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Review

Revision of the lifestyles of phytoseiid mites (Acari: Phytoseiidae) and implications for biological control strategies

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ABSTRACT

A new classification of lifestyles of phytoseiid mites is proposed based on the findings and suggestions from many studies conducted in the fifteen years since the publication of the lifestyle system by McMurtry & Croft (1997). In this newly proposed classification, Type I (Specialized mite predators) is divided into three subtypes to highlight mite prey specificity: subtype I-a—Specialized predators of *Tetranychus* species (Tetranychidae); subtype I-b—Specialized predators of web-nest producing mites (Tetranychidae); subtype I-c—Specialized predators of tydeoids (Tydeoidea). Type II (Selective predators of tetranychid mites) remains essentially the same. Type III (Generalist predators) is a huge and diverse group of general feeders; predators in this category are now grouped into five subtypes based on the microhabitat occupied and morphology: subtype III-a—Generalist predators living on pubescent leaves; subtype III-b—Generalist predators living on glabrous leaves; III-c—Generalist predators living in confined spaces on dicotyledonous plants; III-d—Generalist predators living in confined spaces on monocotyledonous plants; III-e—Generalist predators from soil/litter habitats. Type IV (Pollen feeding generalist predators) also remains essentially the same. Two possible additional lifestyles include phytoseiids living on aquatic plants and phytoseiids able to pierce leaf cells. Behavioral and biological information is updated and implications for biological control strategies are discussed.

Key words: Ecology, predator, feeding habit, biological control

INTRODUCTION

Phytoseiid mites are important biological control agents of other mite groups, thrips and whiteflies. They have been extensively used in biological control programs (Helle & Sabelis 1985; Lindquist *et al.* 1996; Sabelis & Van Rijn 1997; McMurtry & Croft 1997; Gerson *et al.* 2003). The general biology of these mites has been thoroughly studied. Despite being known mainly as predators of small arthropods and nematodes, most phytoseiids also have other feeding habits, consuming food items such as fungi, plant exudates, pollen, etc. Some are even able to extract liquid from leaf cells.

Although apparently all phytoseiids avoid exposure to direct sunlight, they vary in relation to their preferred substrates. Some are often found in smooth microhabitats, where they find their food sources, resting near the main leaf veins or under non-plant structures, such as webbing produced by insects, spiders or mites, or particles carried by the wind and deposited on plant parts, especially leaves and fruits. Others are favoured by non-homogeneous microhabitats, such as pubescent leaves, natural plant structures (domatia, meristematic regions) or structures produced by plants because of exogenous determining factors (galls or erinea). Still others seem to commute regularly between plant microhabitats showing those two extreme characteristics while looking for food or protection. McMurtry (2010) diagrammed hypothetical pathways of evolution of phytoseiid food habits.

This paper presents a revision of the lifestyle system of McMurtry & Croft (1997) as well as a summary of new behavioural and biological information related to this aspect (without intending to be an all-inclusive review). It also discusses the implication of this new information on the establishment of new biological control programs involving the use of phytoseiid species.

THE MODIFIED LIFESTYLE SYSTEM

An overview of the relation between the previous (McMurtry & Croft 1997) and the newly proposed systems is shown in Table 1. One of the main differences between them refers to the relation of some species to more than one lifestyle. McMurtry & Croft (1997) had already emphasized the absence of discrete lines between types.

TABLE 1: Old and proposed new system of lifestyles of Phytoseiidae.

Old (McMurtry and Croft 1997)	Proposed New System
TYPE I—Highly specific on <i>Tetranychus</i> spp	TYPE I—Subdivided according to mite prey specificity: I-a, b, c
TYPE II—Broadly specific—tetranychids most favoured	TYPE II—Nearly the same
TYPE III—Generalists—wide range of foods acceptable	TYPE III—Subdivided according to habitat: III-a, b, c, d, e
TYPE IV—Primarily pollen feeders Generalist predators	TYPE IV—Same, but with new information

Type I is now divided into subtypes to highlight the specificity of phytoseiid assemblages to different groups of mite prey. Type II remains essentially the same as defined previously. Type III is a huge and diverse group of generalists, now divided into subtypes according to microhabitat and morphology (McMurtry & Moraes 2012). Type IV also remains basically the same as previously defined.

Type I lifestyle—Specialized mite predators

Since the first attempt to classify the phytoseiids according to their feeding habits (McMurtry & Croft 1997), the specificity of certain phytoseiid assemblages to mite prey groups other than tetranychids was pointed out by different authors. Thus, Type I lifestyle is now considered to include phytoseiids that are specialized predators of different mite groups. This led to the need to divide this lifestyle type into three subgroups.

Subtype I-a—Specialized predators of *Tetranychus* (Tetranychidae)

This subtype contains phytoseiids that have adapted to attacking spider mites producing the so-called “complicated web” (CW-u life type of Saito 1985). Until now, the examples refer to phytoseiids associated with *Tetranychus* species. However, it is possible that these predators can also be effective as control agents of spider mites of other genera, also known to produce the CW-u web type. Saito (1985) mentioned some species of *Eotetranychus* as also producing that web type.

It corresponds to the species included in the Type I lifestyle of McMurtry & Croft (1997), containing *Phytoseiulus* species. These predators could have coevolved with *Tetranychus* species, which have highly clumped distributions (see McMurtry & Croft 1997).

There is a vast literature indicating the association of *Phytoseiulus* with *Tetranychus* species under field conditions. Several new studies under laboratory conditions confirm the ability of *Phytoseiulus* to develop and reproduce when feeding on *Tetranychus* species (e.g., Pratt *et al.* 2003; Kazak 2008; Abad-Moyano *et al.* 2009). *Phytoseiulus persimilis* (Athias-Henriot), *Phytoseiulus fragariae* Denmark & Schicha and *Phytoseiulus macropilis* (Banks) are the most comprehensively studied species. The first species has been extensively used commercially for the control of pest *Tetranychus* mites, especially *Tetranychus urticae* Koch, a major pest of many crops in temperate and tropical countries, but its performance seems to be limited on solanaceous plants, apparently because of the action of trichomes present on the aerial parts of those plants (Krips *et al.* 1999; Skirvin & Fenlon 2001; Sato *et al.* 2011).

