the population growth of *M. tanajoa*, but it cannot cause extinction of local populations alone. Only when a high initial ratio of infectious to susceptible mites or when the mite population is sufficiently reduced by other factors (e.g., low temperatures, low food quality of the host plant, dislodgement and death by rain or wind, and predation) will the fungus be capable to decimate cassava green mite populations. The fungus can apparently play a role in controlling spider mites on plants, where r_m of spider mites is low, in addition to other natural enemies. However, the conclusions of Oduor *et al.* (1997b) were based on properties of only one strain.

Significant reductions in CGM populations in cassava fields were observed in semiarid regions in the state of Bahia, Brazil from January to August, corresponding to the wet season (Delalibera *et al.*, 1999). Infection levels by *N. floridana* reached more than 75%. Reductions in CGM populations were not only caused by the fungus, but also by increase of the density of three predatory mite species.

Yaninek *et al*. (1996) surveyed fungi occurring on mites in the Republic of Benin, West Africa, and found *N. floridana* on both CGM and *Oligonychus gossypii*. The fungus was present throughout the entire year, but incidence of fungus infection during the dry season was very low in both mite species. The incidence of the disease was considerably greater in the wet season, although the impact of infection on the population density of the CGM was only moderate. The fungus strain from Benin has apparently a low virulence towards the CGM, or is poorly adapted to climatic conditions, in contrast to isolate from Brazil, in which country nearly 100% of the adult female cassava green mite can be infected, depending on density, location, season and climate. Disease incidence in *O. gossypii* was about twice as high: This mite species is indigenous to Africa, in contrast to the introduced cassava green mite. Up to 75% mortality due to a local strain of *Neozygites* was recorded in cassava green mite populations in western Kenya by Bartowski *et al.* (1998).

Elliot *et al.* (2000) conducted a 4-year field study during which the pathogen was monitored in cassava fields in a semi-arid region of northeastern Brazil. They found that the pathogen had a significant, but sporadic effect on

CGM populations. The fungus was not found in live mites during the four dry periods, so they considered resting spores the most feasible mechanism by which the fungus could survive these unfavourable climatic conditions. In a subsequent study, resting spores were found in great numbers during an epizootic in 1995 but not in epizootics in early and mid 1998 (Elliot, 1998). Elliot (1998) did not consider mummies (dried mites, killed by the fungus and containing hyphal bodies) as a possible mechanism for perennial survival as no viability of the fungus present in the mummies could be demonstrated beyond two months of hot and dry storage in the field or laboratory.

Elliot *et al.* (2000) showed that CGM population fluctuations in Brazil are driven by the climate as was apparent from the yearly patterns of abundance of the spider mite and its natural enemies. However, no specific consistent relationships of the cassava green mite with the climate were found. Such relationships were found with biotic factors, in particular inverse density dependence, cassava leaf injury and natural enemies. It was shown that predators had a smaller impact than the pathogens over the study period although this may have been an artefact of the sampling and analysis. The pathogen was found to be regulating the CGM populations at some times, but not at others. Epizootics in early and mid 1996 led to complete decimation of the mite population, in the first instance, and a much slighter apparent regulation of host population growth in the second (Elliot, 1998). Monitoring of the second epizootic confirmed the overriding importance of saturation deficit as the best measured climatic parameter for predicting epizootic progress (Elliot, 1998). A simple regression model to predict epizootic progress was derived from one field where the fungus was naturally present and applied to another where it was not (Elliot, 1998). Together with monitoring transmission in the field, the conclusion was that any applications of the fungus for pest management within an inundative or inoculative strategy would have had a very narrow window of opportunity in this second field. In this field, CGM numbers reached extremely high levels (c. 1,600 per leaf) leading to complete defoliation while predatory mites (*Neoseiulus idaeus)* tracked the population and also reached very high levels (c. 120 per leaf) but did not control the CGM population. Meanwhile, natural occurrence of the pathogen did not reach 0.1% of mites on plants bearing fungal structures. From the results obtained, the author suggested that the pathogen would have a negative impact on CGM populations when introduced into a new area. Various different control strategies were considered: classical biological control, environmental manipulation, inoculative biological control and inundative biological control. The most promising method seems to be classical biological control; the pathogen could either be released as mummies or as resting spores. Environmental manipulation may be feasible: providing a more humid habitat at the leaf by watering

the crop is hardly possible in the water-short areas where cassava is grown in many parts of Africa and northeastern Brazil, but cassava varieties may be selected for a closed canopy to provide high relative humidities. Inoculative and inundative releases also seem control strategies that are unsuited for the marginal cassava crop in many parts of Africa and northeastern Brazil, because of the economic costs, difficulties of producing enough inoculum, finding windows of opportunity and targeting successive generations of mites as they develop.

Other entomophthoralean fungi in mites

Bałazy and Wisniewski (1982, 1984, 1989) isolated several species of entomophthoraceous fungi in Poland from mites in anthills, forest litter and galleries from subcortical insects. These studies were merely inventories; no data are given on the biology and the frequency of occurrence of these fungi. The results of these inventories have been included in Table 1. Several of the fungi were only present in the form of resting spores and were therefore placed in the genus *Tarichium*, a provisional taxon in which species are discerned on the basis of the shape of the resting spores (Keller, 1991).

During a survey for natural enemies of earth mites in pastures in the Leeton-Narrandera district of New South Wales, infection of earth mites by *N. acaracida* were observed in 0–50% of the mites. The disease was noted in the red-legged earth mite *Halotydeus destructor* (Penthaleidae), but was even more prevalent in the blue oat mite, *Penthaleus major* (James, 1994). Infected mites are yellowish (red-legged earth mite) or red (blue oat mite) and become sterile before their death. The pathogen appears to be most common during wet winters. James (1994) considered the disease as the prime cause of frequently observed population crashes of earth mites in July–August. *Neozygites* infections have also been observed in populations of the red-legged earth mite *Halotydeus destructor* in pastures of southwestern Australia (Ridsdill-Smith and Annells, 1997). The authors tentatively identified the fungus as *N. acaridis*, but it is very likely that we are dealing with the same fungus species as in New South Wales. The disease incidence in the latter report was lower than 4% in mainly adult mites during late spring. No data are available on whether *N. acaracida* and *N. acaridis* are different from or synonyms of *N. floridana.*

Entomophthoralean fungal infections in mites were observed by Petch (1944) on *Pergamasus crassipes* and by Milner (1985) on *Macrocheles peregrinus*, both in Australia. Populations of the prickly pear spider mite, *Tetranychus desertorum*, on *Lantana camara* in Queensland, Australia were found to be decimated by fungal epizootics (Walter, 1999). No information is given on the species of fungus involved in these epizootics.

Entomophthorales as possible control agents

The effect of Entomophthorales on natural populations of spider mites and some insect species (e.g. aphids) is impressive: Populations of spider mites and insects can be decimated by fungi from this group, and it is therefore not surprising that research has been conducted to evaluate the potential of these fungi as biocontrol agents. A drawback is that culturing of the fungi can be usually only accomplished inside the arthropod hosts. Dissemination of the fungus as infected mite mummies is a possible way to spread the pathogen in a spider mite population. This method has been patented for the biological control of *T. urticae* in field crops and greenhouse crops (Kennedy and Smitley, 1988). They infected cultures of *T. urticae* on Lima beans with the fungus by adding field-collected, infected mites. Dead, infected mites were collected and were stored over calcium carbonate at 4°C or in a freezer until they were needed for application. Large scale production of mummies of the CGM is more problematic, as mass rearing of the CGM is only possible on cassava plants. The vast cassava growing areas in Brazil and Africa would need a very large production facility of mummies, which would be too expensive for a marginal crop such as this. Inundative releases of the pathogen in this form are therefore not feasible for biological control of the CGM. The fungus may have a future as a classical biological control agent of the CGM, as is presently being studied. One real advantage of these fungi is their host specificity: usually only one or a few very closely related hosts can be infected and non-target species will not be affected. Phytoseiid mites, for example, do not seem to be very susceptible to fungus infections, since only a few observations have been reported of the occurrence of fungus disease in members of this mite family. Furtado *et al*. (1996) reported on a *Neozygites* infection of the predatory mite *Euseius citrifolius*, one of the most common predators of the cassava green mite in Brazil. Infection was observed in mites that were contained on rearing arenas in the laboratory when kept at high relative humidity. The authors did not only observe conidiophores with pear-shaped conidia, but in some mites also black spherical structures. They assumed that these structures were resting spores. However, in another study, De Moraes and Delalibera (1992) did not succeed in infecting *Amblyseius idaeus* and *A. limonicus* under laboratory conditions with *Neozygites* that had been isolated from the cassava green mite.

Recently culture media have been developed for *N. floridana* from *T. urticae* (Leite *et al.*, 2000) and for *Neozygites parvispora* from thrips (Grundschober *et al.*, 1998). The media are very complex and consist of tissue culture media supplemented with fetal bovine serum and/or other adjuvants. The authors were able to obtain growth and multiplication of hyphal bodies.

However, we are still a long way off a commercially viable product. Application of these fungi as inundative biological pesticides is, therefore, out of reach.

It seems worthwhile to investigate the efficiency of these pathogens with respect to conservation biological control strategies, possibly by the judicious use of fungicides to avoid harm to the mite pathogens. The fungus is able to cause widespread occurrence of natural epizootics, which can make the use of acaricides unnecessary. The management of habitats in which the pathogen survives between epizootics, the choice of varieties of crop varieties (e.g. canopy structure affecting microclimate) may allow the fungus to survive and to develop epidemics in spider mite populations (Elliot, 1998).

Deuteromycetes

General characteristics

The Deuteromycetes, formerly called the fungi imperfecti, are combined in a single group, since they do not seem to possess a sexual stage. It is very difficult to place these fungi in the remaining fungus classification system, since this is mainly based on the mode of sexual reproduction. It is generally assumed that the majority of the Deuteromycetes are the nonsexual stages of sexually reproducing fungi that belong to the Ascomycota and the Basidiomycota, with the largest number occurring in the Ascomycota. The large number of fungi (approximately 17,000 species) in the Deuteromycota (or Deuteromycetes) lack any common phylogenetic origin or relationship and have been grouped together for the sake of convenience.

