

# PREDATION IN SUSPENDED AND FOREST FLOOR SOILS: OBSERVATIONS ON AUSTRALIAN MESOSTIGMATIC MITES

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**SUMMARY:** This paper reviews the feeding habit of mesostigmatic mites from soil and litter of Australian forests. It reports on the feeding habit of 69 species-level taxa (39 newly observed; 30 from the literature) belonging to 36 genera and 16 families of Mesostigmata. Feeding observations were made in small laboratory arenas where mites were offered sympatric arthropods or cultured rhabditid nematodes, springtails and mites. Most species tested readily fed on nematodes and springtails and many attacked the nymphs of mesostigmatic mites. A few fed on the fluids of crushed or decomposing arthropods. As indicated by studies on other continents, our results support the hypothesis that many soil Mesostigmata, including both ground and canopy species, are generalist predators that feed on nematodes and a variety of arthropod prey. These findings also suggest that some Mesostigmata are opportunistic scavengers.

ACARI, MESOSTIGMATA,  
COMPORTEMENT ALIMENTAIRE,  
PRÉDATEURS GÉNÉRALISTES,  
CHAROGNARDS, NEMATODES,  
COLLEMBOLA

**RÉSUMÉ** Cet article fait la revue des connaissances sur le comportement alimentaire des acariens mésostigmatés habitant le sol et la litière des forêts australiennes. Des données sur la diète de 69 taxons identifiés au niveau de l'espèce (39 nouvelles observations et 30 provenant de la littérature) appartenant à 36 genres et 16 familles de Mesostigmata sont présentées. Les acariens ont été observés en laboratoire dans de petites arènes où ils ont été mis en présence de proies, soit des arthropodes provenant du même milieu édaphique, soit des nématodes (rhabditides), collembolés ou acariens provenant d'élevages en laboratoire. La majorité des espèces étudiées se sont nourrit de nématodes et de collembolés et plusieurs ont aussi attaqué les nymphes d'autres acariens mésostigmatés. Quelques-uns ont ingurgité les fluides corporels d'arthropodes écrasés ou partiellement décomposés. Tels que des études effectuées sur d'autres continents, nos résultats sont en accord avec l'hypothèse que de nombreux mésostigmatés des sols, incluant des espèces habitant le sol forestier ainsi que des espèces en milieu arboricole, sont des prédateurs généralistes se nourrissant de nématodes et d'une variété d'arthropodes. Ces résultats suggèrent aussi que certains mésostigmatés sont des charognards opportunistes.

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## INTRODUCTION

Mesostigmatic or gamasid mites (Acari: Parasitiformes: Mesostigmata) are among the most numerically abundant and species-rich arthropod predators in soils (PETERSON, 1982; WALTER *et al.*, 1988). Their significance in detrital food webs is substantial (MOORE *et al.*, 1988) and some soil mesostigmatans have shown high potential for the biological control of crop pests (LESNA *et al.*, 1995; WIETHOFF *et al.*, 2004). However, the feeding behavior of only a few species of soil-inhabiting Mesostigmata have been studied, mostly in Western North America and Europe, and many of our inferences about their trophic functions come from their better known plant-inhabiting relatives.

Unlike soil systems, where several to many families of predatory Mesostigmata commonly coexist, vegetation is dominated by members of a single family, the Phytoseiidae. Most phytoseiid mites feed on a diverse range of mite and insect prey, as well as plant material, especially pollen and honeydew, with little indication of specialization on particular prey types. Only a few phytoseiids are known to be specialists: some show a preference for various spider mites (Tetranychidae), although they will accept other mites and pollen, and a few species specialize on spider mites that form dense webbing (mostly species of *Tetranychus*) (MCMURTRY & CROFT, 1997; GERSON *et al.*, 2003). In tropical regions, two non-phytoseiid genera (*Asca*: Ascidae; *Lasioseius*: Blattisociidae) complement the generalist predator fauna on vegetation, but the other arboreal mesostigmatans that have been studied live in flowers and feed mainly on pollen and nectar (SEEMAN & WALTER, 1995; NASKRECKI & COLWELL, 1998).

For mesostigmatans, the soil habitat is strikingly different from vegetation in at least four aspects: the scarcity of alternative plant foods such as pollen, nectar, and honeydew; the high family, genus and species diversity of Mesostigmata present in soils; the range of available invertebrate prey types; and the ecological partitioning of these prey types into two functional groups based on soil moisture: those dependent on water-films for most movement and feeding (nematodes and other small worms) and air-space inhabitants (arthropods). Mesostigmatans are

generally air-space inhabitants, but are able to use their mouthparts to capture prey in water films (WALTER & PROCTOR 1999). Research in North American grassland soils demonstrated that many soil mesostigmatans feed on worm-like prey (nematodes, small oligochaetes) that are generally absent from vegetation. Additionally, most of these species will take lightly sclerotized arthropods (e.g. mites, springtails, other insect eggs or juveniles), and rarely fungal hyphae and spores (WALTER, 1988; WALTER *et al.*, 1988; WALTER & IKONEN, 1989; WALTER & LINDQUIST, 1989). The few 'specialists' encountered took only a single general type of prey, nematodes or arthropods, but fed on a variety of species within each type. Similarly, in seashore habitats, some mesostigmatans are reported to feed mainly on nematodes and copepods that they pluck out of water films (AVDONIN & STRIGANOVA, 2004). A few may consume principally fungal spores and hyphae or other microbes associated with decaying plant matter, although it is likely that most of them also include nematodes and/or soft-bodied arthropods in their diet (ATHIAS-BINCHE, 1981; OCONNOR, 1984; NAWAR *et al.*, 1993).

