

Free-living mesostigmatic mites in Australia: their roles in biological control and bioindication

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Abstract. The taxonomy, biology and ecology of free-living mesostigmatic mites in Australia and their current and potential use in biological control and bioindication is reviewed. Most current research on free-living Mesostigmata in Australia focuses on species with an established role in the biocontrol of crop pests, such as members of the family Phytoseiidae. Three introduced species and at least seven native species of Phytoseiidae are presently used for the control of phytophagous mites in Australia. The introduced phytoseiids are mostly specific to spider mites and have been selected for resistance to some of the common pesticides. Native species provide the advantage of being generalist feeders and are capable of using alternative food in the absence of mite pests. Therefore they can persist more effectively in the environment and contribute to the control of several pests. The reduced and selective use of pesticides, accompanied by scouting services, has allowed the successful control of phytophagous mites by native species in several Australian tree crops, especially grapevine and citrus. In soils, Mesostigmata are extremely abundant, species-rich and play significant ecological roles. They feed on a broad range of invertebrates, including phytophagous pests that spend part or most of their lives on or in the soil or root systems. However, the majority of mesostigmatic mite species are unknown in Australia. Nevertheless, recent research indicates that many species are habitat-specific, and that they may be sensitive to agricultural practices and other land management systems. Mesostigmata have great potential for biological control of pests, and as indicators of soil quality and sustainable agricultural practices. However, the current paucity of research and information on the taxonomy, life-history and ecology of native species in natural and managed landscapes will continue to hinder their use in biological control and as bioindicators.

Additional keywords: agroecosystems, community structure, ecological indicators, insect pests, species diversity.

Introduction

The Mesostigmata are a group of mites (Acari) comprising a large diversity of vertebrate parasites, symbionts of insects, and for the most part, free-living predators (Krantz and Walter, in press). Soil, litter, plants, dung and decaying wood are all inhabited by a range of free-living mesostigmatic mites (Walter *et al.* 1998b; Halliday 2000b; Shaw and Walter 2003), but current knowledge in Australia is generally limited to the plant-associated family Phytoseiidae. The feeding preference of phytoseiids for phytophagous mites has made them valuable biocontrol agents of spider mites (Tetranychidae) and gall mites, rust mites and relatives (Eriophyoidea), which are pests of a wide range of greenhouse, field and tree crops in most countries, including Australia (James 2001; Steiner and Goodwin 2001; Gerson *et al.* 2003). However, most species have a broad diet (generalist feeders) and have the potential to control other invertebrate pests such as thrips and scale insects.

Free-living Mesostigmata are one of the most abundant and species-rich arthropod groups in soils (Peterson 1982; Walter

et al. 1988; Koehler 1999; Behan-Pelletier 2003). They feed on a variety of soil invertebrates and may regulate the populations of many of their prey (Moore *et al.* 1988; Walter and Ikonen 1989). However, relatively little is known about their biology, particularly in Australia. Soil Mesostigmata have the potential to control herbivorous pests that spend some time in the soil or litter, or that attack plant roots (Eickwort 1983; Lesna *et al.* 1995; Gerson *et al.* 2003). Moreover, dung-breeding forms can reduce the populations of noxious flies (Wallace *et al.* 1979; Krantz 1983). As pest management evolves towards the use of more selective ('soft') pesticides and careful habitat manipulations, there is a prospect for better exploitation of predatory Mesostigmata in Australian crops.

The ubiquity, taxonomic and ecological diversity of soil Mesostigmata and their crucial position in soil foodwebs could potentially make them key biological indicators of environmental quality (e.g. soil health), including the impact of agricultural practices and other landscape uses (Karg and Freier 1995; Koehler 1999; Ruf *et al.* 2003). They have shown

promising results in Europe and North America and are considered sensitive to agricultural practices (Koehler 1999), pollution (Ruf *et al.* 2003) and habitat restoration (St. John *et al.* 2002). However, the potential use of Mesostigmata as bioindicators remains largely unexplored in Australia. In this paper, we review the taxonomy, biology and ecology of free-living mesostigmatic mites in Australia and their current and potential use in biological control and bioindication.

Taxonomy

The large majority of species of Mesostigmata in Australia are undescribed. Halliday (2000a) lists only 739 species of Mesostigmata in a recent inventory of Australian species, with fewer than 500 species of free-living forms. However, samples taken from a range of habitats and locations indicate that there are several thousand free-living species still to be described in Australia (Walter *et al.* 1994; Walter and Proctor 1998b; Walter *et al.* 1998b; Halliday *et al.* 2000; Beaulieu 2005).

Many publications are available for the identification of free-living mesostigmatic mites but they are scattered and generally incomplete (Table 1). Recently, Walter (2001) developed a computer-based interactive key (LuCID) for the identification of Mesostigmata at the family level (for a dichotomous key, see Krantz and Walter, in press). The identification of specimens to genera and species is more difficult, with few dichotomous keys available. Even in the case of the family Phytoseiidae (see Fig. 1b), where most taxonomic work has been conducted, species have only been described from a limited range of habitats in Australia and it is likely that many species remain to be discovered in tropical

areas, including the inland, semiarid woodlands of most states (Walter and Beard 1997; Beard 1999).

The Macrochelidae (Fig. 1c) are principally associated with animal dung and the species are relatively well known in Australia (Halliday 2000b). However, poorly studied habitats in more natural situations (mammal and bird nests, fungi, decaying fruits, forest litter) probably contain many undescribed species (Halliday 2000b). Ologamasids are highly diverse and are the dominant family in the soil and litter of Australian forests (Osler and Beattie 2001; Beaulieu 2005). Despite the extensive work of Lee (1970, 1973a) on the family Ologamasidae (Fig. 1a), especially in South Australia, the large majority of soil-inhabiting members of this family are unknown. Although good keys to generic level (and species keys for some genera) were made for the large family Ascidae and the family Ameroseiidae (Table 1), most species are seemingly undescribed (Halliday *et al.* 1998; Colloff *et al.* 2003; Beaulieu 2005). The Laelapidae and families of Uropodina are highly diverse in Australia (Halliday 2000a) but their taxonomy remains largely unresolved. Several other families include species for which the main habitat is soil and/or litter, such as Digamasellidae, Eviphididae, Leptolaelapidae, Parasitidae and Pachylaelapidae, although little or no taxonomic information exists for Australia (Walter 2001; Beaulieu 2005).

Geographic distribution

Given the paucity of studies on Mesostigmata in most habitats throughout Australia, it is difficult to draw conclusions about the geographic distribution of species. In groups where studies are more numerous, endemism appears to be high. For instance,

Table 1. Available taxonomic keys for the identification of free-living Mesostigmata in Australia

Symbols for 'completeness' are as follows: + most (>50%) taxa not included; ++ most (>50%) taxa included; +++ nearly all or all taxa included

Taxonomic group	Main habitat(s)	Resolution of the key	Completeness	References
Soil Mesostigmata	Soil, litter, etc.	Families	+++	Walter (2001)
Family Ameroseiidae	Soil, litter, flowers, stored products	Genera and species	+	Halliday (1997)
Family Ascidae	Soil, litter, plants, etc.	Genera	++	Halliday <i>et al.</i> (1998)
Genus <i>Asca</i>	Soil, litter, plants, etc.	Species	+	Walter <i>et al.</i> (1993a)
Genus <i>Gamasellodes</i>	Soil, litter	Species	+	Walter (2003)
Genus <i>Lasioseius</i>	Soil, litter, plants, etc.	Species	+	Walter and Lindquist (1997)
Genera <i>Arctoseius</i> , <i>Blattisocius</i> , <i>Proctolaelaps</i> , <i>Protogamasellus</i>	Soil, litter, plants, etc.	Species	+	Halliday <i>et al.</i> (1998)
Family Davacaridae	Soil, litter, moss	Genera and species	++	Walter (2004)
Family Laelapidae				
Genus <i>Stratiolaelaps</i>	Soil, litter	Species	+	Walter and Campbell (2003)
Family Macrochelidae	Dung, compost, litter	Genera	+++	Halliday (1986)
Genus <i>Macrocheles</i>	Dung, compost, litter	Species	++	Halliday (2000b)
Genus <i>Glyphtholaspis</i>	Dung, compost, litter	Species	++	Halliday (1986)
Genus <i>Holostaspella</i>	Dung, compost	Species	++	Halliday (1988)
Families Ologamasidae and Rhodacaridae	Soil, litter, moss	Genera	+	Lee (1970) (see also Lee 1973a)
Family Phytoseiidae	Plants, litter	Genera and species	+	Schicha (1987)
Subfamily Amblyseiinae	Plants, litter	Genera and species	+	Beard and Walter (1996); Walter (1999); Beard (2001)
Subfamily Phytoseiinae	Plants	Genera and species	+	Walter and Beard (1997)
Subfamily Typhlodrominae				
Genus <i>Australiseiulus</i>	Plants	Species	+	Beard (1999)
Genus <i>Neoseiulella</i>	Plants	Species	+	Walter (1997)
Family Podocinidae	Soil, litter	Species	+	Halliday (1990)

within the Phytoseiidae, more than half of the known species appear to be endemic to Australia (Schicha 1984, 1987; Walter and Beard 1997; Walter 1999) and most ologamasid species are not known from other countries (Lee 1970). Many species seem to have restricted distributions within Australia. In Far North Queensland, collections indicate that several phytoseiids have a very narrow distribution, with specimens found only in a few sites within the wet tropics (Walter and Beard 1997; Walter and Proctor 1998b). Further, the wet tropics, monsoonal areas of the Northern Territory, and subtropical forests of south-east Queensland all have quite distinct faunas that are largely absent

from other regions. Species in temperate areas usually show a broader distribution, with some species found from south-eastern Queensland down to Victoria.