A recent laboratory study has suggested that *P. macropilis* can be an effective predator of *T. urticae* on tomato (Sato *et al.* 2011). This predator may make use of the webbing produced by *T. urticae* to avoid contact with deterring glandular trichomes of tomato leaves (Sato *et al.* 2011).

Significant efforts have been dedicated in the last decade to the determination of prospective predators of *Tetranychus evansi* (Baker & Pritchard), an actual or potential pest of solanaceous plants in African, American, Asian and European countries that produces profuse webbing (Navajas *et al.* 2013). Despite that effort, only a single species of predator, *Phytoseiulus longipes* (Evans), was found as potentially useful for the control of that pest, showing preference for *T. evansi* over *T. urticae* as prey (Furtado *et al.* 2006, 2007; Ferrero *et al.* 2007; Silva *et al.* 2010).

Subtype I-b—Specialized predators of web-nest producing mites (Tetranychidae)

This subtype contains phytoseiids that have adapted to attacking *Schizotetranychus*, *Stigmaeopsis* and some *Oligonychus* spider mites producing the so-called web-nests (WN-u life type of Saito 1985). These phytoseiids also seem to show co-evolution with their prey (Saito 1990). *Typhlodromus (Anthoseius) bambusae* (Ehara) has been considered an effective biological control agent of *Schizotetranychus celarius* (Banks) in China (Zhang *et al.* 1999). This predator apparently evolved with that prey, having the ability to penetrate its web-nests.

Subtype I-c—Specialized predators of tydeoids (Tydeoidea)

This group was suggested by C. Duso (pers. comm. with JAM, 2009). It comprises representatives of *Paraseiulus* and *Typhlodromina*. It may also contain some species of *Proprioiseiopsis* (Momen 2011).

Paraseiulus talbii (Athias-Henriot) is the most extensively studied member of this group. Camporese & Duso (1995) showed that it was closely associated with tydeoid mites in Italy, and that in laboratory studies it had a higher reproductive potential on *Tydeus caudatus* (Dugès) than on other food items. Of several phytoseiid species inhabiting European vineyards, only *P. talbii* has been mentioned to feed on tydeoids (Camporese & Duso 1995). Its impact on tydeoid population densities was determined to be moderate, but apparently insufficient to maintain these mites at low population levels in vineyards (Camporese & Duso 1995).

Typhlodromina eharai Muma & Denmark is associated with *Tydeus californicus* (Banks) on avocado trees in California, USA, on which it has been observed to prey (J.A. McMurtry pers. obs.). *Proprioiseiopsis cabonus* (Schicha & Elshafie) was reported by Momen (2011) in association with the tydeoids *Neapolorryia aegyptiaca* (El-Bagoury & Momen), *Lorryia aegyptiaca* (Rasmy & El-Bagoury) and *T. caudatus* in soils of Egypt. In a laboratory study, Momen (2011) showed the ability of *P. cabonus* to feed, develop and reproduce efficiently on *N. aegyptiaca* and *L. aegyptiaca*, but not

on pollen of *Ricinus communis* or *Phoenix dactylifera*, reported to be suitable for laboratory rearing (Abou-Setta *et al.* 1997) of *Proprioseiopsis cannaensis* (Muma) and *Proprioseiopsis rotundus* (Muma). Life table parameters of a Brazilian population of *Proprioseiopsis cannaensis* were calculated by Bellini *et al.* (2010) on four different food items, including species of Eriophyidae, Tenuipalpidae and Tetranychidae, as well as *Typha angustifolia* pollen. In that paper, the authors reported difficulties in maintaining a colony of this predator on a mixture of *Typha angustifolia* pollen and all stages of the mite *Tyrophagus putrescentiae* (Schrank) (Acaridae). The results suggested that neither of those items were adequate as food sources to the predator. Laboratory studies are needed to assess the possible preference of *P. cannaensis* for tydeoids as food sources. The suitability of tydeoids as prey for some phytoseiids has been known for a long time. Knop & Hoy (1983) reported *Homeopronematus anconai* (Baker) as an important prey to maintain the population of *Galendromus occidentalis* (Nesbitt) under field conditions, when the population of *Tetranychus pacificus* (McGregor), a major pest of grape, was low. However, *G. occidentalis* should not be included in this group, given that it is not a specific predator of *H. anconai*.

Type II lifestyle—Selective predators of tetranychid mites

This category includes selective predators of tetranychid mites, most often associated with dense web producing species, such as *Oligonychus* and *Tetranychus* species. It includes species of *Neoseiulus*, *Galendromus* and apparently, the *rickeri* group of *Typhlodromus* (*Anthoseius*). These are associated with *Tetranychus* species (CW-u life type) or species of other genera producing other types of webbing (WN-u web and WN-c life types; see McMurtry & Croft 1997). Unlike Type I species, members of Type II have a preference for a broad range of tetranychid species, but they also feed and reproduce on mites of other groups, including Eriophyidae, Tarsonemidae and Tydeoidea, and also on pollen.

It has been questioned (Croft *et al.* 1998a) whether *Neoseiulus californicus* (McGregor), one of the main phytoseiids placed by McMurtry & Croft (1997) in this group, should not be better classified as a member of Type III group. However, it is kept here in the Type II group because it is nearly always associated with tetranychids producing heavy webbing; Type III phytoseiids do not do well on mite prey of this type, often getting stuck in their webbing. *Neoseiulus californicus* shows adaptations for living in spider mite colonies with heavy webbing; it has the ability to cut strands of webbing with the chelicerae (Shimoda *et al.* 2009) and to use the front legs to tear holes in web-nests of *Oligonychus perseae* (Tuttle, Baker & Abatiello) (Montserrat *et al.* 2008).