Hirsutella sp. *infections in eriophyids*

Only fungal infections are known from eriophyids (McCoy, 1996). The study of pathogens of eriophyoids is difficult as the mites are extremely small, generally only 100–250 μm in length. Field observations of the presence of pathogens in eriophyoids are therefore almost impossible, and it is necessary to take field collected material to the laboratory to examine this for the presence of pathogens with a stereo- or compound microscope.

The first published record of a disease in an eriophyoid goes back to 1924: Speare and Yothers (1924) observed a sudden decimation of large populations of the citrus rust mite *(Phyllocoptruta (= Phyllocoptus) oleivorus)* on grapefruit in Florida. Population densities in June were sometimes around 5,000 mites on a single grapefruit, but shortly after the maximum density had been reached, populations were reduced to almost zero. The authors could discern fungal hyphae in mite cadavers and also showed that the incidence of the fungus disease was lower after the use of fungicidal copper sprays. Fisher (1950) described the fungus as *Hirsutella thompsonii*. In the same article, she

described *H. besseyi*, also from the citrus rust mite, but the taxonomic status of this latter species is unclear (Minter and Brady, 1980).

Conidia are the infective propagules of *Hirsutella*. The spores possess a mucous coat that facilitates adhesion to the host cuticle. The conidia germinate and may penetrate all body parts, although on spider mites, penetration is usually through the legs. Entomogenous fungi enter their host through the cuticle, which consists of about 30% chitin surrounded by a protein matrix. The fungi often produce proteases that play a major role in the early stage of penetration by exposing the chitin fibrils. Subsequent excretion of chitinolytic enzymes causes degradation of the fibrils into chains of glucose-N-acetyl of variable length. Cehrnin *et al*. (1997) studied the chitinolytic activity of two isolates of *H. thompsonii* and of *H. necatrix*. The *H. thompsonii* isolates excreted amylase, α-esterase and proteolytic enzymes, including elastase in addition to chitinase. The *H. necatrix* isolate does not produce elastase and differs also with respect to the production of chitinase and some of the proteolytic enzymes. This correlates with the pathogenicity towards the carmine spider mite *Tetranychus cinnabarinus*: the *H. thompsonii* isolates were found to be much more infectious than the *H. necatrix* isolate. However, the ability of the latter to kill is to a certain extent an indication that other enzymatic activities can partially substitute for elastase and chitinase deficiencies (Chernin *et al*., 1997).

Vey *et al.* (1993) observed the production of a toxic protein by *H. thompsonii* when the fungus is grown in artificial cultures. Filtrates were tested against several insect species both by injection and *per os*. Strong cytotoxic effects (pycnosis of the nucleus and lesions in the cytoplasm) were observed in the midgut, malpighian tubules, hypodermis, fat body, hemocytes, muscle and silk glands of larvae of *Galleria mellonella* (Lepidoptera: Pyralidae), but it was also pathological in other insect species. It caused pycnosis of the nucleus and reduction in cytoplasm density. One of the proteins, Hirsutellin A (HtA), inhibits insect cell growth in culture, causing cells to become hypotrophied and disrupting internal organelles and membranes (Boucias and Pendland, 1998). It is a 15–16 kDa thermostable, non-glycosylated protein with properties similar to ribosome-inhibiting proteins. However, the nucleotide and amino acid sequence of HtA are very distinct from other ribosome-inhibiting proteins (Boucias *et al.*, 1998). Later work showed that it affects a wide range of arthropods including mites (Omoto and McCoy, 1998). It is toxic to a wide range of arthropods including mites: in the citrus rust mite, *P. oleivora*, it causes a mortality of nearly 100% at a concentration of 100 μg/ml. HtA also seems to reduce fecundity of the rust mite.

The fungus, causing regular epizootics under natural conditions in Florida, affects both nymph and adult stages. The asexual conidia are produced out-

side the infected mite cadavers on the plant substrate. Conidia germinate under favourable conditions (high relative humidity) and enter the body of the mite by means of a germ tube. The mycelium forms a ramifying growth inside the hemocoel of the mite. The fungus erupts after death of the host through the integument and forms new spores. It takes at least 4 h for a spore to penetrate the cuticle of the host while time from infection to sporulation is around 4 days at 25–30°C. Over 50 species of entomogenous fungi have been reported in the genus *Hirsutella*, but only few have been reported as pathogens of eriophyoids (McCoy, 1996).

Hirsutella species produce conidia on solitary phialides that radiate from the host on the plant substrate. Hyphae exit through the body openings (mouth, anus, and genital opening) and through the cuticle. Hyphae may also break up within the body cavity and form multinucleate chlamydospores. These spores germinate and produce mycelium that can penetrate into the body cavity of the mites or reproduce asexually on the foliar surface (see McCoy, 1996).

Hirsutella thompsonii can easily be cultivated on artificial media, in contrast to most Entomophthorales. It grows on a variety of agar-based and liquid media (McCoy and Kanavel, 1969). Many isolates of the variety *H. thompsonii* form primary conidia and display distinct pleiomorphism in artificial media (Van Winkelhoff and McCoy, 1984). Conidia produced in submerged cultures seem to have a smoother outer cell wall than those produced in aerial cultures. On the basis of ultrastructural analysis of the conidiogenous structure, Samson *et al.* (1980) distinguished three morphologically distinct groups, which have been defined as three different varieties. *H. thompsonii synnematosa* seems to be restricted to the tropics on *Aceria* and related genera. The two other varieties, *H. thompsonii thompsonii* and *H. thompsonii vinacea* are encountered in the subtropical and temperate zones.

Identification of the different isolates is difficult because of the pleiomorphic character of the fungus. Boucias *et al*. (1982) conducted an isozyme analysis of mycelial preparations of 17 geographical isolates of *H. thompsonii*. Results showed the existence of extensive differentiation among the isolates without attendant morphological differences. On the basis of isozyme differences, they were able to distinguish three different varieties of *H. thompsonii*. Molecular data should be used as well for the discrimination of varieties and species. The authors suggest that for fungi belonging to the Deuteromycetes, isozyme analyses should be performed in conjunction with cytological studies throughout the developmental phases to verify whether parasexuality and other sources of genetic variability exist.

Fungi of the genus *Hirsutella* are considered candidates for biological control of mites and insects. In particular, *H. thompsonii* has been studied in this respect because of its effect on the citrus rust mite after periods of hot and

humid weather (McCoy, 1996). However, the fungus is polymorphic in regard to several biological characteristics, including its virulence to arthropods. Mozes-Koch *et al*. (1995) collected isolates from different geographical and climatic regions and tried to increase intraspecific variation by conducting hyphal anastomosis experiments. In this way, heterokaryons were obtained, leading to new fungal strains respect to virulence. This increased variation may allow improved selection of strains for biocontrol. The authors used the Random Amplified Polymorphic DNA technique (RAPD) for discrimination between different isolates of *H. thompsonii*, *H. necatrix* and *H. kirchneri*. Three different species could be discerned and the *H. thompsonii* isolates divided into specific groups each characterised by a different primer. An interesting aspect was that the *H. thompsonii* isolates could be divided into groups according to their RAPD patterns and that the distribution of the DNA patterns corresponded with the genus of the host mite and the geographical origin.

Yang *et al.* (1997) developed an age-structured model in order to study the interactions between orange fruit, the citrus rust mite, *P. oleivora*, and its fungal pathogen *H. thompsonii*. The model consisted of a set of difference equations incorporating age and stage change of the rust mite and its fungal pathogen. Abiotic factors in the model included daily mean temperature and daily dew period, while the biotic factors were mite density (egg, protonymph, deutonymph and adult) and pathogen density (latent pathogen, and infectious pathogen) and undamaged fruit surface area. The authors observed a good correlation of the observed data with the results of the simulation model. They concluded that the model could be used to predict citrus rust mite population trends and resulting fruit damage. If the model were used for estimating damage and population trend estimates, a pesticide-induced mortality model would need to be incorporated.

Hirsutella *infections in other mite taxa*

Hirsutella thompsonii has also been reported from mites other than Eriophyoidea: Gerson *et al.* (1979) showed that the fungus was highly pathogenic to *T. cinnabarinus* when it was grown on potato-dextrose agar or on sterile wheat bran, and pathogenic to *Eutretranychus orientalis* when grown on potato-dextrose agar. Penetration of the fungus into the host usually occurred in the legs, although other penetration sites were sometimes also observed. Mycophagous mites, such as *Tarsonemus* sp. and *Tyrophagus palmarum* were not infected by the fungus, but could use it as food (Gerson *et al.*, 1979). Attempts to use the fungus for control of spider mites (*T. cinnabarinus, E. orientalis* and *T. urticae)* in greenhouses were unsuccessful (see Rombach and Gillespie, 1988).

Hirsutella kirchneri is also considered a candidate for the control of plant-inhabiting mites. Sztejnberg *et al*. (1997) tested the pathogenicity of this fungus towards a number of different mites. It was infective towards the eriophyoid *Phyllocoptruta oleivora*, towards *Eutetranychus orientalis*, *Panonychus citri*, *T. cinnabarinus* (Tetranychidae), and to some degree towards *Hemisarcoptes coccophagus* (Hemisarcoptidae). No infectivity was found towards *Polyphagotarsonemus latus* (Tarsonemidae), *Rhizoglyphus robini*, *Tyrophagus putrescentiae* (Acaridae) and *Typhlodromus athiasae* (Phytoseiidae). The fungus has also no effect on beneficial insects such as the coccinellids *Coccidophilus citricola* and *Lindorus lophantae* (Sosa Gomez *et al.*, 1985).

Bałazy and Wisniewski (1982) observed *Hirsutella thompsonii* on *Trachyuropoda coccinea* (Trachyuropodidae). This is probably the first record of this fungus as pathogen of a non-phytophagous mite.

A few reports deal with the occurrence of *Hirsutella* sp. in the cassava green mite in the cassava belt in Africa. Yaninek *et al*. (1996) observed *H. thompsonii* on GCM and on *Oligonychus gossypii* during an inventory of fungi occurring on mites in Benin, West Africa. The frequency of sites with infected mites was 3.5 times greater in the wet season than in the dry season. Approximately 19–29% of dead CGM on cassava leaves were infected, but infected *O. gossypii* were seldom found. Fungus infections in the CGM were also observed by Bartkowski *et al*. (1988) in Kenya. The authors isolated many different species of fungi, including *Neozygites* sp. and *Hirsutella* sp., but also several other species that may have been saprophytic.