Cosmopolitan or introduced species (e.g. *Phytoseiulus persimilis* Athias-Henriot, *Macrocheles merdarius* Berlese, *Parasitus longicornis* Berlese) are widespread in Australia, but there is a tendency for these species to be found in disturbed habitats such as agricultural fields, pastures and roadside weeds (Walter *et al.* 1998a; Halliday 2000b; Ireson *et al.* 2001). There is little data on the distribution of soil dwelling Mesostigmata to make any general conclusions. However, Beaulieu (2005) has

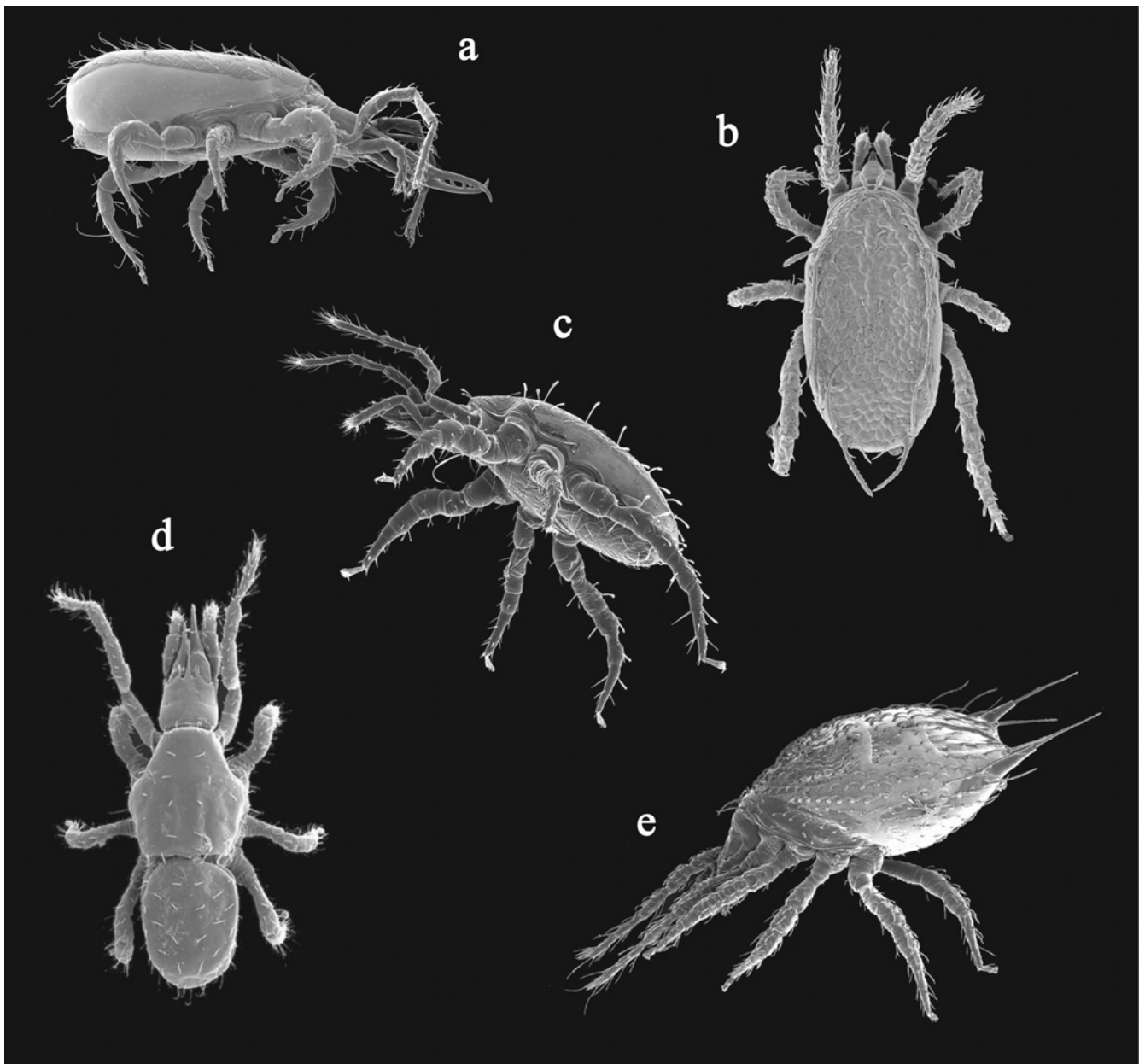


Fig. 1. Scanning electron microscope images of (a) *Athiasella* n. sp. (Ologamasidae), (b) *Phytoseius oreillyi* Walter & Beard (Phytoseiidae), (c) *Macrocheles novaezealandiae* Emberson (Macrochelidae), (d) *Rhodacarus* sp. (Rhodacaridae), and (e) *Sejus* n. sp. (Sejidae). Images courtesy of David E. Walter, University of Alberta, Canada.

recently shown a high level of local endemism of species associated with rainforests/wet sclerophyll forest fragments in eastern Queensland.

There are many factors that will determine the distribution of Mesostigmata within Australia, although climate appears to be the main determinant, either directly or indirectly. For instance, the phytoseiid *Euseius victoriensis* Womersley is found in all states of Australia but is restricted to warmer, dryer, mostly inland areas (Walter 1999). Other factors that likely affect the distribution of Mesostigmata include host plant availability, soil type, prey species and competition.

Biology and ecology

Research on the life-history, ecology and basic biology of Australian Mesostigmata is centred primarily on species that have potential in biological control programs. These studies have focussed on both introduced and native species from the family Phytoseiidae that are associated with agricultural crops and their invertebrate pests (Table 2). Few studies have focussed on the ecology of phytoseiids outside agricultural systems and these are restricted to scattered records of host plant associations, inferences on feeding behaviour from taxonomic studies (Schicha 1987; Walter and Beard 1997) and surveys from rainforest and woodland plants. Biological surveys have given some insight into the distribution of phytoseiids and indicate that species can occur on a diversity of native trees, shrubs and vines (Walter 1992; Walter *et al.* 1994) and are generally not host plant specific (Schicha 1984; but see Beard and Walter 2001).

Plant morphological features appear to influence the distribution of many phytoseiid species with the genera *Phytoseius* and *Paraphytoseius* almost completely restricted to the leaves of plants with well developed tomenta (hairiness) and *Euseius* preferring plants with glabrous leaves (Walter 1992;

Beard and Walter 1996). Other leaf features, such as domatia and strong veins, can influence the distribution of species by providing shelter for oviposition and from natural enemies as well as against microclimatic extremes (Walter 1996). Similarly, extrafloral nectaries on rainforest plants appear to positively influence the abundance of phytoseiids and other predatory mites by providing a source of carbohydrates (Walter and O'Dowd 1995).

Although soil-inhabiting mites are extremely diverse in Australia, very little information is available on their biology and ecology. Ecological surveys in native or agricultural soils are rare (see Table 3) and detailed biological studies are few. Lee (1973b, 1974) described the development, reproductive behaviour, predatory habits, habitat distribution and other components of behaviour (i.e. locomotion) of various species of Ologamasidae that he collected around Adelaide. There are also scattered studies on some species of Ascidae (Walter and Lindquist 1995, 2000). Some of the species having cosmopolitan distribution or that have a clear overseas origin (i.e. introduced) are often better known (e.g. *Arctoseius cetratus* (Sellnick)). This leaves over 95% of species (including described and undescribed species) inhabiting natural and agricultural soils of Australia with little or no specific life-history data. However, some very general information on habitat type, feeding and dispersal behaviour at the family or generic level can be found in Walter (2001) or other general publications (e.g. Krantz and Walter, in press; Ruf 1996).

Among the seven families of Mesostigmata associated with dung or dung-breeding insects in Australia (Wallace 1986), little is known about their biology and ecology. Most species of *Macrocheles* are confined to discrete accumulations of organic matter, especially dung, and are phoretic on insects (Halliday 2000b). The feeding behaviour, interspecific competition and seasonal abundance patterns were studied for a few species of

Table 2. Phytoseiid mites involved in biological control programs in Australia

Parentheses indicate that the role of the predator in controlling the mite pest is minimal, not established, or its release may not be economically viable (in hop); data mainly from James (2001) and Steiner and Goodwin (2001), but also from Beattie *et al.* (1991), Goodwin (1990), James (1990), Smith and Papacek (1991), Schicha (1984), Waite (1988a, 1988b, 2001, pers. comm.) and Whitney and James (1996)

Phytoseiid species	Origin	Pest species	Horticultural crop(s)
<i>Amblyseius deleoni</i>	Native ^C	<i>Polyphagotarsonemus latus</i> , <i>Panonychus citri</i> , eriophyid spp., <i>Tetranychus urticae</i>	Citrus, (lychee)
<i>Amblyseius lentiginosus</i>	Native	Eriophyid spp., <i>P. citri</i>	Citrus, (grapes)
<i>Euseius elinae</i>	Native	<i>P. latus</i> , <i>P. citri</i> , eriophyid spp.	Citrus
<i>Euseius victoriensis</i>	Native	<i>P. latus</i> , eriophyid spp., <i>Brevipalpus</i> spp., <i>T. urticae</i>	Citrus, grapes, peach
<i>Galendromus occidentalis</i> ^{A,B}	Introduced	<i>T. urticae</i> , (<i>Panonychus ulmi</i>)	Apple, citrus, (ornamentals), peach, pear
<i>Neoseiulus womersleyi</i>	Native	(<i>T. urticae</i>)	Hops, strawberry
<i>Phytoseiulus persimilis</i> ^{A,B}	Introduced	<i>T. urticae</i> , (<i>T. lambi</i> (Pritchard & Baker))	(Apple), (banana), citrus, (hop), ornamentals, peach, strawberry, vegetables
<i>Phytoseius fotheringhamiae</i>	Native	Eriophyid spp.	Grapes
<i>Typhlodromus doreenae</i> ^A	Native	<i>Brevipalpus</i> spp., eriophyid spp., (<i>T. urticae</i>)	(Apple), grapes
<i>Typhlodromus dossei</i>	Native	Eriophyid spp.	Grapes
<i>Typhlodromus pyri</i> ^A	Introduced	<i>P. ulmi</i> , <i>T. urticae</i>	Apple

^AStrains show some insecticide resistance.