Because of the widely known efficiency of *N. californicus* as a control agent of tetranychid mites, many new publications have dealt with different aspects of its biology, ecology and practical use to control tetranychid mites (i.e. Jolly 2000; Zalom 2002; Nancy *et al.* 2005; Pringle & Heunis 2006; Walzer *et al.* 2007; Abad-Moyano *et al.* 2009; Elmoghzy *et al.* 2011; Toldi *et al.* 2013). It has also been evaluated as a predator of *T. evansi*, with poor performance (Escudero & Ferragut 2005). *Neoseiulus californicus* has been used for the biological control of *O. perseae* in the USA (Hoddle *et al.* 1999, Hoddle *et al.* 2000), and was recommended for the control of this pest in Spain (Montserrat *et al.* 2008). This predator has also been mentioned as potentially effective for the control of *Phytonemus pallidus* (Banks) on strawberry (Easterbrook *et al.* 2001) and *Polyphagotarsonemus latus* (Banks) on pepper (Jovicich *et al.* 2008), both Tarsonemidae, and for the control of thrips on pepper (Van Baal *et al.* 2007, Rahman *et al.* 2009).

Several studies on the closely related *N. fallacis* were also conducted in recent years. This phytoseiid was reported to feed on a wide range of mite pests of ornamentals (Pratt & Croft 2000). Minimum inoculations of this species were reported to provide successful control of *T. urticae* on strawberries in the USA (Croft & Coop 1998). In field experiments, *N. fallacis* was reported to be effective in controlling *T. urticae* on *Malus* rootstocks or *Acer* shade trees, as well as *Oligonychus*

ilicis (McGregor) on *Rhododendron* (Pratt & Croft 2000). Releases of *N. fallacis* provided effective control of *T. urticae* on apple seedlings in Oregon (Croft *et al.* 2004). It was also reported as effective for management of *Schizotetranychus longus* (Saito) on bamboo in the USA (Pratt & Croft 1999). *Neoseiulus fallacis* has been reported to be able to control *P. pallidus* on strawberry (Croft *et al.* 1998b), and to develop and reproduce adequately when offered *Aculops lycopersici* as prey (Brodeur *et al.* 1997).

As observed for *N. californicus* in the American and European continents, *Neoseiulus longispinosus* (Evans) has received extensive attention in Asia, according to Nusartlert *et al.* (2010), for the control of spider mites. These authors reported its development on species of the tetranychids *Eutetranychus*, *Oligonychus* and *Tetranychus*. This range of prey includes species that web profusely and species that produce little webbing. They did not observe the development of this predator on *Oligonychus mangiferus* (Rhaman & Sapra), a species that produces little webbing. Yet, the potential of this predator to control *Oligonychus coffeae* (Nietner), a serious pest of tea plantations that also produces little webbing, was reported by Vattakandy *et al.* (2013). *Neoseiulus longispinosus* was also observed to develop and reproduce on *Eotetranychus cendanai* (Rimando), so it might be used to control this spider mite pest in greenhouses (Tongtab *et al.* 2001). Works by Zhang *et al.* (1999) showed the potential of this predator as a biological control agent of *Stigmaeopsis nanjingensis* (Ma & Yuan) on bamboo in China. *Neoseiulus longispinosus* has also been observed to feed on the tenuipalpid *Raoiella indica* (Hirst), a serious pest of coconut, especially in the Caribbean area (Carrillo *et al.* 2012).

The preference of *Neoseiulus womersleyi* (Schicha) for *Amphitetranychus viennensis* (Zacher) over *T. urticae* was reported by Furuichi *et al.* (2005). The authors attributed this difference to the more favorable web produced by the former prey. The potential of *N. womersleyi* to control the spider mite *Tetranychus macfarlanei* (Baker & Pritchard) was recently evaluated under laboratory conditions by Ali *et al.* (2011). Reduced predation of *Tetranychus kanzawai* (Kishida) by *N. womersleyi* was attributed by Oku (2008) to the presence of the yellow excreted pellets deposited by the spider mite prey on its own web.

Galendromus occidentalis was found to be effective in the control of *O. perseae*, whereas the opposite was observed for *Galendromus annectens* (DeLeon) (Hoddle *et al.* 1999). *Galendromus helveolus* (Chant) was shown to be one of the most promising predators for that purpose, as it readily entered the nests of *O. perseae* to feed on the prey (Takano-Lee & Hoddle 2002).

Some *Neoseiulus* and *Galendromus* species have been found in association with web-net producing spider mites. However, they are not specific predators of those mites, and for that reason they are placed in Type II lifestyle, rather than in subtype I-b. *Neoseiulus fallacis* has shown some potential in controlling *S. longus* in the United States (Pratt & Croft 1999), being able to successfully invade the nests of this species, at least up to ten days after the beginning of nest building process by the mite. Zhang *et al.* (1999) showed the ability of *N. longispinosus* to consume *S. nanjingensis* in short duration laboratory experiments, but the authors pointed out that this predator is rarely found on bamboo, the host plant on which *S. nanjingensis* should be controlled. *Neoseiulus cucumeris* (Oudemans) has also been shown to feed and develop when offered *S. nanjingensis* as prey under laboratory trials (Zhang *et al.* 2000). However, they are only able to enter broken web-nests. *Neoseiulus californicus* and *G. helveolus* have been reported to provide effective control of *O. perseae* (Tuttle, Baker & Abatiello), also a web-nest producing mite (Kerguelen & Hoddle 1999; Takano-Lee & Hoddle 2002).

Type III lifestyle—Generalist predators

Species in this category feed and reproduce on a wide range of prey (at least under laboratory conditions), including mites of families belonging to Astigmata such as Acaridae and Pyroglyphidae,

and Prostigmata, particularly Eriophyidae, Tarsonemidae, Tetranychidae, Tenuipalpidae and Tydeidae, as well as thrips, whiteflies, mealybugs, nematodes, etc. Many species in Type III have been shown to be able to feed and reproduce well on pollen. They can utilize plant exudates and honeydew as survival food in the absence of prey, or as complementary food, which increase their reproductive capacity when prey is present (McMurtry & Croft 1997).