Odongo *et al.* (1998) carried out small field experiments in which CGM infested cassava plants were treated with suspensions of *H. thompsonii* conidia. The fungus strain was obtained from infected cassava mites in the western part of Kenya and grown on a standard potato-dextrose agar in the laboratory. Suspensions containing 1.2×10^{11} and 6.0×10^{10} ha^{-1} spores were sprayed on CGM infested plants and the effect of the treatment was compared to water-treated plants and plants on which the predatory mite *Neoseiulus teke* had been released. In the treated plots up to 76.6% of the cadavers developed disease, in contrast to only 0.6% of the control plots. Rainfall caused a reduction in disease incidence in the mites. The authors concluded from their work that the application of the fungus has promise for controlling *M. tanajoa*, but the fungus should be applied in harmony with other natural mortality factors, such as rainfall. The negative effect of rainfall was mainly due to the fact that the cadavers and the fungus inoculum were washed from the plants. This can probably be overcome by more appropriate formulations, such as the addition of stickers for a better adhesion of the spores to the leaves. Also, formulations of the fungus in a non-evaporative

diluent such as oil could improve its pathogenicity and its longevity in the field.

A fungal pathogen of the scavenger mite *Tydeus gloveri* (Tydeidae) was described by Samson and McCoy (1982). Citrus groves in central Florida infested with this mite were surveyed in 1979 and 1980. Leaf samples from unsprayed orange trees contained numerous mite cadavers that were apparently killed by a fungus. The fungus was described as *Hirsutella tydeicola* and appeared to be related to the species *H. besseyi*. The fungus has probably also been found on two other tydeid species, *Lorryia formosa* and *Tydeus californicus* in Cuba by Cabrera (cf. Samson and McCoy, 1982).

Hirsutella *species as possible control agents*

The high infective potential of *H. thompsonii* towards the citrus rust mite has led to research aimed at the development of this fungus as biological control agent. Large-scale laboratory mass production and industrial production methods have been developed in order to produce mycelial and conidial formulations (McCoy *et al.*, 1975; McCoy, 1981). The fungus was introduced into the field early in the season as a prophylactic to reduce rust mite populations. The fungus forms grey patches on the leaves under optimal weather conditions. Commercial production of conidial preparations in the USA was developed in 1975–1976 by Abbott Laboratories. After safety testing (McCoy and Heimpel, 1980), full registration was received for a mycoacaricide for the control of eriophyoids on citrus and turf under the trade name Mycar™. Several hundreds of kilograms of the product were sold in the USA, but commercial production was discontinued in 1985. Too many factors affected the stability and reliability of the acaricide (McCoy, 1996). Commercial development of mycelial preparations failed because of lysis of hyphae during storage (McCoy, 1981). Cold storage could prevent this lysis, but was not economical. The fungus has also been tried against other pest species in various countries. For details the reader is referred to McCoy (1996).

Interest in the production of *H. thompsonii* based acaricides for application against eriophyids continued in Brazil and Argentina even after Mycar™ had been taken out of production in the USA. Sosa Gomez (1991) studied conidium production by three pathotypes of *H. thompsonii* on semi-solid media. An isolate of *H. thompsonii* var. *synnematosa* showed the highest spore production on all media tested, compared to the other two isolates. The author also found that copper oxychloride suppressed conidium production completely, although mycelial growth was only reduced. Sulphur as wettable powder also caused reduction in conidiogenesis and mycelial growth, but the effect was less pronounced than for copper oxychloride. Several other pesticides (the acaricide chlorobenzylate, the herbicide paraquat, and the in-

secticides parathion, malathion, chlopyrifos and mineral oil), were found to be detrimental to the development of epizootics (Sosa Gomez *et al*., 1987; Sosa Gomez, 1991). Control measures have been tried in Argentina with a local isolate of *H. thompsonii* (Sosa Gomez and Nasca, 1983) and two strains obtained from the USA (Sosa Gomez, 1991).

Studies are presently being conducted on the control of *Aceria guerreronis* on coconut by means of *Hirsutella thompsonii* (J.M.S. Ferreira, pers. comm.). Five *Hirsutella* strains were introduced from Mexico into Brazil, but initial mortality due the fungus was only 35%. It was possible to increase the virulence of the fungus by passage of the pathogen in its host. The fungus has been established in the field, but damage due to *Aceria* is still present on the fruits. The fungus is mass produced on rice and corn grits. Further subjects of study are the effect of solar radiation on the survival of the conidia, and the infection process in the field.

Other Deuteromycetes infecting mites

Mycosis has also been recorded to occur in the blackcurrant mite *Cecidophyopsis ribis.* The causative agent initially found in Reading, England, was described as *Botrytis eriophyes*, but this description was later reconsidered and the fungus was redescribed as *Paecilomyces eriophytis* (Leatherdale, 1965). The fungus has probably also been observed in Italy on *Phytoptus avellanae* (Eriophyoidea), a mite associated with big-bud of hazel, and was identified as *Cephalosporium* sp. (cf. Leatherdale, 1965). Infection experiments with the isolate from *C. ribis* were performed with the European red mite *Panonychus ulmi* and with the eriophyoids *Aceria hippocastani* (from horse chestnut) and *Cecidophyes galii* (from goosegrass). The fungus infected the first two species but no infection was obtained in *C. galii.* The fungus is also known to infect the blueberry bud mite, *Aceria vaccinii* (Eriophyoidea): Baker and Neunzig (1968) observed high infection incidences in North Carolina, USA in late June and early July, when high temperatures coincided with high rainfall and high relative humidity. Disease incidence declined from August onwards, when conditions were less favourable for the development of the fungus. Population density of the blueberry bud mite then increased.

Sannasi and Amirthavalli (1970) conducted experiments in which the velvet mite, *Trombidium gigas* (Trombidiidae) was infected with spores of *Aspergillus flavus*. Three different means of inoculation were used: injection of spore suspensions into the body cavity, spraying of spore suspension on the integument and dusting of spores on the integument. In all cases, it was possible to infect the mites with the fungus. Changes in the structure of the integument of the infected mites have been described by Sannasi and Oliver (1970). The first sign of disease is the loss of the scarlet-red plumose cuticular

setae of the mites. Each seta consists of a main central stem from where minor secondary branches arise. The base of the central stem is slightly enlarged and is buried in sockets present in the epi- and procuticle. The fungus apparently digests the lipoproteinaceous epicuticular layer that fastens the base to the cuticular sockets. Subsequently, the process is followed by additional chemical changes in the composition of the cuticle. In addition, epidermal cells display pathological symptoms. In uninfected mites, epidermal cells form a syncytium, but after infection, a remarkable reaction occurs in the epidermis. The cells line up in almost a single row just below the outer limiting border of the epidermis. Mucin secretion occurs, a substance found in the endocuticular layer. Subsequently, vacuoles appear in the cytoplasm of the epidermal cells, whereas organelles such as mitochondria and Golgi apparatus are not anymore discernible.

Peña *et al*. (1996) investigated the potential of three different fungus species as biocontrol agents of the broad mite *Polyphagotarsonemus latus* (Tarsonemidae). Fungal pathogens seem promising as the broad mite thrives under warm and humid conditions. The pathogenicity of conidia of *Beauveria bassiana*, *H. thompsonii* and *Paecilomyces fumosoroseus* were tested in the laboratory under controlled temperature and humidity conditions and in the greenhouse. All fungus species tested were able to infect the broad mite; higher doses of conidia resulted in a faster death of the mites, while density of the mites on the leaves also affected disease incidence. For example, mortality caused by *B. bassiana* was fastest among densities between 65 and 125 mites per (bean) leaf. From the results of their study, the authors concluded that the fungus selected for its control should be one that causes epizootics within 2–3 days following application.

The broad mite has also been found in association with *Hirsutella nodulosa* (see Peña *et al*., 1996). Other reports on the occurrence of natural infections of this mite by fungi are not known.

Other Deuteromycetes as control agents

One of the earliest experiments in which a fungus was tested against a phytophagous mite was probably a field application of *B. bassiana* spores for the control of *T. urticae* by Dresner (1949). He treated two-spotted spider mites on kidney beans with a dust containing 0.5% spores of the fungus and obtained a mortality of 71%.

Research is being conducted in Brazil to evaluate several Deuteromycetes as possible control agent of the two-spotted spider mite. Tamai *et al.* (1998) tested 152 different isolates of the fungi *B. bassiana*, *B. brongniartii*, *Beauveria* sp., *Metarhizium* sp., *Paecilomyces lilacnus* and *P. farinosus.* Only the *Beauveria* spp. tested caused mortality between 35 and 95%. The patho-

genicity of one of the *B. bassiana* isolates (# 447), was further tested in the laboratory against *T. urticae* on leaf disks of the jack bean *Canavalia ensiformis* at a temperature of 25°C, at 70% relative humidity and a photoperiod of 12 h (Tamai *et al.*, 1999). The pathogen was applied in a concentration range from 5×10^6 to 1×10^9 conidia per milliliter. A mortality higher than 50% was not reached at any of the concentrations after 6 days following the application. Another *B. bassiana* isolate was tested in a semi-field experiment on two-spotted spider mites in chrysanthemum. The isolate, PL-63, was applied in a concentration of 2×10^8 conidia per milliliter and gave good control when four treatments were carried out in a period of 14 days. Results were even better than those obtained with chemical control. The fungus was also effective against other pests in chrysanthemum, such as thrips and aphids (Alves *et al.*, 1998).

Ascomycetes

The Ascomycota is a very large division of fungi with almost 2,000 genera and over 30,000 species. The group is characterised by the fact that they bear their sexual spores within an ascus, originally a cell that at first contains a diploid nucleus resulting from karyogamy. This nucleus undergoes subsequent meiosis and then haploid ascospores are formed inside the asci. These asci are often borne in or on top of a sporocarp. Very few Ascomycetes have been isolated from mites. The observations only concern Laboulbeniales infections in a number of mite species. This order consists of over 2,000 species of morphologically unusual fungi. They have obligate associations with arthropods, mostly insects, and lack mycelium. The entire thallus (body) is derived from enlargement and subsequent cell divisions of the two-celled ascospore. Fungi of this group do not appear to cause much damage to the host. Several genera of Laboulbeniales have been found on mites, including a species of *Rickia* (see Poinar and Poinar, 1998) and an unknown species on *Hirstionyssus* sp. (Dermanyssidae) (Steinhaus and Marsh, 1962).