^BSpecies available commercially in Australia.

^CKnown distribution suggests that these species are native to Australia, but future studies may reveal that some of them originated elsewhere. *Amblyseius deleoni* is considered by some authors to be a junior synonym of *A. herbicolus* Chant and to have a widespread distribution. *Neoseiulus womersleyi* (Schicha) is also found throughout Asia.

Table 3. Density and number of species of Mesostigmata collected in different regions and vegetation types in Australia

Region	Vegetation type	Habitat	No. of morphospecies	Average densities	Total abundance	Comments	References
Queensland	Tropical lowland rainforest	Litter	40	14–37/L	597	–	Beaulieu (2005)
Queensland	Subtropical rainforest (montane)	Soil, litter	29–61 (per site)	1926–3736/m ²	259–923	Many species show preference for rainforests or open forests	Walter <i>et al.</i> (1998b); Beaulieu (2005)
Queensland	Subtropical, tall open forest (montane)	Soil, litter	28–52 (per site)	512–3904/m ²	157–835	–	Beaulieu (2005)
Queensland	Subtropical rainforest, tall open forest (montane)	Soil, litter	185 (25 m ² area)	–	15343	> 85% are undescribed species	Beaulieu (2005)
Queensland	Subtropical rainforest, tall open forest (montane)	Soil, litter	76	40900–51700/m ² A	–	Many species prefer litter or soil	Plowman (1981)
Tasmania	Warm temperate, tall open forest	Litter	45	71/L	856	–	Beaulieu (2005)
Tasmania	Warm temperate, tall open forest	Logs (rotting wood and moss)	43	23/L	417	Nearly half of species were absent from litter	Beaulieu (2005)
New South Wales	Temperate, open forest	Soil, litter (under 3 tree species)	33	3130/m ²	3630	No species show preference to a tree species	Osler and Beattie (2001)
South Australia	Temperate, open forest and woodland	Moss or litter	22 (only Ologamasidae)	3080–6660/m ²	–	Densities twice higher in litter than moss	Lee (1985)
South Australia	Temperate, open forest	Soil, litter	–	1770–3100/m ²	–	Densities were maximum during winter	Hutson and Veitch (1987)
Western Australia	Temperate, jarrah forest	Soil, litter	13	100–28000/m ² (for soil)	–	–	Adolphson (2000)
Western Australia	Temperate, bluegum plantation	Soil, litter	4	200–41000/m ² (for soil)	–	–	Adolphson (2000)
New South Wales	Semi-arid chenopod shrubland	Soil (under shrubs)	–	0–442/m ²	–	Abundance varies highly across plant spp. and seasons	Noble <i>et al.</i> (1996)
Western Australia	Semi-arid chenopod shrubland	Soil (within & between bluebush mounds)	11	0–599/m ²	58	Most individuals confined to the shrub mounds	Kinnear and Tongway (2004)
Western Australia	Semi-arid woodland and shrubland	Soil	6	88–725/m ²	115	Abundance increases with litter cover	Kinnear (1991)
Western Australia	Grazed pasture	Soil	3	200–10800/m ²	–	–	Adolphson (2000)
Western Australia	Agricultural (canola-wheat-lupin)	Litterbags	8	–	835	Composition does not reflect stage of decomposition	Osler <i>et al.</i> (2004a)
Western Australia	Agricultural (canola-wheat-lupin)	Soil	6	100–2800/m ²	–	–	Osler <i>et al.</i> (2000); Osler <i>et al.</i> (2004b)
South Australia	Citrus orchards (9 sites)	Soil	17	198–5150/m ²	–	Higher densities associated with low thrips infestation	Colloff <i>et al.</i> (2003)

A Juveniles were included in the counts and represent 29–35% of individuals.

Macrocheles (Macrochelidae) and *Parasitus* (Parasitidae) (Wallace and Holm 1984, 1985), and Manning and Halliday (1994) compared the reproductive mode and distribution of several macrochelids.

Mesostigmatic mites show a range of reproductive modes. The majority of species for which the reproductive systems have been studied are arrhenotokous (haplodiploid), with virgin diploid females producing haploid male progeny, and fertilised females giving rise to diploid daughters (Norton *et al.* 1993). Some taxa are parahaploid (pseudoarrhenotokous), where males and females arise from fertilised eggs, but in males the paternal genome is lost soon after fertilisation. Parahaploidy may be the dominant reproductive mode in the Phytoseiidae and Ascidae (Norton *et al.* 1993). Some taxa are mainly represented by diploid species and thelytokous or female parthenogenesis (asexuality) occurs in a range of taxa.

Biological control agents

Predatory Mesostigmata have considerable potential for use in biological control programs aimed at invertebrate pests of plants. Because of their plant-dwelling habits, however, most research has focussed on the family Phytoseiidae, both in Australia and abroad. Their short generation times, wide dispersal ability, general association with plant fauna and voracious feeding behaviour make them excellent candidates for inundative, augmentative and inoculative biological control programs (Gerson *et al.* 2003). In Australia, introduced phytoseiids have formed the basis of biological control programs, although native phytoseiids can provide endemic control of some pests, especially in agricultural systems that do not rely on the continual use of pesticides (James 2001). Although their role in biological control has yet to be established, other predatory Mesostigmata (mainly from soil and litter) are also likely to be important in pest control and act as part of an assemblage of generalist predators within an agroecosystem. In this section, we review the current literature in Australia on the use of phytoseiids in biological control programs and then provide some insight into the role that other Mesostigmata may play in the control of agricultural pests.

Introduced Phytoseiidae

Within Australia, four introduced phytoseiids have been used in biological control programs in horticultural crops: *Galendromus occidentalis* (Nesbitt); *Typhlodromus pyri* Scheuten; *Neoseiulus fallacis* (Garman); and *Phytoseiulus persimilis*. These Phytoseiidae have largely been introduced due to their specificity to pest species from the family Tetranychidae (spider mites) and/or because they have been selected for resistance to particular pesticides (James 2001). At least three strains of the spider mite specialist *G. occidentalis* have been introduced into Australia, although only one strain is known to have established successfully (Readshaw 1975; James 2001). The successful *G. occidentalis* strain, which is resistant to azinphos-methyl (used for the control of oriental fruit moth), was introduced from North America in 1972, to apple orchards in all mainland states for the control of the two-spotted spider mite *Tetranychus urticae* Koch (Tetranychidae) (Readshaw 1975). The strain is now established in apple, pear and peach orchards where azinphos-methyl is used (Table 2) and can

survive year-round. In orchards that do not use pesticides intensively, *G. occidentalis* is often displaced by native species (i.e. *Euseius victoriensis*) which are sufficient to control *T. urticae* (James 1990).

Typhlodromus pyri and *N. fallacis* have both been introduced for the control of the European red mite *Panonychus ulmi* (Koch) (Tetranychidae) and/or *T. urticae* in apple orchards in several states in the late 1970s (James 2001). The generalist *T. pyri* is now established on apples in Tasmania and New South Wales and provides good control of *P. ulmi* (Table 2). Despite initial control of *P. ulmi* and *T. urticae* on apples in the season of release, *N. fallacis* has failed to establish at release sites and it is now considered incompatible with the microclimates and overwintering areas available in Australian apple orchards (James 2001).

Probably the most successful of all mite biocontrol agents across the world has been the Chilean predatory mite *Phytoseiulus persimilis*. This species is a strict specialist of spider mites from the genus *Tetranychus*. It is used overseas largely for the control of *T. urticae* in greenhouse crops (Gerson *et al.* 2003). *Phytoseiulus persimilis* was found in commercial strawberry crops in New South Wales in 1978 (Goodwin and Schicha 1980), but there are no records of when it was introduced into the country (James 2001). This introduced strain is resistant to several fungicides, insecticides and acaricides (Goodwin 1984). It has been used in Australia for the control of *T. urticae* on a variety of greenhouse ornamental plants, vegetable crops, field strawberries and, to a lesser extent, deciduous fruit crops (Table 2). This predatory mite can locally decimate populations of *Tetranychus* spp. but, in doing so, often results in its own local extinction due to a lack of alternative prey. Populations of *P. persimilis* have been found to persist and invade other host plants, where some *Tetranychus* spp. persist year-round (Waite 1988a, 1988b). Generally, however, in seasonal crops such as strawberries, seasonal releases of *P. persimilis* are necessary for the control of *Tetranychus* spp. The recent introduction of the western flower thrips *Frankliniella occidentalis* (Pergande) into Australia has resulted in the use of pesticides that are not compatible with current strains of *P. persimilis* and has limited their use somewhat in strawberry fields and greenhouses (Steiner and Goodwin 2001). This has forced researchers to look for other phytoseiids and soil mites as biocontrol agents of thrips (Steiner *et al.* 2003).