In addition, several phytoseiids of this group have the ability to feed on fungi. Association or actual development and/or reproduction have been reported for the following phytoseiids on different plant pathogenic fungi: *Typhlodromus* (*Typhlodromus*) *pyri* (Scheuten) by Chant (1959), Eichhorn & Hoos (1990), Zemek & Prenerova (1997) and Pozzebon & Duso (2008); *Ricoseius loxocheles* De Leon by Flechtmann (1976) and Oliveira (2012); *Amblydromalus manihoti* (Moraes) (mentioned as *Typhlodromalus limonicus* s.l.) by Bakker & Klein (1992); and *Amblyseius andersoni* (Chant) by Pozzebon & Duso (2008). Some phytoseiids have been found to consume the microcrustacean species *Artemia franciscana* (Kellogg) (Artemiidae) as factitious food (Vangansbeke *et al.* 2013). *Amblydromalus limonicus* (Garman & McGregor) and *Amblyseius swirskii* Athias-Henriot have been reported to feed and maintain themselves on those organisms when the latter are placed on plant leaves (Audenaert *et al.* 2013).

The subsequent grouping of these mites in subtypes is based on their preferred microhabitats.

Subtype III-a—Generalist predators living on pubescent leaves

Species of *Paraphytoseius*, *Phytoseius* as well as some *Kampimodromus*, *Typhlodromalus* and *Typhlodromus* species are commonly found on pubescent leaves (leaves with trichomes). The typically small and laterally compressed idiosoma of these species apparently aids them in moving between leaf trichomes (Duso 1992; Walter 1992; Karban *et al.* 1995; Kreiter *et al.* 2002; Kreiter *et al.* 2003; Tixier *et al.* 2007). Those phytoseiids characteristically have some of the dorsal shield setae stout and usually serrate. These morphological characteristics enable those mites to colonize microhabitats not occupied by larger phytoseiids, avoiding possible competition and escaping predation by the latter (Seelman *et al.* 2007), while taking advantage of the presence of prey which also prefer the same microhabitat.

Also, the elongate gnathosoma of *Eharius* phytoseiids seems to be an adaptation to aid them in reaching the leaf surface from the trichomes of *Marrubium vulgare* foliage. *Eharius chergui* (Athias-Henriot) has been observed on this plant in the apparent absence of any prey or pollen grains, possibly piercing leaf cells (D. Mahr pers. comm.).

Trichome shapes and structures are widely variable (Metcalf & Chalk 1979). Some authors have pointed out their deleterious effect on some phytoseiid species, whereas others have reported the opposite (Sato *et al.* 2011). While the non-glandular trichomes conceivably affect the phytoseiids and other mites physically, glandular types may also cause chemical interference with them. Walter (1996) conducted a thorough revision about the effect of different types of trichomes on mites. The author referred to several studies showing that plants with pubescent leaves had a higher diversity and density of predatory mites than plants with glabrous leaves, which was especially true for the small phytoseiid species. Different authors mentioned by Walter (1996) reported the following phytoseiids to predominate on pubescent leaves: *Euseius victoriensis* Womersley, *G. occidentalis*, *Kampimodromus aberrans* Oudemans, *Phytoseius* species, *Typhlodromus* (*Anthoseius*) *caudiglans* Schuster and *T. (T.) pyri*. As explained elsewhere in this text, the first and the second species are not classified as Type III lifestyle. *Kampimodromus aberrans* has been widely known to occur mainly on plants with pubescent leaves (Kreiter *et al.* 2002; Kabicek 2008). Kreiter *et al.* (2003) observed that leaf characteristics (trichomes, domatia) as well as pollen densities and plant species influenced greatly the occurrence and abundance of this predator. Additional supporting information has been published about the importance of *K. aberrans* as a biological control agent of spider mites on some

grape varieties in Europe, especially in France and Italy (Duso *et al.* 2009; Kreiter *et al.* 2000; Ozman-Sullivan 2006). It has also been reported from hazelnut orchards in Turkey in association with the eriophyoid mites *Phytoptus avellanae* (Nalepa) and *Cecidophyopsis vermiformis* (Nalepa) (Ozman-Sullivan 2006). In a laboratory study, these authors reported the ability of *K. aberrans* to develop and reproduce on *P. avellanae*. This predator has also been reported to prey, develop and reproduce on *Cecidophyopsis vitis* (Nalepa) (Schausberger 1992). Higher density of *T. (T.) pyri* was reported by Duso *et al.* (2003) on an apple variety with highly pubescent leaves as compared to varieties with less pubescent leaves. The preference of *Typhlodromalus aripo* De Leon for cassava varieties with pubescent tips over varieties with glabrous tips was reported by Onzo *et al.* (2012).

Many studies have been published about the association of *Phytoseius* species with tetranychid, eriophyid, tarsonemid and tenuipalpid mites (e.g., El-Laithy & Fouly 1998; Tixier *et al.* 1998; Mailloux *et al.* 2010; Vassiliou *et al.* 2012). Differently from what was reported by McMurtry & Croft (2007) in relation to the potential of species of this genus as biological control agents, a species reported as *Phytoseius finitimus* (Ribaga) was mentioned by Duso & Vettorazzo (1999) as potentially useful for the control of *Panonychus ulmi* Koch on grape. In laboratory experiments, Pappas *et al.* (2013) observed phytoseiids identified as *P. finitimus* to feed and reproduce on larvae of *T. urticae*, as well as on crawlers of the greenhouse whitefly, *Trialeurodes vaporariorum* Westwood. Populations from Iran identified as *Phytoseius plumifer* (Canestrini & Fanzago) have been mentioned as predators of tetranychid and eriophyid mites on various crops (Hajizadeh *et al.* 2002; Kodayari *et al.* 2013; Nadimi *et al.* 2009).