Diseases Caused by Viruses

Virus diseases in mites have been observed in Tetranychidae, in particular in the citrus red mite, *Panonychus citri*, and the European red mite, *P. ulmi*. Muma (1955) reported the first indication of the occurrence of a virus disease in mites: He observed diseased specimens in a natural population of the citrus red mite (CRM) in Florida. Affected mites showed symptoms of diarrhoea and, when dead, were often stuck to the leaf surface by a smear of black resinous material that was excreted through the anus. Smith *et al.* (1959) reported

the disease in CRM also from California. A virus disease was suspected; spherical particles inside the diseased mites were presumed to be the virus particles. Later, however, it was shown that a rod-shaped, non-inclusion virus causes the disease (Reed and Hall, 1972). The virus particles are approximately 194 × 58 nm in size and are enclosed in an envelope of c. 266 × 111 nm. They are formed inside the nucleus of the midgut epithelial cells, but later they move out of the nucleus into the cytoplasm. Reed and Desjardins (1978) studied the spherical particles in more detail, found spherical particles of three different sizes in only laboratory reared CRM and assumed that these were acquired by the mites from the green lemons on which they were grown. The particles seem to have no detrimental effect on the mites, although they do multiply inside their hosts. Estes and Faust (1965) demonstrated the presence of RNA in these particles.

Diseased mites can easily be recognised by the presence of birefringent bodies of irregular shape of a few microns up to 50 μm in diameter (Smith and Cressman, 1962), although the mites do not always form the bodies, for example when grown under humid conditions (Reed *et al.*, 1974). The bodies are distributed throughout the host and occasionally in the legs. The bodies are believed to be associated with the formation of the so-called faecal pellets which probably contain guanine as excretion product (McEnroe, 1961). Similar bodies have been observed in other mites and are discussed in the section 'symptoms ascribed to poor condition'.

The virus disease is common in natural populations of the citrus red mite throughout the citrus groves in California and Arizona, USA, where it may cause a large reduction in population density of this mite (Reed, 1981). In the late 1960s, extensive research was carried on the development of the virus as a microbial insecticide. Shaw *et al*. (1968) applied the virus as an aqueous suspension of macerated diseased mites. The virus can only be cultured in live citrus mites that are usually grown on green lemons. This procedure is laborious and expensive and therefore only feasible for small field applications. A cheaper way to produce the virus in large quantities is the collection in the field of infected mites by means of a vacuum-suction machine (Shaw *et al.*, 1971). The mites are subsequently kept on green lemons for 6–7 days in order to increase the level of infection (Reed *et al.*, 1972). Application of field-collected diseased mites rendered a higher incidence of disease than dissemination of infected mites that were reared in the laboratory. Satisfactory control was obtained in small field experiments, but large field applications have never been successful for various reasons. The virus becomes rapidly inactivated by sunlight after application in aqueous formulations. High temperatures also have a negative effect on the virus although it is less affected when present in mite bodies than when free on the foliage. The host

range of the virus seems limited: Phytoseiid mites are not susceptible to infection (Shaw *et al.*, 1967), and of seven other spider mites tested, only *T. cinnabarinus* developed the birefringent bodies (Beaver and Reed, 1972). For a more complete survey on this virus disease the reader is referred to Van der Geest (1985).

Steinhaus (1959) studied a virus disease that affects the European red mite in California, USA. A spherical, non-occluded virus with a size of 40–60 μm was isolated. Later, Putman and Herne (1966) described a disease in the same mite species from Ontario, Canada, caused by a rod-shaped virus that develops inside the cells of the fat body of the mite (Bird, 1967). There is no conclusive evidence that this report concerns the same disease as found in California. Diseased mites can easily be recognised by the darker red colour of the immature mites, but adult mites do not show a difference in colour. The most conspicuous symptom, however, is the presence of birefringent inclusions inside the midgut of the mite with a radiating crystalline structure, probably also consisting of guanine. The virus causes only natural epizootics in dense populations. Putman (1979) performed field applications by introducing infected immature mites into a peach orchard. A considerable reduction in the population density was obtained. Application of aqueous suspensions of the virus was less successful, probably due to inactivation of the virus by the release of virus inhibitors from the leaf surface. No recent studies have been conducted on virus diseases in tetranychids.

Unidentified, non-occluded virus particles have also been observed in the egg yolk of eggs developing in gravid females of the predatory mite *P. persimilis* and *Neoseiulus cucumeris* (Figure 3a and 3b). Birefringent crystals were also noted in adults of this species, but no relation seems to exist between crystal formation and the presence of the virus in the eggs (Bjørnson *et al.*, 1997).

Honeybees *(Apis mellifera)* are subjected to many viruses, five of which seem to be associated with the varroa mite *Varroa jacobsoni* and the honeybee tracheal mite (HBTM) *Acarapis woodi* (Sammatoro *et al.*, 2000). It is assumed that these viruses are always present in bees, either in a latent or an inapparent form. The viruses may be activated in the bees by wounds inflicted by the mites. They are probably not capable to infect the parasitic mites, but the presence of varroa mite and/or HBTM causes a higher incidence of virus disease in honeybee colonies.

Two reports have been published on virus diseases in bee parasitic mites. One concerns virus particles observed in varroa mites that were present in a moribund honeybee colony in the northeastern United States (Camazine and Liu, 1998). The hexagonal, isometric particles showed features that are typical of iridescent viruses (iridoviruses), a group of viruses infecting many

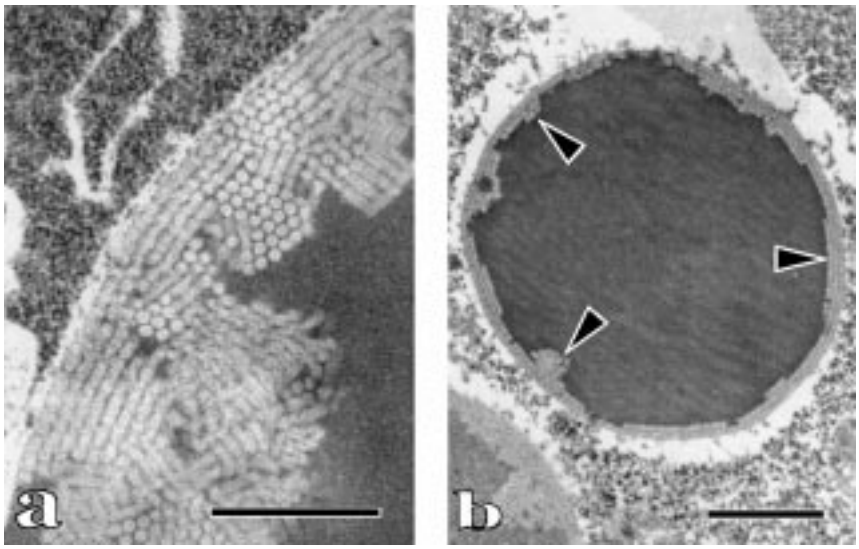

Figure 3. Unidentified, non-occluded virus-like particles (arrowheads in Figure 3(b)) in the yolk of a developing egg within a gravid *Neoseiulus cucumeris* female. Scale bar: (a) 0.5 μm, (b) 1 μm. Published with permission of Susan Bjørnson and Marilyn Steiner.

different groups of cold-blooded animals, including insects from several different orders, and other organisms. The authors assumed that the virus is lethal to both the honeybee and the mite. The mite may serve as vector of the virus to the honeybee, but further research is necessary to prove the role of varroa mites as vectors of honeybee viruses.

During a search for diseases in varroa mites in parasitised bee colonies, mites were found with characteristic internal black-coloured changes of the gut and the fat body (Kleespies *et al.*, 2000). On living bees, 3.6% of the mites showed this anomaly, in brood cells, even 8% of the juvenile mites were affected. Frequency and intensity of the symptoms can be enhanced by changes in environmental conditions (deficiency of bee brood, deficiency of pollen, abnormal brood temperature or death of the host). Longevity of black-coloured mites was reduced by 43% compared to normal looking individuals. (Cytopathological studies revealed the presence of a large number of spherical virus-like particles primarily in the nuclei of fat body and muscle tissue. The vir8s-partickes measure approximately 27–60 nm in diameter and resemble the particles found by Liu (1991) in HBTM. The authors performed *per os* transmission experiments with extracts of fat body tissue derived from symptomatic mites, but the experiments failed.

Virus-like particles were found in a sample of HBTM that originated from Scotland (Liu, 1991), but mites collected in California did not show the

presence of these particles. Tissues of affected mites were extensively lysed and most of the cells were tightly packed with virus-like particles. The ultrastructural appearance of these particles resembles insect picornaviruses, also known from honeybees. The size of the particles, however, is either smaller or larger than the bee virus. The author assumed from his histopathological studies that the virus multiplies inside the mite and is not derived from honeybees.

Diseases Caused by Bacteria

We realise that *Bacillus thuringiensis* is not a pathogen in the true sense of the word, as its mode of action on arthropods is mainly due to the presence of toxins. Nevertheless, we included *B. thuringiensis*-related work on mites in this article, as the study of this organism has traditionally been considered as part of the field of invertebrate pathology.

Mites are apparently not very susceptible to bacteria, since only a few reports deal with diseases in mites caused by this type of micro-organism. Lipa (1971) states in his review that "no bacterial diseases of mites have so far been recorded". However, data were already available on the action of the β-exotoxin of *B. thuringiensis* (see Šebesta *et al*., 1981). This toxin, also named thuringiensin, is heat stable and is excreted *in vitro* by the bacterium into the culture medium. Thuringiensin is nucleotide-like in chemical structure and inhibits DNA-dependent RNA polymerase, resulting in blockage of mitosis. The substance may cause deformations when applied to young insects, in particular holometabolous insects. Field applications were successful against the *P. citri* (Hall *et al.*, 1971) and *T. pacificus* (Hoy and Ouyang, 1987). Later, Royalty *et al*. (1990) conducted experiments in which two formulations of thuringiensin were tested on the *T. urticae*. Results were promising, and indicated that the compound is a potential acaricide. Young instars are especially susceptible, since these have a high growth rate. Physiological processes that occur in young organisms require higher rates of RNA synthesis than in older, slower growing adults. Thuringiensin is toxic for a wide range of organisms, including spider mites. It is not a very selective acaricide: *Metaseiulus occidentalis* (Phytoseiidae) treated with field-recommended doses fail to develop to adult, although eggs do hatch. Guo *et al.* (1991) also showed the toxic effect of thuringiensin on *T. urticae* and *P. persimilis*: oviposition started to decline after two days and ceased completely after 3–4 days in both predator and spider mite at doses of 115 and 211 μg/ml, respectively. The authors concluded from their experiments that thuringiensin is a non-selective acaricide that should not be used in combination with predatory mites.