Despite the fact that *G. occidentalis*, *T. pyri* and *P. persimilis* are now widespread in Australia, none appear to have invaded native habitats and they seem to be restricted to crops, weeds or other exotic plants in disturbed habitats (Schicha 1987; Walter *et al.* 1998a). This may, in part, be due to their preferred prey (*Tetranychus* spp.) not being common on native plants (Walter 1992). The apparent absence of the introduced phytoseiids in natural, undisturbed habitats indicate that they have not damaged or perturbed native ecosystems and native fauna, and that it may be safe to import predatory mites as biological control agents as long as they show a moderate to high degree of prey specialisation (Schicha 1984). Both *G. occidentalis* and *P. persimilis* are available commercially within Australia for augmentative, inoculative or inundative release.

Native Phytoseiidae

In Australian agriculture, there are two industry success stories that show how native Phytoseiidae can play a major role in the control of invertebrate pests when incorporated in an integrated pest management (IPM) system.

In citrus orchards throughout inland regions of Queensland, New South Wales, Victoria and South Australia, there are several mite pests, including the citrus rust mite *Phyllocoptruta oleivora* (Ashmead) (Eriophyidae), the broad mite *Polyphagotarsonemus latus* (Banks) (Tarsonemidae), the brown citrus rust mite *Tegolophus australis* Keifer (Eriophyidae), *Brevipalpus* mites (Tenuipalpidae) and the two-spotted spider mite *T. urticae* (Beattie *et al.* 1991; Smith and Papacek 1991; James 2001). In the past, control of these mites relied heavily upon regular indiscriminate pesticide applications throughout the year (Smith and Papacek 1993). However, the switch to an IPM strategy, which depended largely on the service of scouts who monitored pest population numbers, released biocontrol agents and gave growers advice on the optimal time to spray, meant that the use of native phytoseiids for biocontrol was possible (Smith and Papacek 1993). The native species *Euseius victoriensis* (formerly *Amblyseius victoriensis*) is now established in most citrus orchards practicing IPM and is largely responsible for keeping population numbers of the above mite pests below economic damage thresholds (Smith and Papacek 1991; James 2001). In coastal citrus areas of New South Wales, three other native phytoseiid species, *Amblyseius deleoni* Muma & Denmark, *A. lentiginosus* (Denmark & Schicha) and *Euseius elinae* (Schicha) control mite pests including the citrus red mite, *Panonychus citri* (McGregor) (Tetranychidae) (Table 2; Beattie *et al.* 1991; James 2001). The long-term establishment of these phytoseiids and others in citrus is probably due to several factors and not just the move away from non-targeted pesticide applications. Citrus trees are evergreens, which means that a year-round microhabitat is provided in these trees for phytoseiids and their prey (Beattie *et al.* 1991). Also, these phytoseiids are generalists (feeding type III and IV, McMurtry and Croft 1997), consuming a variety of mites, small insects (including scale insects and whiteflies) and pollen. In some instances, however, the use of either augmentative releases of commercially available phytoseiids (*G. occidentalis* or *P. persimilis*) or targeted pesticides is still recommended in citrus groves when large outbreaks of pest mites occur (James 2001).

There are several mite pests of grapevines (Table 2). However, both the grape blister mite (and the grape bud mite; see Carew *et al.* 2004), *Colomerus vitis* (Pagenstecher) (Eriophyidae) and the grape rust mite, *Calepitrimerus vitis* (Nalepa) (Eriophyidae) are considered the major mite pests of viticulture. This is due to their association with the phenomenon known as restricted spring growth (Bernard *et al.* 2005). In vineyards that practice targeted IPM strategies and limit pesticide use to inorganic fungicides, an assemblage of native phytoseiids, dominated by *Typhlodromus doreenae* Schicha and *E. victoriensis*, is present and keeps these pests under economically damaging thresholds (Table 2; James and Whitney 1993). In fact, in vineyards where *T. doreenae* and *E. victoriensis* are present, there is no need to spray acaricides (James and Whitney 1994). Both are resistant to inorganic

fungicides (copper and sulfur) and *T. doreenae* is also resistant to some synthetic fungicides and insecticides, including azinphos-methyl (Smith and Papacek 1991; James 2001). In a survey of vineyards throughout 29 viticultural regions of Australia, a total of 31 native phytoseiid species has been recorded (Whitney and James 1996). Several of these species, including *Phytoseius fotheringhamiae* (Denmark & Schicha), *Typhlodromus dossei* (Schicha), *Amblyseius lentiginosus*, *A. helmi* (Schicha) and *A. loxtoni* (Schicha), are thought to contribute to the control of invertebrate pests (James and Whitney 1993; Whitney and James 1996).

The success of native phytoseiids in citrus and grapevines for controlling acarine pests shows the potential that these predators have in IPM programs, as long as pesticides are either kept to a minimum or targeted specifically at a pest species (e.g. insecticides based on *Bacillus thuringiensis*) and that appropriate scouting services are provided, at least for the first year(s) of the program. Reductions of pesticide use in other agricultural systems have also resulted in native phytoseiids providing adequate control of acarine pests. For instance, *Euseius victoriensis* colonised peach fruit trees where broad-spectrum insecticides had been replaced by mating-disruption pheromones for oriental fruit moth (Table 2). The native predator controls the peach silver mite, *Aculus cornutus* (Banks) (Eriophyidae) and prevents outbreaks of *T. urticae* (James 1990). *Euseius victoriensis* cannot develop or reproduce on *T. urticae* alone (James 1989a), so other food sources (e.g. eriophyids, pollen, honeydew) on these crops are needed for this predator to maintain populations year-round (James 1990). A reduction in pesticide use has also resulted in substantial control of the lychee erinose mite, *Aceria litchii* (Keifer) (Eriophyidae) by native phytoseiids (G. Waite, Department of Primary Industries and Fisheries, Queensland, pers. comm.). Overall, the use of native phytoseiids can result in considerable net cost savings associated with the reduction in use of pesticides (Barrass and Brown 1993; Smith and Papacek 1993; James and Whitney 1994).

Cultural methods and habitat manipulation also appear important to the persistence of both native and introduced phytoseiids, by providing overwintering sites and additional food sources (e.g. pollen, alternative prey). The maintenance of Rhodes grass in inter-rows of citrus orchards enhances population growth of *E. victoriensis* by providing access to pollen, and windbreak rows of *Eucalyptus torrelliana* F. Muell. appear to act as reservoirs of *E. victoriensis* for nearby citrus blocks (Smith and Papacek 1991). Providing cover crops and adjacent evergreen vegetation in vineyards and peach orchards is also important for overwintering of phytoseiids, including *E. victoriensis*, and enhances recolonisation in spring (James 1989b, 1990).

The choice of plants is also important, especially the morphology of the leaves, since many phytoseiid species are associated with particular features (hairy surfaces, domatia), and alternative food sources may or may not be present on different plants (James 1989b, 1990). Overseas research also indicates surrounding vegetation and habitat manipulation influence phytoseiid numbers (Ragusa and Paoletti 1985; Gurr *et al.* 1996; Paoletti *et al.* 1997). However, it has received only minor consideration in IPM programs to date and further work

is required to understand its potential role for enhancing native phytoseiids and other predators for biocontrol.

Native (and naturalised) phytoseiids provide a rich assemblage of predatory species that can provide a stable predator-prey system that is sustainable, cost effective and environmentally sound. They are generally better adapted to local conditions than introduced phytoseiids (James and Taylor 1992), are able to persist year-round on alternative prey and have short generation times and rapid searching behaviours (James 1990; James *et al.* 1995). Developing mass rearing techniques for some of the key native phytoseiids would also provide the opportunity to augment existing populations when pest pressures are high and also for reintroduction after pesticide applications. Such techniques have recently been developed for *E. victoriensis* and *T. doreenae* (James and Whitney 1993; James 2001) and are in the process of commercialisation (Steiner and Goodwin 2001).

Non-phytoseiids

In Australia, the use of phytoseiid species in biocontrol is largely restricted to crops associated with spring–summer growing periods (e.g. orchards, strawberry fields). However, a large section of Australian agriculture is geared towards the cool winter growing season in southern Australia, where crops include cereals, canola, field peas, fodder crops, lucerne and pastures. In these highly disturbed environments, the use of phytoseiids may be somewhat limited due to the largely annual turnover of plants. However, a broad diversity of other free-living ‘generalist’ Mesostigmata belonging to families that inhabit soil and litter could play a major role in providing endemic control in these environments (Tsitsilas *et al.* 2006). Non-phytoseiid Mesostigmata also have the potential for controlling pests in greenhouses and stored grain products, as well as noxious flies associated with animal dung (Gerson *et al.* 2003). This diversity remains largely unexplored in Australia.