Subtype III-b—Generalist predators living on glabrous leaves

This is probably the most diverse subgroup. It seems to contain most of the species of large genera, e.g. *Amblyseius* and *Neoseiulus*, but also species of smaller genera, such as *Amblydromalus*. This subtype contains phytoseiids that are not particularly small.

Amblyseius swirskii has been extensively used for thrips and whitefly control in greenhouses (e.g., Bolckmans *et al.* 2005; Messelink *et al.* 2005, 2006; Kutuk *et al.* 2011). It can be mass produced at relatively low cost on acarid mites. Provision of pollen to this predator in the field may enhance its efficiency in controlling whiteflies (Nomikou *et al.* 2010; Kutuk & Yigit 2011). This predator was mentioned by van Maanen *et al.* (2010) as useful for the control of *P. latus*.

Amblydromalus limonicus is often found on the glabrous leaves of citrus and other plant species (Moraes *et al.* 1986), whereas the closely related *A. manihoti* is a common predator on cassava plants in South America (Yaninek *et al.* 1998). The latter species is found mostly on leaves of the median section of cassava plants, where leaf pubescence is less than those of the apical section (Bonato *et al.* 1999). In the last few years, *A. limonicus* has been commercialized for the control of whiteflies and thrips in protected crops, following the discovery of successful off-plant rearing on factitious prey. *Amblydromalus manihoti* was reported (as *Amblyseius limonicus* s.l.) to feed on thrips (Noronha & Cobo 1990) and whiteflies (Noronha & Moraes 1992). *Amblydromalus lailae* (Schicha) was reported as potentially useful for the biological control of thrips, *A. lycopersici* and *P. latus* in Australia (Steiner *et al.* 2003b).

Amblyseius andersoni was observed to be abundant and more effective as a predator of spider mites on grape varieties with more glabrous leaves (Camporese & Duso 1995; Duso *et al.* 2003). Studies conducted under laboratory and greenhouse conditions also indicated the potential of *Transeius montdorensis* Schicha to control *A. lycopersici*, *P. latus* and thrips (Steiner *et al.* 2003a). It can be reared exclusively on *Typha* pollen. Given the successful adoption of off-plant rearing methods using factitious prey, this predator is now produced commercially in Europe and Australia mainly for thrips and whitefly control in greenhouses.

Studies in China (Wu *et al.* 2010) have shown *Amblyseius eharai* Amitai & Swirski and *Scapulaseius newsami* Evans to be effective natural enemies of *Panonychus citri* (McGregor). The potential of the former species to control thrips has been reported by Kakimoto *et al.* (2004).

Subtype III-c—Generalist predators living in confined space on dicotyledonous plants

Examples are phytoseiids (Walter 1996) on galled leaves of willow and poplar trees. Gall-forming eriophyids are often present as possible food sources, but so are spider mites (JAM, pers. obs.). Thus, these phytoseiids are apparently distinguished by the type of microhabitat they favour, represented by the galled leaf surface, rather than by the available prey type. They are elongate but not particularly small, comprising mostly the *desertus* group of *Neoseiulus* (Prischmann *et al.* 2005). Little is known about the potential of species of the *desertus* group of *Neoseiulus* as biological control agents of gall-forming eriophyid mites on willow and poplar trees.

Domatia are structures of different constitutions always corresponding to a confined space on leaves of some plants (O'Dowd & Willson 1989; Walter 1996). They have been reported on over 2000 plant species of nearly 300 families (Brouwer & Clifford 1990). As previously mentioned, domatia favor the survival and development of several mites, including phytoseiids. Pemberton & Turner (1989) hypothesized the existence of a widespread facultative mutualism between plants with leaf domatia and beneficial mites. The following phytoseiids have been noted to occur in domatia: *Amblyseius herbicolus* (Chant), *Euseius hibisci* (Chant), *Galendromus longipilus* (Nesbitt), *Phytoseius hawaiiensis* Prasad, *Typhlodromus (Anthoseius) haramotoi* Prasad and *Typhlodromus (Anthoseius) rhenanoides* (Athias-Henriot), by Pemberton & Turner (1989); *Euseius elinae* (Schicha) and *Typhlodromus (Anthoseius) dossei* Schicha, by Walter (1992); *Iphiseius degenerans* (Berlese), by Faraji *et al.* (2002); *Iphiseiodes zuluagai* Denmark & Muma, by Matos *et al.* (2004); *Typhlodromus (Anthoseius) doreenae* Schicha, by Rowles & O'Dowd (2009).

Although several other phytoseiids have been noted to occur in domatia, it does not seem appropriate to include them as part of this subtype because they are also often found on leaves (either pubescent or glabrous) of plants that do not have domatia. Thus, it seems that they may benefit from the presence of domatia, but that domatia are not essential for them (Ferreira *et al.* 2008). For example, *I. zuluagai* is one of the common predatory mites found in domatia of coffee leaves in Brazil (Matos *et al.* 2004). However, it has also been commonly reported on the glabrous leaves of several plant species, including citrus (Albuquerque & Moraes 2008) and other plant species that do not have domatia (Moraes *et al.* 1986). Thus, we do not consider it appropriate to include this species as a member of subtype III-c.

Similarly, *T. aripo* has been reported to spend the day between the unfolded leaves within the growing tips of cassava plants (Onzo *et al.* 2005, 2009). Growing tips of cassava could be considered as a confined space (Onzo *et al.* 2005), but *T. aripo* has also been reported from leaves of several plant species (Moraes *et al.* 1986). Even on cassava, this predator is found at night wandering on the upper leaves searching for its preferred prey, *Mononychellus tanajoa* (Bondar) (Tetranychidae). Thus, here it is considered as belonging to subtype III-a, given its preference for plants with pubescent tips (Onzo *et al.* 2012). The preference of *K. aberrans* and *Neoseiulella tiliarum* (Oudemans) to inhabit pubescent domatia has been reported (Kreiter *et al.* 2000, 2003; Kabicek 2008). However, these mites are commonly found on the surface of pubescent leaves, and are for this reason classified in subtype III-a.