Experiments in which the spore-crystal complex of *B. thuringiensis* was tested on spider mites did not show any mortality among spider mites (Krieg, 1972). However, Chapman and Hoy (1991) conducted experiments in which the *T. urticae* and *M. occidentalis* were treated with 10%, 50% and 100% of the recommended field doses of commercial preparations of *B. thuringiensis* var. *tenebrionis*, a strain which is recommended for use against the Colorado potato beetle, *Leptinotarsa decemlineata* (Chrysomelidae). No effect was noted on the *T. urticae*, but the preparation did show a toxic effect on *M. occidentalis*. The preparations had no effect on eggs, but if immatures were treated, only 65% reached adulthood. Starvation seemed to increase the effect of the *B. thuringiensis* preparation. The authors suggested that starvation probably leads to a higher uptake of the preparation, or that the predators were more exposed to the preparation because starved individuals walk faster. Another explanation was that starvation acts as a stress factor. The colony that was used carries a rickettsia-like organism which can depress survival when the predator is subjected to unhealthy conditions (Hess and Hoy, 1982). Chapman and Hoy (1991) had no explanation for the cause of the toxicity to *M. occidentalis*. It was probably not due to by-products in the preparation, as other commercial preparations based on the same *B. thuringiensis* variety showed the same effect. The preparation did not contain β-exotoxin, which is known to be toxic for predatory mites (see above). More recently, three isolates of *B. thuringiensis* have been found that contain δ-endotoxin with a clear effect on Acari (Payne *et al.*, 1993; 1994). The isolates were found to be toxic to the two-spotted spider mite and to the house dust mite. The δ-endotoxin of these strains can be isolated by, for example ion exchange, and be formulated to commercial acaricides. Another possible approach for phytophagous mites is to clone the genes that encode the toxin and to transfer this gene into a crop plant.

Lighthart *et al*. (1988) exposed *M. occidentalis* to several stress factors and studied the effect of these factors on the susceptibility of the predator to the bacterial pathogen *Serratia marcescens*. This bacterium is considered a weak pathogen for various insect species. Stress factors employed were starvation, high temperature, high relative humidity and crowding, all prior to inoculation with the bacterium. In particular, a high pre-inoculation temperature pulse in relatively uncrowded conditions caused the mites to become susceptible to the bacterium. However, starvation did not produce such an effect.

Control of the house dust mite *Dermatophagoides pteronyssinus* (Pyroglyphidae) by means of *Bacillus sphaericus* and *B. thuringiensis* var. *israelensis* (BTI) has been considered by Saleh *et al*. (1991). The *B. sphaericus* strains were more toxic than BTI: the bacteria not only killed mites, but

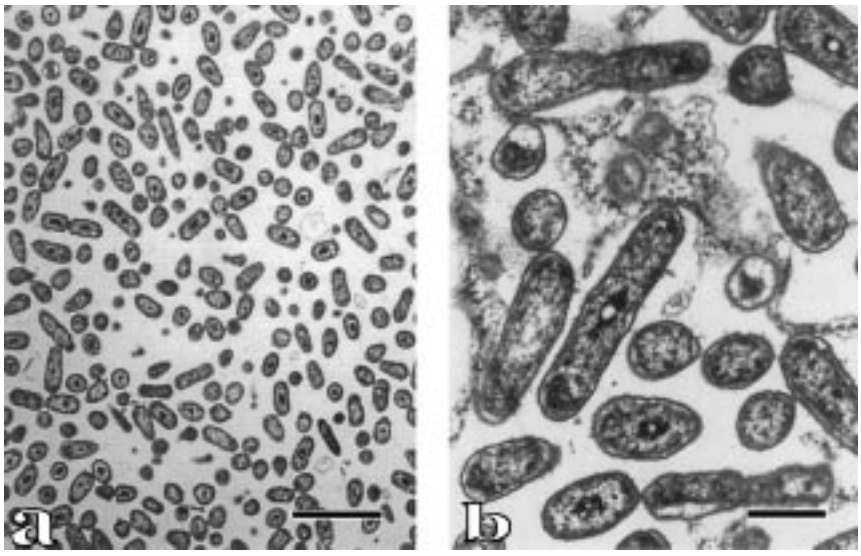

Figure 4. Rickettsia, of the genus *Wolbachia*, within unidentified tissues of *Phytoseiulus persimilis*. Scale bar: (a) 2 μm, (b) 1 μm. Part (a) of the figure published with permission of Susan Bjørnson and Marilyn Steiner and part (b) with permission of Academic Press.

development from the tritonymph stage onwards was considerably retarded. LC_{50}-values were established for three strains of *B. sphaericus* and for BTI. The values obtained were probably too low to proceed with the development of these bacteria as a biocontrol agent.

Diseases caused by α-Protobacteriaceae

Mite and tick species are commonly infected with intra-cellular microorganisms (Šut'áková, 1988, 1994; Steiner, 1993; Munderloh and Kurtti, 1995; Bjornson *et al.*, 1997). Most of these micro-organisms have been placed into the family Rickettsiaceae within the alpha subdivision of the Proteobacteria (Figure 5). The family Rickettsiaceae or rickettsia-like-organisms consists of three tribes – Rickettsieae, Ehrlichieae and Wolbachieae (Weiss and Moulder, 1984) – which have a number of features in common: they are obligate intracellular gram-negative bacteria naturally found in arthropod hosts, they multiply inside eukaryotic cells and are often surrounded by multiple membranes. Some are capable of infecting humans and other vertebrates, but are frequently pathogenic in these secondary hosts causing severe diseases such as spotted fever, typhus and scrub typhus (Hayes and Burgdorfer, 1989). Proper classification of members of this group has been hampered by the fact that classical microbiological identification tools could

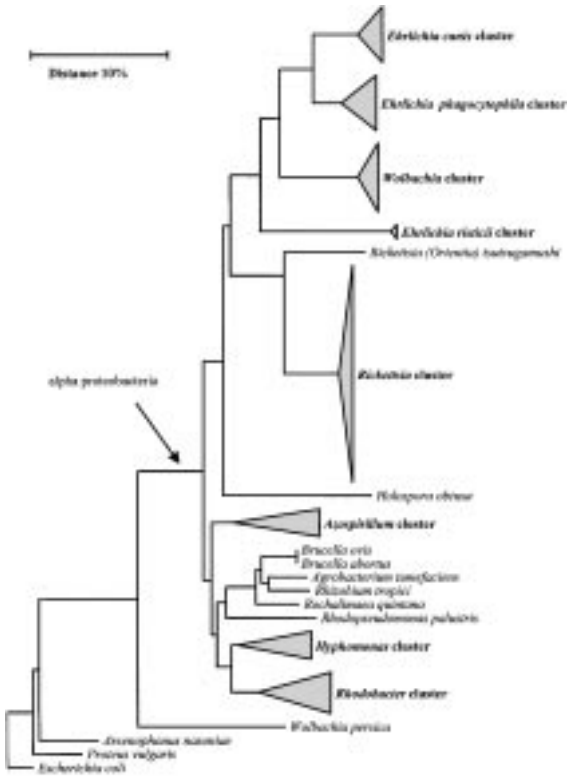

Figure 5. Phylogeny of representatives of the alpha Proteobacteria based on 16S rDNA sequences. Aligned sequences were retrieved from the small subunit RNA database (Van de Peer *et al.*, 2000). Phylogenetic relationships were inferred with Treecon vers. 1.2 (Van de Peer and De Wachter, 1994). The evolutionary distances were determined by the method of Jukes and Cantor. These values were used to construct a dendrogram by the neighbor-joining method. The tree is rooted using *Escherichia coli* as outgroup to the alpha Proteobacteria.

not be used due to their obligate intracellular lifestyle (see Roux and Raoult, 1995).

Recently, sequence information on 16S rDNA genes has revealed a number of interesting evolutionary aspects of the order Rickettsiales, including their phylogeny (Weisburg *et al*., 1985, 1989; Roux and Raoult, 1995; Johanowicz and Hoy, 1996; Noda *et al*., 1997; Andersson *et al*., 1999). For example, a microbe observed in the tick *Argus persicus* (Argasidae), originally placed in the genus *Wolbachia* based on resemblance in intracellular distribution and ultrastructure (Suitor and Weiss, 1961), has been reclassified as a member of the gamma-Proteobacteria (Weisburg *et al.*, 1989). Mitochondria evolved from within the rickettsia (Andersson *et al.*, 1998). Recent molecular phylogenetic studies on reproductive parasites of arthropods

(Werren *et al*., 1995a), including mites (Breeuwer and Jacobs, 1996; Johanowicz and Hoy, 1996), and nematodes (Bandi *et al.*, 1998), revealed that they are all closely related and belong to the genus *Wolbachia* (Figure 5). Unfortunately, molecular identification does not appear to be easily incorporated into the repertoire of bacterial classification tools; still invertebrate pathological studies heavily rely on morphological descriptions.

The best studied group of rickettsia are those vectored by ticks, as they can cause disease in vertebrates. There is a large body of mostly medically-oriented literature which deals with the detection, transmission and treatment of rickettsial diseases (Hastriter *et al.*, 1987; Munderloh and Kurtti, 1995). For example, *Rickettsia* (now renamed *Orientia* (Tamura *et al*., 1995)) *tsutsugamushi* is associated with lack of male offspring in broods of infected females of the parasitic mite *Leptotrombidium* (Roberts *et al.*, 1977; Tkahashi *et al.*, 1997). In other mites, rickettsia-like infections have often been observed in microscopic surveys (Šut'áková and Rüttgen, 1978; Hess and Hoy, 1982; Šut'áková, 1988, 1994; Steiner, 1993; Bjørnson *et al*., 1997) and are described as intracellular microbes often localised in the reproductive tissue of their host without any diagnostic features.