In southern Australia, there are several serious pests of small grain crops and pastures, including the earth mite species *Halotydeus destructor* (Tucker) (redlegged earth mite) and the *Penthaleus* species complex (blue oat mites) (Penthaleidae), as well as the collembolan *Sminthurus viridis* L. (lucerne flea, Sminthuridae). These alone are thought to cause in excess of 200 million dollars in damage to the wool, meat and dairy industries each year (Sloane, Cook, and King Pty Ltd 1988). Biocontrol methods have generally focussed on single predator solutions, including species of introduced and native bdellid and anystid mites (Prostigmata) (Ireson *et al.* 2001; Umina *et al.* 2004), with effective control rarely achieved. However, there are numerous predatory species of native soil-dwelling Mesostigmata that can potentially have a role in control of earth mites and the lucerne flea, and may act as part of a generalist assemblage of predators (Halliday 2003). There is some evidence that continual use of pesticides against earth mites in pasture can result in higher infestation and lower numbers of predatory mites compared to pesticide-free pastures (James 1995). Likewise, continual use of the ‘spring spraying’ method of earth mite control (Ridsdill-Smith and Pavri 2000) can lead to significantly lower numbers of soil Mesostigmata and increased abundance of redlegged earth mites and blue oat mites (J. Gower, University of Melbourne, pers. comm.). In addition,

the type of management of shelterbelts that surround pasture fields has been shown to have a positive impact on the control of earth mites, with fewer pest mites and increased numbers of soil predatory mites found where the understorey of the shelterbelt was not grazed (Tsitsilas *et al.* 2006). Predatory Mesostigmata from the family Parasitidae (*Pergamasus* and *Parasitus* spp.) are found in high abundance in pasture and crop soils (James 2000; Ireson *et al.* 2001). They are known to attack the lucerne flea (Ireson *et al.* 2001) and other mite pests (Lesna *et al.* 1995) and may also contribute to the control of cereal aphids (El Banhaway *et al.* 1993) and the garden symphytan, *Scutigerebella immaculata* (Newport) (Scutigerebellidae), which was recently discovered in Australia (Halliday 2004).

Nematodes are also important pests of crops throughout Australia, causing several hundred million dollars in damage each year by attacking the roots of most crop plants (Curran 1993). Although they are often the preferred prey of predatory Mesostigmata, the potential value of these mites for nematode control has been largely ignored (Gerson *et al.* 2003). There are currently relatively effective cultural control methods, particularly the use of non-host crops and/or resistant cultivars in crop rotations. However, these methods are generally not optimal and chemical nematicides are still widely used (Stanton and Stirling 1993). The manipulation of predatory mite populations, combined with these cultural methods and/or other biological control agents (fungal and bacterial pathogens) could help maximise the control of plant-parasitic nematodes (Sayre and Walter 1991). In various grass-dominated habitats in North America, 57 species out of 63 were feeding on (non-plant parasitic) nematodes (Walter and Ikonen 1989). Also, many species develop and reproduce better on nematodes than on an arthropod diet (Walter *et al.* 1987). The mesostigmatic fauna of Australian forests and open fields appear similar to overseas, in that they are composed of a large proportion of nematophagous species (Walter and Lindquist 2000; Colloff *et al.* 2003; Walter and Campbell 2003; F. Beaulieu, unpubl. data). Although some Mesostigmata have a strict nematode diet (Walter *et al.* 1988), most species are generalist feeders, attacking both nematodes and soft-bodied arthropods (Walter and Ikonen 1989; Sayre and Walter 1991). Reductions in parasitic nematodes have been observed in many experimental and greenhouse situations using inoculation of selected Mesostigmata (Walter *et al.* 1993b; Gerson *et al.* 2003), but field experiments are generally lacking.

Members of the family Laelapidae are common soil dwellers, some of which have shown serious potential in controlling a variety of pests, both in greenhouses and in field crops. Most research on this family is based on overseas studies. *Gaeolaelaps aculeifer* (Canestrini) is an aggressive predator of soft-bodied arthropods and nematodes. It has been shown to significantly reduce populations of parasitic nematodes, bulb mites, western flower thrips, as well as fungus gnats (*Bradysia* spp.) in greenhouse experiments (Lesna *et al.* 1995; Gerson *et al.* 2003). *Stratiolaelaps miles* (Berlese) (or *S. miles* species complex; see Walter and Campbell 2003) is another cosmopolitan, fast-reproducing, fast-moving voracious laelapid. The introduction of *S. miles* in greenhouse pots and mushroom compost resulted in satisfactory control of fungus gnats (*Bradysia* spp. and *Lycoriella solani* (Winnertz), Sciaridae) (Gerson *et al.* 2003). Several species of *Stratiolaelaps* and *Gaeolaelaps* occur in

Australia (Walter and Campbell 2003), and greenhouse experiments have shown that some have the potential to control fungal gnats and thrips pupae by their feeding activity in the soil (I. Vänninen, Agrifood Research Finland, pers. comm.; Goodwin and Steiner 2006). In South Australia (Riverland), citrus orchards characterised by perennial herbaceous cover and dense populations of soil Mesostigmata were generally free of thrips, while orchards with bare soil and few predatory mites had major thrip problems (Colloff *et al.* 2003). Therefore, it may be possible to use both soil predators and phytoseiids to control thrips and other phytophagous pests that spend parts of their lifetime in both plant and soil surfaces (Wiethoff *et al.* 2004). Other soil laelapids have been observed to significantly reduce the populations of phytophagous beetle pests, in the field or in the laboratory, by feeding on the soil-dwelling larvae; some are suggested to enhance the spread of entomopathogenic fungi to beetle hosts (Eickwort 1983). Australian soils have rarely been investigated for potential biological control agents. Open fields, greenhouse soils as well as natural undisturbed habitats may harbour effective predators of various pests (e.g. thrips, beetles, aphids) that could be reared and used for inoculation or inundation, especially in greenhouses, but also possibly in field crops.

A diversity of predatory Mesostigmata belonging to seven families are coprophilous, i.e. breed mainly in animal droppings, and are dispersed phoretically by coprophagous beetles and flies (Krantz 1983; Wallace 1986). Although a large number of dung beetle species were introduced in Australia in order to decrease the nuisance of dung-breeding pest flies (by accelerating the decomposition of their microhabitat), the latter are still a major nuisance in many pastoral situations. In dung habitats, Mesostigmata prey on nematodes and soft-bodied arthropods including the eggs and young instar larvae of flies. Macrochelidae are diverse in Australia and many species occur in cow dung, especially in pastoral situations (Halliday 2000b). The combination of several traits make some macrochelic mites theoretically suitable for fly control: (i) their aggressive behaviour and feeding preference for the eggs and larvae of flies; (ii) their high rate of population increase [e.g. *M. muscaedomesticae* (Scopoli) can increase its populations by a factor of 70 every three days at 30°C; Ho *et al.* 1990]; (iii) their efficient dispersal on a variety of dung-inhabiting beetles; and (iv) the ease of rearing on flies or nematodes (Krantz 1983). Among the resident Australian fauna, *Macrocheles glaber* (Müller) and *M. perglaber* Filiponi & Pegazzano (combined under the name of *M. 'glaber'* at the time of publication) were shown to have a significant effect on the bush fly *Musca vetustissima* Walker (Muscidae) in laboratory dung pad experiments, with 100% control in an optimal situation (Wallace *et al.* 1979). However, the arrival time of mites at the dung pad had a great impact on the success of control. When mites arrived after the fly eggs had hatched, the control dropped to 60%, emphasising the importance of quick and timely dispersal (i.e. concurrent with the dispersal of flies) on their beetle carriers. A South African macrochelic, *M. peregrinus* Krantz, was selected for its climatic ubiquity and its broad range of dung beetle vectors (many of which were introduced and established in Australia) and was introduced at two sites in Far North Queensland in 1980 and 1981, for the control of the bush

fly and buffalo fly, *Haematobia irritans exigua* de Meijere (Muscidae) (Wallace and Holm 1983). It spread rapidly and now occupies most of northern Australia. Field experiments have shown an average suppression of 33% of the buffalo fly by *M. peregrinus*, indicating that alone it is not an effective predator (Roth *et al.* 1988). The limited success of the mite was explained by the feeding preferences for other (non-pest) flies, the inaccessibility of some fly eggs (e.g. underneath the dung pad) and the low predator/prey ratio (Roth *et al.* 1988). Assemblages of macrochelids and other predatory arthropods may be more efficient in controlling the pests than *M. peregrinus* alone, although competitive interactions between predatory mites could have adverse effects and should be considered (Wallace and Holm 1984). The importation of carefully selected and studied species from overseas might assist *M. peregrinus* and other resident macrochelids in the control of the bush and buffalo flies in pastures, but it would be necessary to demonstrate that there would be no harmful effects on non-target species.

In contrast to macrochelids in dung pads in pastoral situations, few species are found in 'domestic' dung piles (e.g. poultry houses, stables). *Macrocheles muscadomesticae* (Scopoli) has a cosmopolitan distribution and has been shown overseas to help control filth flies breeding in poultry manure (Gerson *et al.* 2003). However, an integrated approach combining cultural practices (e.g. for keeping moisture low to decrease fly colonisation), the selective use of insecticides and the enhancement of predatory mites (mainly through manure management) would provide economical control of the pests in poultry houses and cattle feedlots (Krantz 1983; Gerson *et al.* 2003).