Subtype III-d—Generalist predators living in confined spaces on monocotyledonous plants

This includes phytoseiids adapted to living in restricted spaces on monocotyledonous plants, between leaf sheaths or between bracts and subjacent fruit surfaces. The best known case refers to phytoseiids of the *paspalivorus* group of *Neoseiulus*, including *Neoseiulus baraki* (Athias-Henriot),

Neoseiulus neobaraki (Zannou, Moraes & Oliveira) and *Neoseiulus paspalivorus* (DeLeon). These species are small, flat, elongate, and short-legged, which allows them to move into the tiny spaces between the tightly appressed bracts and the subjacent fruit surface of coconut, in search of their eriophyid prey, *Aceria guerreronis* (Keifer) (Moraes *et al.* 2004).

Considerable effort was dedicated in the last decade to the development of a program for the biological control of *A. guerreronis*, a major pest of coconut. In this regard, several studies have been conducted in tropical countries of the American, African and Asian continents to search for prospective biological control agents. *Neoseiulus baraki*, *N. paspalivorus* and *N. neobaraki* have been found in association with *A. guerreronis* (Moraes *et al.* 2004; Lawson-Balagbo *et al.* 2008; Negloh *et al.* 2008; Navia *et al.* 2013). The first two species were most common in Africa, South America and Asia, while the last was only recorded in Africa. Their ability to feed and reproduce on *A. guerreronis* has been shown in studies conducted under laboratory conditions (Lawson-Balagbo *et al.* 2007; Negloh *et al.*, 2008). They have also been reported to develop and reproduce on *T. putrescentiae*, occasionally found in the same microhabitat (Moraes *et al.* 2004; Lawson-Balagbo *et al.* 2007). *Neoseiulus paspalivorus* was also shown to develop and reproduce on *Steneotarsonemus furcatus* (De Leon) and coconut pollen (Lawson-Balagbo *et al.* 2007), whereas *N. baraki* had poor development and reproduction when fed with *Steneotarsonemus concavoscutum* Lofego & Gondim Jr. as well as coconut pollen (Negloh *et al.* 2008; Domingos *et al.* 2012). *Neoseiulus baraki* and *N. paspalivorus* were originally described from grasses, on which they were probably occupying the leaf sheaths, as suggested by the confined microhabitat they occupy on coconuts.

Subtype III-e—Generalist predator from soil/litter habitats

Some species of this group periodically move up onto low-growing plants. These correspond to a diverse assemblage of species that may have secondarily moved from the aerial to the ground habitat (McMurtry 2010). It includes many *Neoseiulus* and *Arrenoseius*, some *Amblyseius* and most *Proprioiseiopsis*, *Chelaseius* and *Graminaseius* (e.g., Salamane & Patrova 2002; Amano *et al.* 2011). The last three genera could have derived from *Amblyseius*. The *Neoseiulus* probably evolved in a separate event and they do not seem to be morphologically distinguishable as a group from the arboreal species.

Two species showing this lifestyle, *Neoseiulus barkeri* (Hughes) and *N. cucumeris*, have been extensively used commercially for the biological control of pest species, especially thrips (Gerson *et al.* 2003). *Neoseiulus barkeri* has also been used for the biological control of *P. latus* in protected crops (Fan & Pettitt 1994). Laboratory and greenhouse experiments conducted by Messelink *et al.* (2012) have shown this predator to be potentially useful for the control of *Steneotarsonemus laticeps* (Halbert), a serious pest of amaryllis in Europe. Its ability to control the western flower thrips, *Frankliniella occidentalis* (Pergande), has also been suggested (Fan & Pettitt 1994). *Neoseiulus cucumeris* is also known to feed on *P. latus*, *P. pallidus*, *T. urticae* and fungi (Gerson *et al.* 2003; Weintraub *et al.* 2003). Both *N. barkeri* and *N. cucumeris* are commercially produced using acarid mites as prey.

Species of *Proprioiseiopsis* are commonly found in the soil/litter habitats. Despite being so common in different parts of the world (Moraes *et al.* 2004), very little has been reported about the biology of mites of this group. The few papers dealing with the biology of these mites refer to their ability to consume mites found on the aerial plant parts as prey (Ball 1980; Meshkov 1996; Fouly 1997; Abou-Setta *et al.* 1997; Momen 1999, 2009; Momen & El-Borolossy 1999; Navasero & Corpuz-Raros 2005).

Type IV lifestyle—Pollen feeding generalist predators

This category contains phytoseiid predators for which pollen constitute an important part of the diet. It includes the genera *Euseius*, with nearly 212 species (Demite *et al.* 2012), *Iphiseius* and *Iphiseiodes* (Reis & Alves 1997; Villanueva & Childers 2007), with a single and a few known species, respectively. These species generally have high reproductive capacity when feeding on pollen, and population increases often follow blossoming periods of the crop or adjacent plants.

Many of these mites prefer glabrous leaves, as inferred from an analysis of the plants on which they have been found (see Moraes *et al.* 1986). However, leaves of some of these plants are covered by trichomes over certain regions. *Euseius finlandicus* (Oudemans) has been reported mainly on glabrous substrates (Tuovinen 1994; Kabicek 2005, 2008). Kabicek (2008) reported the common occurrence of this species on the glabrous regions of the leaves of *Corylus avellana*, moving to pubescent patches when disturbed, where they are more protected. This predator is known to feed on eriophyoid and tetranychid species (Schausberger 1998; Broufas & Koveos 2000; Awad *et al.* 2001). Abundance of this predator was correlated with the presence of pollen on hedgerows adjacent to vineyards in northern Italy (Duso *et al.*, 2004). A positive effect of pollen was also reported by Broufas & Koveos (2000) in some fruit tree orchards. *Euseius victoriensis* has been mentioned as a remarkable predator in Australia, playing an important role in the control of eriophyids (Smith & Papacek 1991), *T. urticae* as well as of *P. latus* (James 2001).