Recently, molecular screening for intracellular micro-organisms has detected *Wolbachia* in tetranychid and phytoseiid mite species (Gotoh *et al.*, 1995, 1999a, b; Breeuwer and Jacobs, 1996; Johanowicz and Hoy, 1996; Tsagkarakou *et al.*, 1996). Rickettsia-like organisms reported in the earlier microscopic surveys are probably all members of the genus *Wolbachia* in the family Rickettsiaceae. *Wolbachia* are widespread among arthropods and filarial nematodes (Werren *et al*., 1995b; Bandi *et al*., 1998). These bacteria are parasites of the reproductive system causing many unusual effects in their hosts (Stouthamer *et al.*, 1999), such as parthenogenesis (infected females produce only females), feminisation (infected male embryo's develop into females), male killing (male embryos die while female embryos develop into adults) and cytoplasmic incompatibility (see below). *Wolbachia* is maternally transmitted through the egg cytoplasm (but see Huigens *et al.*, 2000). It is estimated that *Wolbachia* occur in up to 16% of the insect species (Werren *et al.*, 1995b). They seem also to be common in Acari but their presence in this group has only been recently documented.

Wolbachia can induce cytoplasmic incompatibility (CI) resulting in reduced numbers of offspring and/or male biased sex ratios. This phenomenon is wide-spread in insects and has been described in both phytoseiid mites (Hess and Hoy, 1982; Hoy and Cave, 1988; Johanowicz and Hoy, 1998a, b) and spider mites (Breeuwer, 1997). The incompatibility is expressed in crosses between infected males and uninfected females. If no other genetic incompatibility factors are present, all other cross combinations should produce normal

offspring. Uninfected individuals may be obtained from naturally uninfected strains or by curing the infection through antibiotic or temperature treatment (Johanowicz and Hoy, 1996; Breeuwer, 1997; Van Opijnen and Breeuwer, 1999). Apart from the incompatibility, no obvious pathogenic symptoms are associated with the *Wolbachia* infection, other than that infected females have a somewhat lowered fecundity (F. Vala, pers. comm.). In some tetranychid species, *Wolbachia* infection does not cause cytoplasmic incompatibility (i.e. lowered offspring production or deviant sex ratios) (Gotoh *et al.*, 1995, 1999a, b; Gomi *et al.*, 1997). There are at least three explanations for the absence of cytoplasmic incompatibility that are dependent upon both genetic interactions between host genotype and *Wolbachia* strain: *Wolbachia* cannot induce CI (Bourtzis *et al.*, 1998; Merçot and Poinsot 1998); incompatibility is not expressed until the F2 causing hybrid breakdown (F2 male mortality) (F. Vala, pers. comm.) and bacterial density in the parental strain is too low and incapable of eliciting CI (cf. Breeuwer and Werren, 1993). Interesting point is that *Wolbachia* infections may provide an explanation for the frequent observations of incompatibility and hybrid breakdown in crosses between and within closely related mite species.

It is likely that surveys for microbial parasites of the reproductive tract in the Acari will yield patterns of abundance and diversity similar to that found in insects. Such micro-organisms are easily overlooked if one only screens for classical pathogenic symptoms such as mortality of infected individuals. Other possible symptoms associated with infection, such as CI or sex ratio distortion, should be investigated. The phenotypic effects of microbial infections may only be apparent in crosses between different mite strains or by comparing field collected strains. Infections may easily be lost or go to fixation during lab culturing. For example, the intracellular bacteria (named *Rickettsiella persimilis)* found in some, but not all strains of the predatory mite *P. persimilis* (Šut'áková and Arantunyan, 1990) may very well be a CI *Wolbachia*. A survey among thelytokous oribatid mites using *Wolbachia* specific *ftsZ* primers did not detect infected species (Perrot-Minnot and Norton, 1997). However, this does not rule out the possibility that parthenogenesis-inducing *Wolbachia* exist in other thelytokous mite species. Indeed, recently Wolbachia have been found in several thelytokous *Bryobia* (Tetranychidae) species (A. Weeks, pers. comm.). The molecular tools for the detection of these microbes and the knowledge of possible phenotypic effects that they may have on their arthropod host, will open up new fields for acarologists.

Diseases Caused by Protozoa

General characteristics

Two phyla of the subkingdom Protozoa, the Apicomplexa and the Microspora, have members that occur in arthropods: some are pathogens, occasionally found in both arthropods and vertebrates (e.g., haemosporidia causing malaria), while others are commensals or weak pathogens, and others are highly virulent organisms (cf. Tanada and Kaya, 1993). Protozoa associated with mites are especially found in the phylum Apicomplexa, with the classes Gregarinia and Coccidia, and the phylum Microspora. The Gregarinia are divided in the orders Eugregarinida and Neogregarinida. Several representatives of the former order have been detected in mites. The phylum Microspora also contains several, often virulent, pathogens of mites.

Apicomplexa infections in mites

Gregarinia, or gregarines, have mature gamonts (trophozoites) that are large and extracellular. The gamonts are found in the digestive tract and body cavity of invertebrates and possess attachment organelles (see Tanada and Kaya, 1993). They generally have similar gametes (isogametes) and undergo syzygy, whereby mature gamonts detached themselves from the midgut and line themselves end to end in pairs or in larger numbers to form a prenuptial association. The zygotes form oocysts within gametocysts. Eugregarines have a life cycle that consists only of gametogony and sporogony, but the neogregarines, considered to be more primitive, have an additional schizogony (a multiple fission process). This schizogony, or merogony, occurs intra- or extracellularly and causes the presence of higher numbers of the pathogen than in case of the eugregarines. These higher numbers result in a more virulent infection.

As early as 1855, the eugregarine *Gregarina oribatarum* was reported in an unidentified mite (see Lipa, 1971). Unidentified eugregarine infections were reported in the oribaitid mites *Damaeus oblongus* and *D. geniculatus* (Damaeidae) by Michael in 1884 and Wellmer in 1911, respectively (as reported by Lipa, 1971). Erhardová (1955) described the gregarines *G. corolla* and *G. scutovertexi* from *Scutovertex minutus*, an oribatid mite that serves as a vector of the tapeworm, *Moniezia expansa*. Several other eugregarine species were described from oribatid mites by Purrini *et al.* (1979) and Purrini and Ormieres (1981) (see Table 1). In 1988, Levine (1985) erected the new genus *Erhardovina* and transferred all *Gregarina* species from mites to this new genus in order to differentiate these species from those that occur in insects. We feel that this criterion is not a valid one for the taxonomy of organisms. However, in Table 1 we use the genus name *Erhardovina.*

A eugregarine infection of the intestinal wall was also reported from the water mite *Limnochares aquatica* (Hydrachnellidae) (see Issi and Lipa, 1968) and *Erhardovina euzeti* was detected in the oribatid mite *Euzetes seminulum* (Lipa, 1982). Despite these reports, no data are available on the impact of these infections on their mite hosts or the pathological condition that they produce. It is generally believed, however, that gregarines belonging to the Order Eugregarinida (including the genus *Erhardovina*) are of low virulence (Tanada and Kaya, 1993).

Coccidia differ from the gregarines in their gamogony: the female gamont of the gregarine gives rise to a number of gametes whereas that of the coccidians only gives rise to a single gamete. One coccidian species has been described from an (oribatid) mite (Purrini, 1984).

Microspora infections in mites

Microsporidia are obligate intracellular parasites with a wide host range including all major animal groups. They rank among the smallest of eukaryotes and are now considered a separate phylum, the Microspora, within the subkingdom Protozoa (Levine *et al*., 1980), although recent molecular studies indicate that they may be a branch of the Fungi (Hirt *et al.*, 1999). Our knowledge on the life history of microsporidia is mainly based on work that has been done on microsporidiosis in insects. Spores, the infective stage, are ingested by the host and, in the midgut, their polar filament is instantaneously emitted. In this way the sporoplasm is 'injected' into the midgut cells without the destruction of the host cell. Within the host cell, an increase in numbers followed by development into new spores takes place. These so-called 'first spores' from the midgut cells are thought to be responsible for cell to cell spread (Solter and Maddox, 1998). In this way the infection spreads throughout the host. Many different tissues may be infected. The spores are released into the environment during the life of the host or after its death. They are the only stages that can survive outside their host, and act as a source of new inoculum. Many microsporidian species have very complicated life cycles with several spore types and hosts involved. Often microsporidiosis is transmitted vertically (from mother to offspring), usually without spores as an intermediary. Vertical transmission may be transovarial, by passage of the pathogen through the ovary, or transovum, a form of transovarial transmission in which the pathogen enters the egg while it is still in the ovary (S. Bjørnson, pers. comm.).

Classical taxonomy of microsporidia is mainly based on spore size and shape and is unsatisfactory. For several decades, ultrastructural characteristics have been used for taxonomic purposes, which has caused a revision of some of the genera in this group of parasitic organisms (Sprague *et al.*, 1992). Host-

and tissue specificity are now also taken into consideration. In the 1990s, several research groups started to integrate molecular techniques for phylogenetic studies of microsporidia (Franzen and Muller, 1999), conformable to bacteria. This will result in another revision of the Microspora genera and new insights into their evolutionary relationship with other phyla (Canning *et al*., 1998). However, the relevance of molecular data and ultrastructure characteristics for microsporidia phylogeny is an ongoing discussion.

The first microsporidium described in mites was *Nosema steinhausi* (Weiser, 1956) from the stored product mite *Tyrophagus putrescentiae* (Tyroglyphidae). The disease affects both adults and nymphs. Experiments in a colony of this mite showed that the disease progressed from about 10% infection at the start of the experiment to 75% after two months. The culture was completely eradicated after a further two weeks.

Several species of microsporidia have been described in Oribatei: Purrini and Bäumler (1976) described *Nosema ptyctimae* from *Rhysotritia ardua* (Phthiracaridae). Up to 26% of the adults were infected of a population occurring in spruce forest soil. Infected mites could easily be recognised by the presence of a distinct milky spot under the cuticle of the host. Fat body tissue and nephrocytes appeared to be affected by the microsporidium. In another study on microsporidia in Oribatei, Purrini and Weiser (1981) described eight new species: four species in the genus *Pleistophora*, one species belonging to the genus *Thelohania* and three *Nosema* species. Another species, *N. euzeti* was described by Lipa (1982) from the oribatid mite *Euzetes seminulum* (Euzetidae).

Two microsporidian species have been described from the water mite *Limnochares aquatica* (Hydrachnellae): *Gurleya sokolovi* by Issi and Lipa (1968), and the species *Napamichum aequifilum* by Larsson (1990).