Indicators of soil quality

In the last two decades, there has been growing interest in the use of invertebrates as indicators of ecosystem integrity, specifically for determining the impact of anthropogenic disturbances and climate change ('ecological indicators', McGeoch 1998). With the current rate of land degradation in Australia, there is an urgent need to evaluate the effect of agricultural and other land use practices on ecosystems, in order to develop improved management strategies and develop more sustainable practices. In Australia, many insect groups are frequently employed as ecological indicators (e.g. ants, Andersen *et al.* 2002). With the exception of earthworms (Thomson 2006), however, most invertebrate groups intimately associated with soils (e.g. mites, Collembola and nematodes) are generally not used as bioindicators (but see this issue). Given that these invertebrates will be the first to encounter altered or stressful soil conditions, it makes sense to focus on these as indicators of soil quality. Mesostigmatic mites satisfy the common selection criteria for bioindicators: they are abundant and diverse, they have important ecological functions in the soil, they are relatively easily sorted and identified (see Appendix 1) and they are sensitive to environmental conditions. They also have other characteristics, such as high reproductive rates and dispersal abilities, which can allow them to respond quickly to environmental change. In Europe, they are increasingly used as bioindicators (Karg and Freier 1995; Siepel 1996; Ruf 1998; Koehler 1999; Ruf and Beck 2005). However, in Australia the main obstacles facing the use of Mesostigmata as indicators of

soil quality is the general paucity of experts (and identification tools) and the lack of baseline data describing the relationship between community composition and environmental stress.

Soil Mesostigmata

Soil Mesostigmata are very small arthropods, with the large majority of adult females less than 1 mm in body length, although sizes range from 200 μm to 2 mm (Krantz and Walter, in press; Koehler 1999; Ruf and Beck 2005). Size is roughly related to the vertical distribution. Euedaphic species, which live in deeper soil (>10 cm) (e.g. Rhodacaridae) are small (<500 μm), usually narrow and characterised by separate shields that allow higher flexibility to manoeuvre in narrow soil pores. Organic layers (humus and litter) are occupied by hemiedaphic species and surface dwellers, which represent a broader size range and include the largest species (Walter and Ikonen 1989; Koehler 1999). Accordingly, larger species can be absent or rare in cultivated fields or other disturbed areas where the litter layer is not well developed (Buryan and Hartmann 1992; St. John *et al.* 2002).

Many Mesostigmata have specialised dispersal behaviour and are phoretic on winged insects. Phoretic species are usually associated with patchy, transient habitats such as dung, carrion, decaying wood and fungal sporocarps (Athias-Binche 1991). In soils, the few species that disperse by phoresy generally occur in patchy habitats such as compost, mushrooms, animal nests, or tidal debris (Binns 1982; Athias-Binche 1991). These species tend to be opportunistic, and can colonise habitats more readily than non-phoretics. Thus, they are well represented and often dominate recently or frequently disturbed habitats, such as cultivated fields, pastures, early stages of plant succession, burnt soils and mine tailings (Athias-Binche 1989; Siepel 1996; St. John *et al.* 2002).

Although the majority of soil free-living Mesostigmata are primarily predatory, there is variation in the range of prey they can ingest, and some consume plant/fungal material. Laboratory studies on feeding behaviour support the view that the majority of species may be 'generalist' predators, feeding on both worm-like prey (nematodes, small oligochaetes) and soft-bodied arthropods (springtails, mites, insect eggs or juveniles) (Walter *et al.* 1988). However, some appear to feed exclusively or mainly on nematodes and others accept only arthropod prey. Some Uropodina feed on yeast and unicellular algae, and some Ameroseiidae, Ascidae and other Uropodina include both animal prey and fungi in their diet (Halliday 1997; Halliday *et al.* 1998; Athias-Binche 1989). The few studies on the feeding behaviour of Australian species indicate that Australian forest soils include many generalist predators and species that feed primarily on nematodes (Lee 1974; Walter and Proctor 1998a; Walter and Lindquist 2000; F. Beaulieu and D. E. Walter, unpubl. data). The representation of feeding types varies among habitats. Certain nematode specialists often dominate in agricultural fields and other open, disturbed habitats, while species feeding mainly on arthropods are more abundant in wooded areas (Buryan and Hartmann 1992; Madej and Skubala 2002).

Soil Mesostigmata generally have high fecundity and developmental rates (Ruf 1996) and consequently high rates of population increase. Depending on the species, development time from egg to adult varies from 2 to 26 days at 25°C in the

laboratory (Ruf 1996). However, development rate is highly dependent on temperature and species will take 10–163 days to develop at 15–16°C. Depending on climate and the taxon, soil Mesostigmata will have one (univoltine) to many (multivoltine) generations a year (Lee 1985; Athias-Binche 1989). Females will lay between ~10 and 200 eggs, at the rate of 0.1–20 eggs per day (Ruf 1996). Fecundity is independent of temperature and is more determined by the quality of prey (Walter *et al.* 1987; Ruf 1996). Longevity varies with temperature, and adults may live for less than one week to a few months. There are some trends among taxa. For instance, Ascidae, Digamasellidae, Macrochelidae, and *Alliphis* spp. (Eviphididae) generally develop fast, while Rhodacaridae, some Parasitidae, Laelapidae, and Ologamasidae develop relatively slowly (Ruf 1996). However, there is a broad overlap among families and wide variation within families, and so, developmental rate, fecundity, reproductive mode and even feeding behaviour are seldom predictable beyond the generic level (Walter and Ikonen 1989; Ruf 1996).

Abundance and diversity

Mesostigmatic mites occur in the soil and litter layers of virtually all terrestrial ecosystems including agricultural landscapes, forests, saltmarshes, deserts and even Antarctic landscapes (Peterson 1982; Walter and Proctor 1999). Except in arid and some semiarid areas, they are among the most diverse and numerically abundant groups of predatory arthropods in soil-litter (Peterson 1982; Walter *et al.* 1988; Behan-Pelletier 2003). In subtropical wet forests of Queensland, high species diversities are found, with averages of 10–20 species per (1 L) sample and a typical site having around 50 species (Table 3; Beaulieu 2005), although it is likely that more species are present. At a larger scale, nearly 200 species can occur in a ~25 km² area of subtropical rainforests and tall open forests (Table 3). Open forests in temperate areas are also inhabited by rich communities, at least in eastern Australia, but may not reach diversities of subtropical wet areas. The fauna of semiarid areas appear to be represented by very few species (Table 3). North American arid grasslands and shrubland sites are also characterised by low diversities of Mesostigmata (e.g. Wallwork *et al.* 1985). The few surveys conducted in agricultural fields and pastures in Australia also indicate a poor fauna, with fewer than 10 species per site (Table 3). Conventional agroecosystems in Europe and North America show similar levels of diversity (Broadbent and Tomlin 1979; Koehler 1999).

Like species diversity, abundances of Mesostigmata in Australian ecosystems depend heavily on the type of vegetation and soil. In forests, several tens of individuals per litre of litter, or a few thousand individuals per m² are usually found (Table 3). Similar or higher densities are observed in European forests, with 4000–30000 individuals per m² (Peterson 1982). Semiarid woodlands and shrublands have much poorer densities, with sometimes no Mesostigmata recovered from samples collected from bare soil or during the driest seasons (Kinnear and Tongway 2004). In these areas, the few species present may be restricted to soil directly beneath shrubs, where soils are more fertile, have higher organic matter and more litter cover (Table 3; Kinnear 1991; Kinnear and Tongway 2004). Mesostigmata densities in agricultural fields vary in accordance

to the type of crop and the season (Table 3; Osler *et al.* 2000) but data is scarce. Agroecosystems in Europe and North America have recorded abundances of 2000–15 000 per m² (Moore *et al.* 1984; Lagerlöf and Andrén 1988; Paoletti 1988; Buryn and Hartmann 1992; Karg and Freier 1995; Koehler 1999).

Functional roles in ecosystems

Their high density and diversity at very small scales, from organic horizons down to deeper mineral layers, make Mesostigmata an integral component of soils. These attributes and their general high fecundity and developmental rate (Ruf 1996) suggest that they contribute substantially to ecosystem functioning. They are important predators of a variety of soil- and litter-inhabiting invertebrates, including springtails, nematodes and other mites (Moore *et al.* 1988; Edwards 2000). In some North American grasslands, they are the most important group of nematophagous arthropods (Walter *et al.* 1988) and therefore they can regulate populations of fungivorous, bacterivorous, predatory and root feeding nematodes (Moore *et al.* 1988). They are also the top predators of grassland soil food webs, feeding on invertebrate prey that occupy different trophic levels (Moore *et al.* 1988; Walter and Oliver 1989). As a result, they obtain their energy indirectly from plant, fungal and bacterial energy pathways, and are therefore likely to integrate any change occurring in these pathways (Ruf and Beck 2005).

Their feeding activity on soil invertebrates may affect ecosystem processes. Because a large proportion of prey of Mesostigmata are bacterivores and fungivores (i.e. nematodes, microarthropods), which act directly on populations and the activity of primary decomposers (fungi and bacteria), they may have a large impact on decomposition and mineralisation rates (Moore *et al.* 1988; Berg *et al.* 2001). Their effect on prey populations may have a stabilising effect on microbial populations and therefore stabilise rates of ecosystem processes (Tian *et al.* 1997). They may also enhance plant growth and survival via their consumption of plant-feeding mites and nematodes.