Field observations in Saudi Arabia indicated *Euseius* species, particularly *Euseius scutalis* (Athias-Henriot), to be important as predators of tetranychid mites, scale insects and whiteflies (Nomikou *et al.* 2001; Raza *et al.* 2005). A recent study conducted by Al-Shammery (2010) showed *E. scutalis* to be a promising control agent of those pests. *Euseius hibisci* is of some importance to management of the spider mite *Oligonychus punicae* (Hirst) in avocado orchards in California (McMurtry 1985), as is *E. scutalis* of *O. perseae* in avocado orchards in Israel (Maoz *et al.* 2011). In a study conducted by Abad-Moyano *et al.* (2010) in Spain, *Euseius stipulatus* (Athias-Henriot) was found to adversely affect the establishment of *N. californicus* and *P. persimilis*, thus negatively affecting control of *T. urticae* in Spanish Clementine orchards.

Iphiseius degenerans is a common predator on cassava plants in Africa (Yaninek *et al.* 1998; Zannou *et al.* 2005). This species was reported to feed and oviposit when diet consisted of pollen, *T. urticae*, larvae of the thrips *F. occidentalis* or eggs of *Ephestia kuehniella* (Zeller) (Vantornhout *et al.* 2005). Following the determination by van Houten *et al.* (2005) of its potential as a predator of *F. occidentalis*, this predator is now commercialized for thrips control.

Iphiseiodes quadripilis (Banks) could not complete its development when fed *Phyllocoptruta oleivora* (Ashmead) under laboratory conditions, while it could complete its development and reproduce on ice plant or oak pollens, or on *Eutetranychus banksi* (McGregor) and *P. citri* (Villanueva & Childers 2007). These results corroborate previous observations indicating availability of pollen on citrus leaves to be correlated with the abundance of *I. quadripilis* (Villanueva & Childers 2004). *Iphiseiodes zuluagai* is one of the most common phytoseiids in Brazil and a few other south American countries (Demite *et al.* 2012). Independently of its preference for pollen, *I. zuluagai* has also been mentioned as an important predator of *Brevipalpus phoenicis* (Geijskes) in Brazil, and to be able to develop and reproduce when offered eggs of *T. putrescentiae* as factitious food (Albuquerque & Moraes 2008).

Some phytoseiids placed in this group have been shown to be able to pierce leaf cells. This ability will be discussed in the following section of this publication.

POSSIBLE ADDITIONAL TYPES

Two possible new groups might be proposed in the future. However, the official establishment of those groups requires further investigations.

Aquatic phytoseiids

A distinct group of phytoseiids consisting of a single species in each of the genera *Evansoseius* and *Macrocaudus* (Neoseiulini) may constitute a new type (or subtype) of lifestyle. These mites live on floating plants and have similar primitive morphological phytoseiid features, especially the presence of some setae of uncommon occurrence on the posterior half of the dorsal shield. Otherwise they share common features with other Neoseiulini, a tribe considered by Chant & McMurtry (2003) to consist of primitive Amblyseiinae. Both genera were described from South America, and neither has been reported after the original description. Nothing is known about their biology. *Macrocaudus multisetatus* Moraes, McMurtry & Mineiro has been occasionally observed from its type locality and type host plant (unpublished observation). The only obvious arthropods found in association with this species were larvae of an unidentified species of chironomid fly. Attempts to rear that phytoseiid on *T. putrescentiae*, *Typha* pollen or the nematode *Rhabditella axei* (Cobbold) (Rhabditidae) as factitious food sources have not been successful (unpublished observation).

Phytoseiids with plant cell piercing abilities

A “cross type” was suggested by Adar *et al.* (2012) to contain phytoseiids that apparently complement their nutrition requirements by feeding on leaf cells. Although evidence suggests their ability to pierce leaf cells, the primary reason for this type of behaviour is still unknown. Given that the limiting factor for any organism is usually the availability of water, it seems that leaf cell piercing may be related to water uptake (from within cell cytoplasm), the uptake of nutrients being a consequence of their presence in the imbibed liquid.

This potential group contains mostly *Euseius* mites, but also species of *Kampimodromus*, *Phytoseius*, *Typhlodromalus*, *Typhlodromus* (*Anthoseius*), *Typhlodromus* (*Typhlodromus*) and probably some *Amblydromalus*. It is expected that many of the species included in this group are also pollen feeders. However, research suggested that some pollen feeders were unable to take up liquid from at least some of the plant species on which they were found (Porres *et al.* 1975; Adar *et al.* 2012).

Uptake of plant liquid by phytoseiid mites was first reported by Chant (1959) from laboratory experiments with *E. finlandicus*, *Typhlodromus* (*Anthoseius*) *rhenanus* (Oudemans) and *T. (T.) pyri*. It was later suggested by Porres *et al.* (1975) and Congdon & Tanigoshi (1983) for *E. hibisci*, Congdon & Tanigoshi (1983) for *Euseius tularensis* (Congdon), Kreiter *et al.* (2002) for *K. aberrans*, Magalhães & Bakker (2002) for *T. aripo* and Nomikou *et al.* (2003) for *E. scutalis*. Field studies by Grafton-Cardwell & Ouyang (1995, 1996) also provided indications that *E. tularensis* could consume the content of citrus leaf cells. Adar *et al.* (2012) conducted a detailed evaluation of the ability of *E. scutalis* and *A. swirskii* to pierce leaf cells, determining that the former was able to extract liquid from leaf cells but that the latter was not, although it ingested free water on the surface of the substrate. Nomikou *et al.* (2003) also did not find evidence of liquid uptake from leaves by *A. swirskii*. Adar *et al.* (2012) evaluated the cheliceral morphology of several phytoseiid species, including species reported and not reported as plant piercers, concluding that plant piercing phytoseiids had movable cheliceral digit shorter than fixed cheliceral digit and the latter less curved than the non-plant piercers.