Poor performance of phytoseiids, commercially-reared to be used as biological control agents of spider mites and/or small insects such as thrips, have led to studies on the possible involvement of pathogens in predator colonies. Beerling and Van der Geest (1991a, b) studied a microsporidosis in mass rearings of the predatory mites *Amblyseius barkeri* and *Neoseiulus cucumeris* that are being used for the control of the thrips pests *Frankliniella occidentalis* and *Thrips tabaci* (Thripidae) on vegetable and ornamental crops in greenhouses. The predatory mites are reared in large, aerated containers that are filled with wheat bran and kept at approximately 22°C at a relative humidity of about 90%. These conditions allow the growth of fungi on the wheat bran that are grazed by stored product mites, such as *Tyrophagus putrescentiae* and *Acarus siro* (Acaridae). These mites serve as food for the predators. Reproduction of the predator in the mass cultures was low and predation capacity of the mites unsatisfactory. Predatory mites were sluggish in their movement and

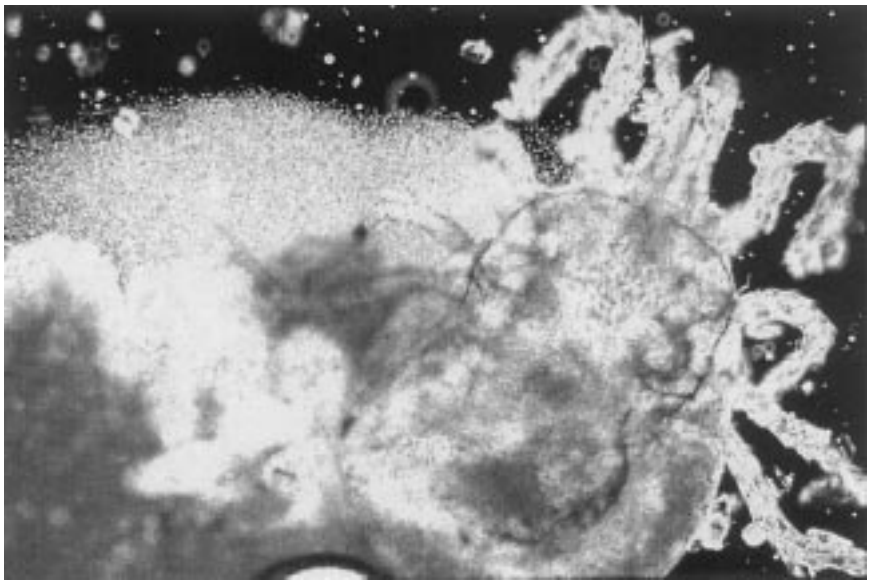

Figure 6. Squash preparation of *Amblyseius barkeri*, infected with a microsporidium. Note the numerous spores on the top half of the picture. Photograph from Ellen Beerling.

had a swollen and whitish appearance (Beerling and Van der Geest, 1991a). Squash preparations of mites showed the presence of numerous spores of microsporidia, probably belonging to the Pleistophoridae (Figure 6). Heavily infected mites died and spores were the released into the culture medium (free-spore pool). The authors also observed stored product mites infected with microsporidia in the rearing containers. As the pathogen was also present in the prey mite, it was assumed that five possible ways of transmission were possible: vertical transmission (from parent to offspring), and four ways of horizontal transmission (by predation or cannibalism, by contact with the free-spore pool, by physical contact with other mites (conspecifics or prey) and by mating).

Further work by Beerling *et al*. (1993) showed that three different spore types are found in the predatory mite rearings. Since a microsporidium life cycle may comprise different spore types with different functions, these spores could belong to one and the same microsporidian species, although two or three different species cannot be excluded. Oblong spores were detected in both prey mites and predatory mites, measuring $1.8 \pm 0.9\,\mu$m. Small and more oval spores ($1.4 \pm 0.8\,\mu$m) were exclusively found in the prey mites. Large spores ($2.6 \pm 1.3\,\mu$m) were occasionally encountered and found in prey mites only. These spores resemble the spores described for *N. steinhausi*, and therefore could be the same species.

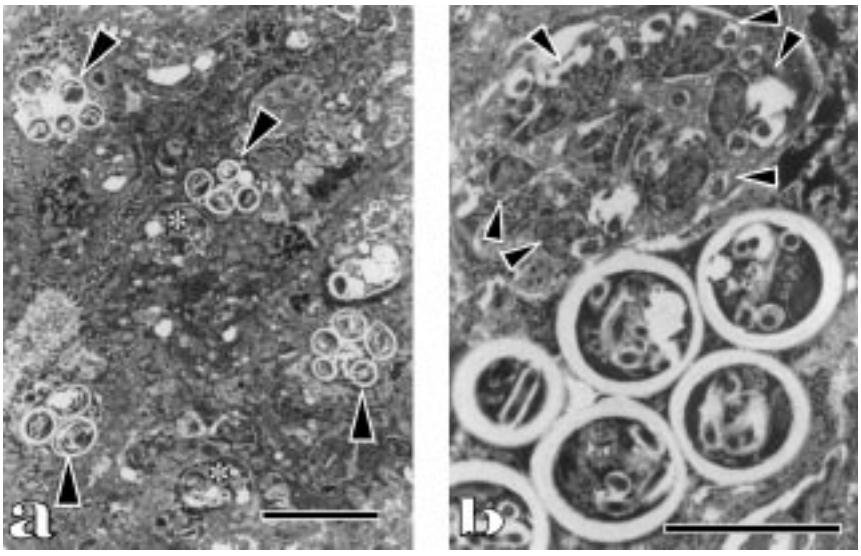

Figure 7. Intexta acarivora mature spores (arrowheads in (a)) and developing spores (∗ in (a), arrowheads in (b)) in unidentified tissue of *Tyrophagus putrescentiae*. Scale bar: (a) 5 μm, (b) 2 μm. Published with permission of Susan Bjørnson and Marilyn Steiner.

Recently, a new species of a microsporidium parasite, *Intexta acarivora*, was observed in the gut epithelium of the forage mite *T. putrescentiae* (Larsson *et al*., 1997), obtained from a commercial culture in The Netherlands. Mites of this culture are used as prey for a commercial rearing of *N. cucumeris*. Beerling and Van der Geest (1991a, b) also studied infected mite strains from a commercial rearing in The Netherlands, but it is not known whether this has the same origin as the samples studied by Larsson *et al.* (1997). The microsporidium *I. acarivora* (Figure 7a and 7b) possesses macrospores with dimensions 1.5–2.3 μm width and microspores of 1.3–1.7 μm width. These values do no correspond with any of the measurements of the spores in Beerling *et al.* (1993).

Bjørnson *et al*. (1996) studied colonies of *P. persimilis* that were obtained from suppliers of biological control agents. On the basis of spore morphology, three distinct microsporidia could be observed in strains of *P. persimilis*, obtained from three different suppliers. The ultrastructure of the pathogen and the course of the disease of a colony obtained from Europe were studied in more detail (Figures 8 and 9). Schizonts were observed inside the nuclei of the digestive cells of the ventriculus and within the protoplasm of cells that line the caecal wall and the muscle tissue underlying it. The properties of the pathogen made it difficult to assign it to an existing genus. For that reason, it was placed in the collective group *Microsporidium*. Prey mites (*T. urticae*)

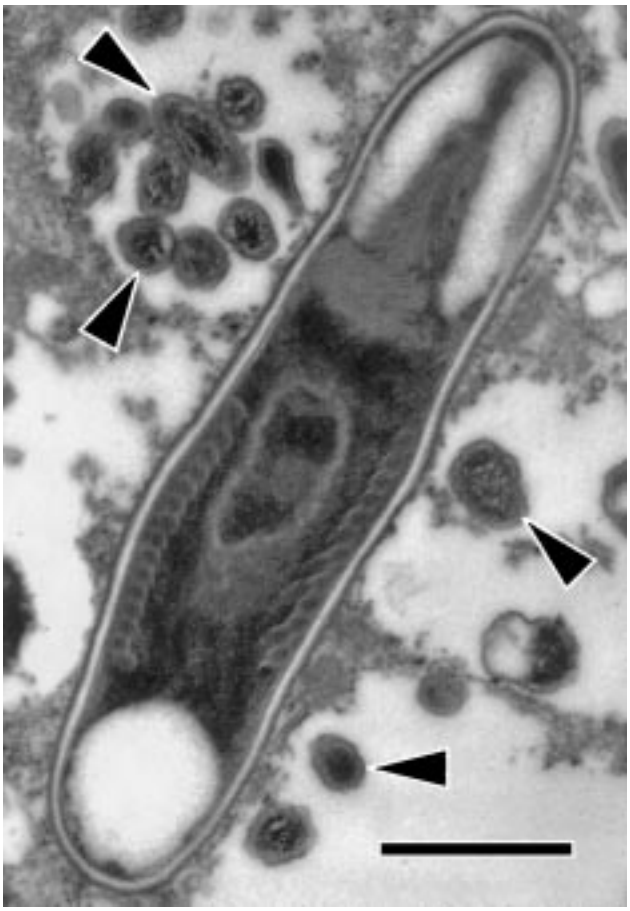

Figure 8. *Microsporidium phytoseiuli* mature spore and rickettsia (arrowheads) in unidentified tissue of *Phytoseiulus persimilis*. Scale bar: 1 μm. Published with permission of Academic Press.

did not show any sign of microsporidiosis making it highly improbable that the disease was obtained through the prey mites. Vertical transmission for this microsporidium was proven, as mature spores were observed in developing eggs inside gravid females. Horizontal transmission seems only possible when uninfected immatures were allowed to develop in the vicinity of infected adults or juveniles. The performance of an infected colony was greatly affected (Bjørnson and Keddie, 1999): mean fecundity and prey consumption of infected mites were significantly reduced. Short-term survivability was variable and was not a good measure of predator quality. However, uninfected females lived longer than infected females.