Finally, soil Mesostigmata contribute to food web functioning as food resources for a variety of invertebrates (e.g. other mites, ants, predatory beetles) and vertebrates (lizards, frogs, birds) which eat mites intentionally or by chance (Walter and Proctor 1999).

Community changes through ecological space and time

A survey in eastern Australia indicates that many species of Mesostigmata are restricted to soils associated with particular forest types (Beaulieu 2005). In several montane areas in south-east and central Queensland, the species assemblages in rainforest and adjacent tall open forest were significantly different. In Lamington National Park, where collecting was more intensive, 36 species were indicators of a specific forest type. That is, they were frequently collected in this particular forest type and were almost absent from other forest types. This includes 18 indicator species of rainforests, 6 of rainforest margins and open forests and 9 indicators of open forests (Beaulieu 2005). Habitat preferences can be observed at the level of families and genera. For instance, Ologamasidae are generally better represented in rainforests while Ascidae

(especially *Asca* spp.) have more affinity with open forests and shrublands (Walter *et al.* 1993a; Kinnear and Tongway 2004; Beaulieu 2005). In addition to the tree composition of the canopy (rainforest v. sclerophyllous trees), the type of understorey also contributes to differences in community structure. Open forests dominated by grasses were more distinct from rainforest and harboured unique species, while open forests with rainforest understorey had species intermediate and more similar to rainforests (Beaulieu 2005). These results suggest that among the broad range of vegetation forms in Australia, each harbours a relatively specific assemblage of Mesostigmata. In Europe, deciduous and coniferous forests generally have a rather distinct fauna, with the type of humus appearing to be a major explanatory variable (Ruf and Beck 2005). Open habitats (meadows, pastures) are characterised by many species absent or rare in forests, and vice versa (Buryn and Hartmann 1992; Madej and Skubala 2002). Within a forest type, there is little influence of the tree species on the underlying soil fauna. Osler and Beattie (2001) did not find any Mesostigmata species restricted to the soil and litter under any of three tree species (two *Eucalyptus* spp. and one *Allocasuarina* sp.). Direct causative factors determining community structure of Mesostigmata and the presence and abundance of individual species are not well understood, even in Europe (Koehler 1999).

Given the rarity of surveys conducted at taxonomic levels finer than 'Acari', the influence of agriculture practices on the mesostigmatan fauna in Australia is difficult to assess. The studies of Osler *et al.* (Table 3) show that cultivated fields are occupied by low numbers of species. In Europe and North America, agricultural fields are usually inhabited by an impoverished fauna compared with undisturbed meadows, with sites often having fewer than 10–15 species, with a few of them highly dominant numerically (Lagerlöf and Andrén 1988; Koehler 1999). Conventional agricultural practices (tillage, intense pesticide use) create a simplified, highly disturbed ecosystem that eliminates microarthropod species most susceptible to desiccation and damage of their microhabitats (Behan-Pelletier 2003). With reduced competition and predation, the remaining species are then free to increase in numbers and dominate. Although several hemiedaphic species are associated with agricultural fields, the most dominant species are usually small and associated with humus or deeper soil layers. These species typically belong to the genera *Arctoseius* (Ascidae), *Rhodacarellus* (Rhodacaridae), *Dendrolaelaps* (Digamasellidae) and *Alliphis* (Eviphididae) and are widespread, opportunistic, and also common in other disturbed habitats such as land fills, mine dumps and early successional habitats in Europe and North America (Lagerlöf and Andrén 1988; Glockemann and Larink 1989; Buryn and Hartmann 1992; Koehler 1998; St. John *et al.* 2002). Most of these species (*Rhodacarellus* spp. excepted) have a high reproductive output and dispersal ability, being phoretic on insects (Binns 1982). These two traits allow them to rapidly colonise new habitats that have been recently disturbed.

Several factors are involved in the alteration of soil fauna in cultivated fields compared with natural habitats. Conventional methods of tillage are a major factor. In Europe, comparison of conventionally tilled agroecosystems with no-tillage or reduced

tillage systems indicate that conventional ploughing results in significant reductions in total abundance and species richness of Mesostigmata (Moore *et al.* 1984; Wardle 1995; Koehler 1999; Minor *et al.* 2004). Ploughing disturbs soil microhabitats by burying surface litter and reducing soil porosity (Gupta 1994). Ploughing especially reduces the abundance of Mesostigmata in the upper horizons and tends to redistribute the overall abundance towards lower depths (Lagerlöf and Andrén 1988; Winter *et al.* 1990). Alternative methods of tillage (rotary cultivation) working at a shallower depth, was found to maintain higher abundances of Mesostigmata than deep conventional ploughing (Butz-Strazny and Ehrnsberger 1991). Soil compaction by heavy wheeled machinery also has an adverse effect on abundance and diversity by reducing soil porosity (Koehler 1999).

Another major practice that can reduce Mesostigmata populations is the use of pesticides. Broad-spectrum pesticides, including organophosphates, organochlorines and carbamates, were shown to decrease overall abundance and diversity of soil Mesostigmata (Koehler 1992; Behan-Pelletier 2003; Beck *et al.* 2004). Some species are particularly sensitive, while others are not affected or can even show an increase (Koehler 1992; Karg and Freier 1995). It may take from several months to over a year after the application for species to recover, even when residues of the pesticide are no longer detected. The effect may be direct or may be the result of a decrease in prey sensitive to the pesticide (e.g. nematodes). Narrow-spectrum biological pesticides (*Bacillus thuringiensis* toxins) appear to have little or no effect on soil Mesostigmata (Al-Deeb *et al.* 2003; Beck *et al.* 2004). The application of herbicides does appear to decrease abundance and species richness (Moore *et al.* 1984; Tomlin *et al.* 1995; Minor *et al.* 2004). However, this may be due to the reduction of surface vegetation rather than to direct herbicide toxicity. Selected species of Mesostigmata can also be used to assess the eco-toxicity of chemicals. The common and easily cultured *Gaeolaelaps aculeifer* is a test species in the European guidelines for risk assessment of pesticides (Heckmann *et al.* 2005). Laboratory cultures of the mite are used to determine the effect of common pesticides on adult and juvenile mortality, as well as population growth rates. Ecotoxicological testing standards for agrochemicals are also being developed using phytoseiid mites in Australia (Bernard *et al.* 2004).

Fertilisers have variable effects, depending on the fertiliser type, concentration, and soil characteristics. In general, they indirectly benefit Mesostigmata, probably by enhancing populations of their prey (Koehler 1999; Minor and Norton 2004). The application of fresh manure, composted manure or sewage sludge (with low heavy metal content) stimulate Mesostigmata by favouring populations of several species (Bühlmann 1984; Glockemann and Larink 1989; Minor and Norton 2004). The effect of mineral fertilisers (e.g. urea, calcium nitrate) on Mesostigmata can be minimal (Lagerlöf and Andrén 1988; Minor and Norton 2004) or increase overall abundance (Bird *et al.* 2004). The application of wood ash (used as fertilisers and for reducing soil acidity) has a minor effect on the communities of microarthropods, including Mesostigmata (Liiri *et al.* 2002).

The small-scale diversity of Mesostigmata is influenced by the development of litter and humus layers (Koehler and Born

1989; Karg and Freier 1995). Thus, the retention of stubble (as opposed to burning, or burying during tillage) is likely to favour the generalist predators such as mesostigmatic mites, through a response to the improved microclimate and the increase in prey populations (e.g. Collembola) (Gupta 1994). The same factors could explain the increase of Mesostigmata with the addition of straw mulch (Karg 1983; Tian *et al.* 1997). The use of live clover mulch in vineyards in Italy resulted in much higher abundances of Mesostigmata, compared to bare plots, but grape yields were reduced (Favretto *et al.* 1992). The presence of tree hedges or grass strips in field margins may benefit the populations of Mesostigmata (Buryn and Hartmann 1992) and favour recolonisation of cultivated soils. Intercropping and crop rotations may also affect the abundance of predatory mites compared to monocropping (Tomlin *et al.* 1995), but species-level data on the effect of such practices is lacking.

Grazing intensity (measured as sheep or cattle densities) was observed to have a negative effect on the total abundance of mites in eastern Australia (King and Hutchinson 1976; Holt *et al.* 1996). In Canada, heavy cattle grazing resulted in significantly reduced abundance of most families, compared to light or no grazing (Clapperton *et al.* 2002). However, only minor effects on family abundances were observed in Colorado, USA (Leetham and Milchunas 1985). Ascidae tend to increase with grazing intensity (Clapperton *et al.* 2002; Leetham and Milchunas 1985). Grazing intensity affects litter accumulation, soil organic matter and soil microclimates (Clapperton *et al.* 2002), and thereby affects populations of Mesostigmata.