Despite the ability of some phytoseiids to take up liquid from plants, economic damage by those mites has not been reported. Feeding scars have been mentioned by Sengonca *et al.* (2004) to be

caused by *T. (T.) pyri* on apple leaves and fruits, but even in total absence of other food items, the damage caused by those mites was minor, represented by few small scars. In addition to the reduced ability of each individual to cause damage, phytoseiid populations rarely attain high levels on plants under natural conditions. High phytoseiid population densities usually only occur when food is abundant, and that circumstance is less conducive to piercing of plant cells by phytoseiids (Sengonca *et al.* 2004).

Some authors have discussed the biological importance of plant piercing by phytoseiids. Grafton-Cardwell & Ouyang (1995) reported that pruning of citrus trees resulted in higher *E. tularensis* population densities. In a subsequent paper, the same authors (Grafton-Cardwell & Ouyang 1996) observed a positive correlation between the number of eggs laid by *E. tularensis* and the concentration of fertilizer supplied to the plants. These observations do not preclude the possibility of the effect being indirect, resulting basically from the effect of better plant nutrition on the prey. Magalhães & Bakker (2002) concluded that *T. aripo* feeds in cells of cassava leaves, suggesting that this habit could increase the survival of the phytoseiid in the absence of its main food source (*M. tanaioa*) on cassava. Gnanvossou *et al.* (2005) observed that males of this species were able to complete immature development when confined on a cassava leaf disk without any prey. It has often been observed under laboratory conditions that some phytoseiid species seem unable to develop and reproduce on non-leaf substrates, as reported by McMurtry & Scriven (1965) for *E. hisbisci* and by Bakker & Klein (1992) for *A. manihoti*. However, it is not known whether they really depend on plants for their survival, or whether other unaccounted factors could be involved. Omnivory is widespread in the animal kingdom, but many predators (canines, for example) are known to directly ingest plant material only under abnormal circumstances, although plant material is often taken by consuming the guts of their prey.

CONCLUSIONS

In this work, it was decided to deviate from the system of McMurtry & Moraes (2012) dividing type I lifestyle into three subtypes. Evolution of specialization to feed on tydeoids may be common to all *Paraseiulus* but not all *Proprioiseiopsis*. It may also be common to *Typhlodromina* but not enough is known for most species of this genus. It is conceivable that many other phytoseiids prey on tydeoid mites, given the very common occurrence of the latter on plants and in the soil. The lack of information in this regard is apparently due to the low economic importance attributed to those mites. Other types of specialization may be detected in the future.

The very large Type III lifestyle could not be subdivided based on food habits, as was previously hoped by McMurtry & Croft (1997); therefore, subtypes based more on microhabitat and morphology were erected. Perhaps the majority of Type III species cannot be placed in a microhabitat subtype. This seems to stem from both lack of knowledge and the diversity of microhabitats that can be occupied by many of them. Can predictions be made based on this classification of species of the lifestyle? Type III-a contains species that are small and laterally compressed and/or with long gnathosoma to reach the plant surface from above. Species with these morphological features could be predicted to be adapted to living on pubescent leaves, and this seems largely to be the case. Considerable numbers of species seem to prefer glabrous leaves, mainly on trees (subgroup III-b). Species with smooth bodies (mostly minute setae and no ornamentation of dorsal shield) such as *Amblyseius* spp. as well as *Iphiseiodes* and *Iphiseius* inhabit smooth leaves. However, mites of the latter two genera were included in this paper in Type IV lifestyle, because of their apparent preference for pollen as food items. This is a clear case of overlapping of two different groups, which is not surprising, given the fact that Type IV species constitute a special group of

generalist predator (that has pollen as preferred food). Small and flattened species (subtype III-d), all in the *Neoseiulus paspalivorus* group, could be predicted to live in small spaces on monocotyledonous plants, and this also seems to be the case. Subtype III-c is probably insufficiently known at present and studies of more species may strengthen the constitution of this group. The soil/litter habitat (Subgroup III-e) is difficult to characterize because of its complexity and wide array of potential foods.

The most consistent group in terms of morphology is still Type IV, with the characteristic shape of small chelicerae and shape of the gnathosoma.

Despite the extensive practical use of phytoseiids for the biological control of pest species, much remains to be known about microhabitat and food preference of the vast majority of the species. Several of the genera are known only from the original description of the corresponding type species, while very little is known about species of most genera. The large number of described phytoseiid species justifies further investigations to determine new prospective species for practical use. Precise determination of the feeding habit of phytoseiid species seems highly relevant for evaluation of their potential for practical use for different purposes. In the 15 years since the review by McMurtry & Croft (1997), the biology of only about 15 additional species (eight belonging to Type III) has been studied, even though the list of described species increased from about 1600 in 1997 to about 2800 today (Demite *et al.* 2012; Prasad 2013).

For better understanding of the behaviour of each phytoseiid group, studies on the factors driving preference for different microhabitats, seem particularly relevant. Some information is already available in this regard, but much more needs to be done. Are the driving factors physical, biological, biochemical or something else? For example, the assumption of many workers that the occupation of heterogeneous microhabitats is exclusively related to protection against predation could be an oversimplification or even misinterpretation of the real factor(s) involved. Similarly, why are some species restricted to or prefer inhabiting the soil? It would also be interesting to understand why some taxonomic groups, like the Neoseiulini for example, are much more diverse than others in terms of food or microhabitat preferences. Is that because it is the most primitive and oldest tribe, as proposed by Chant & McMurtry (2003)?

Because of the considerable attention that phytoseiids have received in the last few decades, this proposed lifestyle classification must be considered as a work in progress. Two possible additional types have been mentioned in this document. While preparing this document, F. Faraji (pers. comm. with the authors, 2013) called our attention to the apparent preference of *Typhlodromus (Anthoseius) bakeri* (Garman) for tree bark. An evaluation of the substrates onto which this species has been mentioned shows a strong predominance of tree hosts, although in most cases the authors do not refer to the exact plant part from which the specimens were collected; this preference is reported however by Faraji *et al.* (2006). Discovery of other species with similar behaviour will justify the creation of a new group for these predators. The growing interest for the study of phytoseiids around the world might lead in the future to a need for further updates of the lifestyles here defined.

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