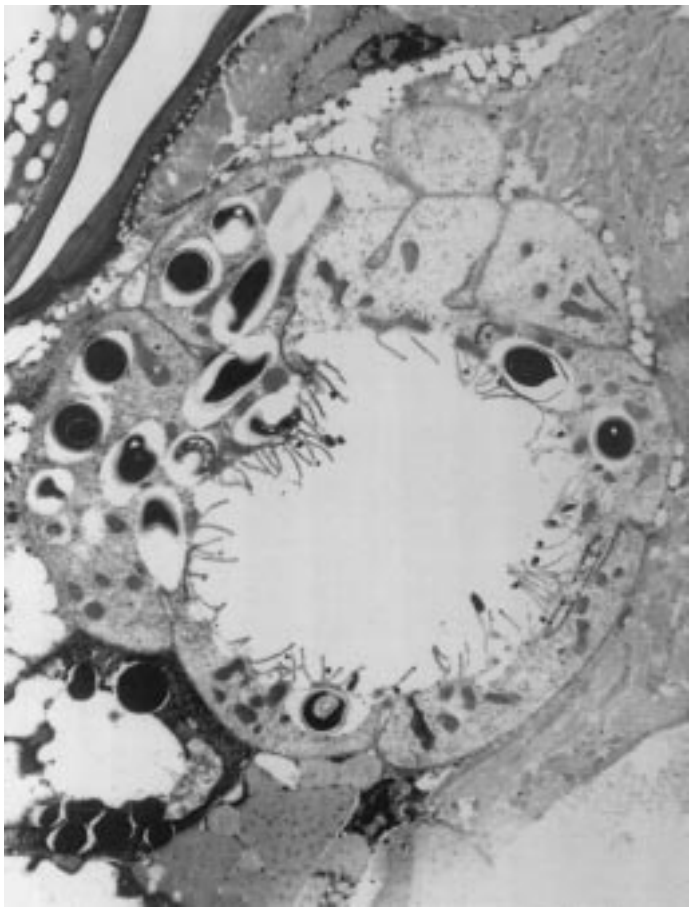

Figure 9. Spores of an unidentified microsporidium in Malpighian tubule cells of *Phytoseiulus persimilis*. Scale bar: 1 μm. Published with permission of Susan Bjørnson.

Mass production of predatory mites has been performed for a large number of years, often without any complications. The predator *P. persimilis* was first discovered in Chile in the 1950s and was subsequently introduced into Germany (Dosse, 1958). After almost 40 years of mass production, three different microsporidian species have now been detected in this predator. Bjørnson (1998) considered it very unlikely that these pathogens originated from the original area of distribution of the predator. She finds it more reasonable to assume that the microsporidians are endemic to the areas where they are being mass-produced. They could have been derived from the prey species on which they are being mass cultured, but these prey colonies seem to be free of disease.

Poor performance of the predators, due to the presence of pathogens in the mass cultures is a threat to integrated pest management in especially glasshouse crops (e.g., Steiner, 1993). It is clear that more attention should be paid to a good monitoring system. The presence of pathogens should be established early in the manufacturing process, which requires a fast and reliable detection method. In the past, visual inspection with the aid of a binocular or compound microscope was the only way to establish the presence of these pathogens. A polarising filter is needed to avoid confusion with the birefringent crystals that are commonly present inside adult phytoseiids (see section on 'Symptoms ascribed to poor condition'). The availability of a method to detect the disease at an early stage is of great importance for the commercial production of natural enemies. Beerling *et al*. (1993) developed an ELISA to detect the presence of microsporidiosis in predator mass-rearings. Monoclonal antibodies were produced against one spore type (oblong), that was present in both prey and predator species. A next step would be the use of more sensitive molecular techniques (e.g., PCR) which makes the detection of microsporidiosis possible regardless of spore type, and even before spores are formed (Malone and McIvor, 1996).

At this moment, no cure exists for microsporidiosis in predatory mite mass rearings. Anti-microsporidial compounds, such as albendazole, fumagillin, metronidazole and nifedipine were not successful in eliminating microsporidiosis in mass cultures of *P. persimilis* (Bjørnson, 1998). Therefore, efforts should be made to keep the starting cultures of predatory mites disease-free. Heat treatment of infected eggs, or rearing infected individuals at elevated temperatures, may reduce disease prevalence in some cases; however, the most effective and practical means for rearing microsporidian-free predatory mites is to start a new rearing with progeny from uninfected females.

Symptoms Ascribed to Poor Condition

Rectal plugs, usually in combination with abdominal discoloration is a well-known phenomenon in phytoseiids (Tanigoshi *et al.*, 1981; Bjørnson *et al.*, 1997). Abdominal discoloration is usually manifested as two white stripes along the dorsal sides of the body within the Malpighian tubules. The condition is frequently found in laboratory colonies of predatory mites and it has been assumed that it is caused by a poor condition of the predator. Tanigoshi (1982), for example, considered the condition a sign of senescence. Affected mites are often lethargic and have often numerous densely packed, birefringent dumbbell-shaped bodies, mainly in the Malpighian tubules, rectum and anal atrium (Figures 10, 11a and 11b). The condition does not seem to be

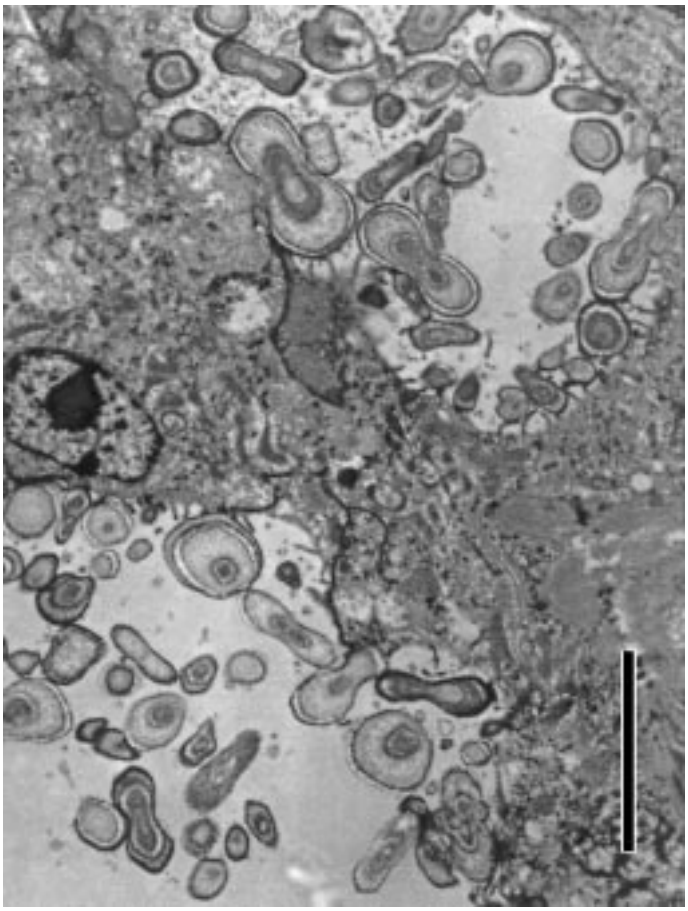

Figure 10. Dumbbell-shaped crystals in the caecal lumen of *Phytoseiulus persimilis* Athias-Henriot. Scale bar: 5 μm. Published with permission of Susan Bjørnson and Marilyn Steiner.

associated with the presence of pathogenic organisms (Bjørnson *et al.*, 1997). In *Cheyletus eruditus*, abdominal discoloration is also associated with the occurrence of birefringent crystals in the excretory organs, especially when reared under crowded conditions. The crystals are considered the normal excretory products (Hughes, 1950). The main excretory product of arachnids is guanine with uric acid, in spider mites is guanine the sole excretion product McEnroe (1961). These compounds are insoluble and are probably stored in the malpighian tubes prior to excretion. The crystals observed in *P. persimilis*, however, contain high levels of potassium, low levels of phosphorous and sulphur and traces of chlorine, very unlike the common waste products of arachnids (Bjørnson, 1998). Large numbers of crystals in

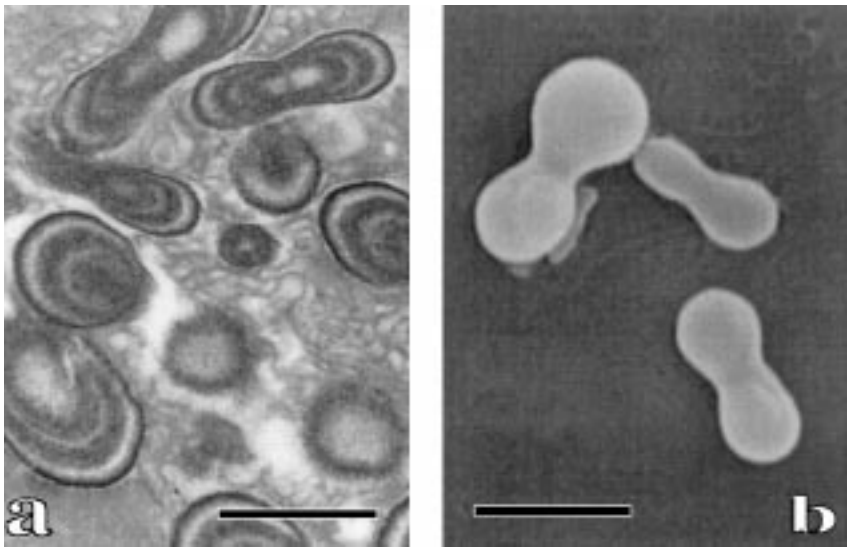

Figure 11. Dumbbell-shaped crystals in *Phytoseiulus persimilis*. Scale bar: (a) 1 μm, (b) 2 μm. Part (a) of the figure published with permission of Susan Bjørnson and Marilyn Steiner and part (b) with permission of Susan Bjørnson.

mites are especially found in laboratory mites, reared under crowded condition. She assumed that they are an indication of poor conditions of the mites.

Schütte *et al.* (1995) showed that mites with heavy loads of the crystals have a lower response to herbivore-induced plant volatiles, which play a role in the foraging behaviour of the predator, than less affected mites. Adult females with crystals also showed a lower oviposition rate and higher mortality. This so-called low responding population of *P. persimilis* was screened for the presence of pathogens (Schütte *et al.*, 1998), but no pathogens could be detected. The authors, however, provided strong evidence that a contagious disease affects the population: The presence of dead individuals of this population induces behavioural changes in predatory mites of a so-called responding strain in only about a week. The disease agent is apparently released by the dead conspecifics of the non-responding strain prior to or after death. Maintenance of a population with a high response to volatiles in a laboratory where also the low responding population is present is only possible by rearing the former under very strict hygienic conditions (Dicke *et al.*, 2000).

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