Mesostigmata may be useful indicators of various pollutants in the soil, including water-soluble toxicants, because of their feeding preferences for prey from several trophic levels, including organisms living in the pore-water systems (nematodes) (Koehler 1996). Mesostigmatic mite communities have been successfully used to evaluate the effect of pollution in Europe. A decrease in total abundance and species richness of Mesostigmata was associated with high nitrogen pollution levels in forest soils (Seniczak *et al.* 1998, 2002). An abundant *Pergamasus* species showed a significant shift towards deeper horizons in polluted sites, while a species of *Rhodacarus* (Fig. 1d) showed tolerance to nitrogen pollution. The abundance of some species (including large litter dwellers) was significantly reduced by the application of sewage sludge contaminated with heavy metals, while the populations of other, especially smaller, opportunistic species were enhanced (Glockemann and Larink 1989; Minor and Norton 2004). Heavy metal pollution in soils also distinctly decreased the abundance and diversity of Mesostigmata in forests (Seniczak *et al.* 2002). Ruf *et al.* (2003) used Mesostigmata and other soil invertebrate groups to evaluate the effect of heavy metal pollution in various forest sites in Europe. They analysed the species composition of polluted sites and compared them with reference, unpolluted sites. They found that the assemblage of Mesostigmata characterised at the species level is a sensitive indicator of pollution; the sites near industrial areas with high concentrations of metals (lead, cadmium and zinc) in soils have assemblages of Mesostigmata that deviate from those of similar but non-polluted sites. Mesostigmata proved to be one of the invertebrate groups most sensitive to this form of pollution. Ruf (1998) also showed a pollution effect on soil Mesostigmata

community using a 'Maturity Index'. The calculation of the index of a site is based on the proportion of species belonging to a family or genus with predominantly 'K-selected' attributes (slow developing and reproducing) and species with mainly 'r-selected' attributes (fast developing and reproducing). Each family or genus is ranked on an r/K scale, according to the life-history traits of known species. The index of a site is compared with values of undisturbed sites with similar humus type. Sites with high levels of heavy metals (lead) in soil were found to have lower index values (occupied by more r-selected and fewer K-selected species), compared to unpolluted, reference sites. The pollution effect on Mesostigmata tended to be correlated with adverse effect on plant communities (herbaceous plants, lichen) (Ruf 1998). The use of life-history traits at the family or genus level compensates for a limited knowledge of traits at the species level. One must be cautious in this approach, however, as biological attributes are rarely predictable above the generic level (Walter and Ikonen 1989).

Mesostigmatic mites can be useful for the study of the impact of forestry practices and restoration management. Clear-cutting, forest floor (litter) removal, heavy soil compaction, and bedding treatment can temporarily reduce densities of soil Mesostigmata compared to control plots (Battigelli *et al.* 2004; Bird *et al.* 2004). Many species of free-living Mesostigmata, as well as many symbionts of wood-inhabiting arthropods, are mainly or exclusively found in decaying logs in Australian forests (Table 3; Seeman 2001; Beaulieu 2005). This suggests that the rarity of mature timber in intensively managed forests, and the removal of dead trees in salvage logging, may put such species at risk (Grove 2002). Fire management practices have an effect on soil Mesostigmata, with frequent (annual) fires characterised by an impoverished fauna (Athias-Binche 1989; Dress and Boerner 2004). However, as for other forestry practices, species-level data is largely lacking.

In Canada, St. John *et al.* (2002) studied the rehabilitation of copper and nickel mine tailings. They found that Mesostigmata, Oribatida and Prostigmata are good indicators of rehabilitation parameters (development of vegetative cover and soil organic matter), although assemblage structure is still altered and the mine tailings have not fully restored their original mite fauna, even after 40 years (St. John *et al.* 2002). Cuccovia and Kinnear (1999) made similar observations on oribatid mites in rehabilitated bauxite mine pits in Western Australia. The inclusion of Mesostigmata and other microarthropod groups in the study of rehabilitation of rainforests (Nakamura *et al.* 2003) or mine sites in Australia would likely contribute to the improvement of restoration techniques.

Conclusions

Mesostigmata is one of the least known invertebrate groups in the world, especially in tropical and subtropical areas, including Australia (Halliday *et al.* 2000). Their small size, cryptic habits and their high and unknown diversity may be the three main factors that prevent people working on them (Walter and Proctor 1998b). The lack of funding for an area where model organisms are rare is also an additional impediment. The work of several taxonomists in Australia (e.g. Womersley 1954; Lee 1970; Schicha 1987; Walter and Beard 1997; Halliday 2000b) has shown that Mesostigmata is a group for which the taxonomy can

be determined and be particularly useful (e.g. James 2001; Steiner and Goodwin 2001). The potential applied use of soil Mesostigmata is not as obvious as Mesostigmata associated with plants and their pests (Phytoseiidae). This is, in part, because the science of biological indication is still particularly young and there is a lack of studies that have focussed on using soil mites as bioindicators and biocontrol agents.

The integration of phytoseiids in biological control programs in Australia has been especially successful where the reliance upon broad-spectrum pesticides has been diminished, such as in vineyards and citrus groves. Native and naturalised phytoseiid species that can persist all year round are likely to be important for endemic control of invertebrate pests, whereas introduced phytoseiids (*P. persimilis*, *G. occidentalis*) are more likely to be important for augmentative releases when pest pressures are high. Non-phytoseiid Mesostigmata may also play an important role in the control of invertebrate pests in Australian agriculture, particularly as assemblages of generalist predators, although a lack of studies makes it difficult to determine their direct role. The incorporation of Mesostigmata into IPM programs, based on use of less harmful (or 'soft') pesticides as well as habitat manipulation aimed at the conservation of Mesostigmata, may provide a cost effective and more environmentally friendly approach to the control of pest species.

Free-living Mesostigmata are major components of soil faunas and represent the most important predatory microarthropods in most soil types. Their high densities, ecological and taxonomic diversity, and their ecological functions as consumers of a range of soil invertebrates make them potentially valuable bioindicators. The status of soil Mesostigmata (composition, diversity) in a given site may be a reflection of the abundance and diversity of their prey, of habitat quality (e.g. soil porosity, soil fertility, humus development), and of the impact of pesticides and other pollutants. Recent studies in eastern Australia (Beaulieu 2005) and in Europe (Ruf *et al.* 2003) suggest that, with increased knowledge, Mesostigmata could be incorporated into multi-taxon studies on the environmental impact of agricultural practices and other land uses. Their use as bioindicators in Australia, however, will be limited until more baseline research is conducted on the taxonomy, abundance and diversity as well as correlations between soil quality, land use and species occurrences.

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Appendix 1. Sampling and sorting Mesostigmata

The collection of mites almost invariably involves the collection of habitat samples (Krantz and Walter, in press). For plant inhabitants, leaves or stems should be sampled and scanned under a stereomicroscope. Faster methods like leaf washing and leaf brushing can be used but should be followed by direct observation under microscope to check for mites lodged in cavities such as domatia. For soil mites, soil and litter samples are taken. Litter samples can be based on area (e.g. 20 × 20 cm) or volume (e.g. 0.5–1 L samples). Soil samples are usually obtained using cores of variable diameter and depth (2–10 cm diameter × 5–30 cm deep), depending on the soil type and the collector's preference. Core samples can be separated in two or more vertical layers. Samples are put in plastic or cloth bags and brought into the laboratory for specimen extraction. For the appropriate assessment of a community at the species level, it is necessary to take several samples (e.g. 6–12 samples per site) for each sampling date. Moreover, large samples (e.g. 1 L of leaf litter or 0.5 L of soil) are useful in that they may optimise the use of multivariate analyses.

Soil and litter mesostigmatic, oribatid and many prostigmatic mites are most easily extracted using the Berlese–Tullgren funnel or its various modifications (Krantz and Walter, in press). This method is based on a humidity gradient, which forces mites to escape the drying substrate down the funnel into a receptacle. The latter can contain a killing and preservative agent (usually 75% alcohol) or a charcoal-plaster mix that retains moisture for live extraction (Koehler 1999). Mesostigmatans are usually extracted efficiently from plant litter; soil extraction is not as satisfactory and only a portion of individuals may be extracted (see André *et al.* 2002). Fine soils, sandy soils and soils in semiarid areas may necessitate special extraction methods (e.g. infrared extraction, flotation methods), especially if one wants to extract soft-bodied mites such as juveniles of Mesostigmata and many adults of Prostigmata (Krantz 1978; André *et al.* 2002; Kinnear and Tongway 2004).

Mesostigmata specimens are usually cleared with lactic acid or Nesbitt's fluid and mounted on slides using Hoyer's medium for semipermanent preparation. More permanent mounting can be done, but requires more time and effort. The identification of family, genera and species are done using a compound microscope, preferably with phase contrast or differential-interference contrast systems, under 200–1000× magnification. Walter and Proctor (1998b) measured the time required for slide-mounting and identifying Mesostigmata (mainly phytoseiids) collected from leaf samples. It takes ~150 h to process ~600 specimens, representing 76 named and undescribed species. This represents 15 min per specimen. Although this would take substantially more time for an inexperienced worker, the processing time decreases significantly with an increase in samples and specimen numbers from a given site; once the most common species of a local fauna are recognised, it may not even be necessary to slide-mount specimens, as some can be identified directly under a stereomicroscope. Mesostigmatic mites are characterised by a broad range of morphological characters, many of which vary among taxa. Body size, the position, numbers and shape of setae ('hairs') of shields and appendages, the texture of ventral and dorsal shields, cheliceral teeth, and the shape of primary and secondary sexual characters can be useful characters to sort specimens into species-level taxa or 'recognisable taxonomic units' (morphospecies). Some publications are excellent for the sorting of families and the learning of morphological characters (e.g. Walter 2001). Despite their small size, given similar infrastructure (i.e. identification tools, appropriate microscopes) and taxonomic experience, mesostigmatic mites can be as easy to identify and may not require substantially more time for specimen preparation than common, diverse insect groups such as flies, beetles or ants.