The importance of assemblages of generalist predators in biological control is unclear, but as has been shown for other generalist predator assemblages (SYMONDSON *et al.*, 2002), mesostigmatic mite communities are likely to exert a significant impact on crop pests that spend some time in soil or litter. Australia has a wealth of Mesostigmata (HALLIDAY, 1998; BEAULIEU, 2005), but most species are undescribed and their life histories are unknown. This paper compiles feeding data on 67 species-level taxa (36 newly observed; 31 from the literature) belonging to 33 genera and 16 families of Mesostigmata collected from Australian forest soil-litter and other detritus-based habitats, including from the canopy, based mainly on qualitative laboratory observations. We use these data to address the hypothesis that soil Mesostigmata tend to be prey generalists and opportunistic scavengers.

## MATERIALS AND METHODS

Collections. Specimens for newly observed species were collected between November 2002 and October 2004 from four sites in subtropical montane rainfo-

rests and wet sclerophyll forests (tall open forests) in Lamington National Park (28°14'S, 153°09'E) and Brisbane Forest Park (27°18'S 152°45'E), Southeast Queensland, Australia. Species studied by the junior author in previous publications were mainly obtained from subtropical and tropical rainforests in Southeast Queensland and Far North Queensland, and secondarily from open forest and urban sites in Southeast Queensland. Habitats sampled include soil and surface litter, suspended soil, decaying fungal sporocarps and rotting wood. Suspended soil was sampled from tree hollows or from inside the crown of epiphytic ferns (*Asplenium australasicum* (J. Smith) Hook) attached to tree trunks at various heights (2-16 m). Studies by other authors were based on collections from soil-litter in open forest (Mount Lofty, Southern Australia; LEE, 1974) and rainforest (New South Wales and Far North Queensland; HALLIDAY, 1990, 1993), or decaying wood in rainforest (Lamington; SEEMAN, 2000). Feeding observations from mites collected from compost, dung, or disturbed habitats (e.g., agricultural fields) or made overseas (even if the species occur in Australia; e.g., *Arctoseius cetratus* (Sellnick)) were excluded from the study. In the laboratory, the samples were placed in standard Berlese-Tullgren funnels over containers with floors made of moistened plaster of Paris and powdered, activated charcoal (7:1 by volume, respectively). As samples dried under the funnel lights, arthropods left the soil and tumbled into the containers. Some predator-prey observations were obtained as the extracted arthropods interacted.

Laboratory feeding tests. Mites were sorted roughly into morphospecies using a fine camel hairbrush and observed individually in small vials of 5 cm deep × 1.1 cm diameter, or as a group of one or more species in 4 cm high × 5.5 cm diameter containers with moistened charcoal-plaster floors. Large containers were closed with a screw plastic lid and vials were sealed with parafilm ventilated with a minuten pin. Containers were kept in incubators at 25° C and observations were made at room temperature (20-30° C). Most feeding tests used cultures of bacterivorous nematodes (Nematoda: Rhabditida, mainly *Panagrellus silusiae* (de Man) and secondarily *Rhabditis* sp.), a springtail (Collembola: Isotomidae, *Folsomia candida* Willem), and a mesostigmatic mite

(Acari: Mesostigmata, *Gamasellodes adriannae* Walter). Arthropod prey were usually offered in large numbers (>20 in the large containers) to accelerate contact. The eggs of the grain moth (Lepidoptera: Gelechiidae, *Sitotroga* sp.) and crushed arthropods were sometimes offered. Observations were made under a stereomicroscope using fiber optic illumination. Tests were mainly made within 24h after extraction, although some species were kept longer to establish cultures or to determine feeding rates.

After feeding tests, mites were cleared in Nesbitt's solution, mounted in Heinze PVA or Hoyer's medium on glass slides, identified to family, genus, and species or morphospecies under a differential-interference contrast microscope. Voucher specimens are deposited in the University of Queensland Insect Collection, School of Integrative Biology, St Lucia, Queensland 4072, Australia. The morphospecies codes presented in the results are, with a few exceptions (*Cheiroseius*, *Iphidozercon*, *Zerconopsis*, *Sejus*), the same as those used in BEAULIEU (2005) and habitat distribution of species were determined using the same source (BEAULIEU, 2005) and other published (sources indicated in the table) or unpublished data from other surveys in South East Queensland. Authorship for named species is indicated in TABLE 1.

## RESULTS

TABLE 1 summarizes feeding observations that were made on Australian free-living Mesostigmata inhabiting forest soil and litter. We provide information on the habitat and the degree of feeding that was noted on nematodes, Collembola, small mites and crushed arthropods. Cohorts, families and genera are ordered alphabetically.

— Ascidae & Blattisociidae: Two species associated with suspended soil, *Arrhenoseius gloriosus* and *Gamasellodes adriannae*, are voracious predators of nematodes. Both have been reared successfully on nematodes alone (WALTER & LINDQUIST, 2000; WALTER, 2003b; TABLE 1). An adult of *A. gloriosus* was seen carrying a dead mesostigmatan nymph in its chelicerae, but no feeding was noted (TABLE 1). *Asca garmani*, *A. aphidioides*, *Lasioseius boomsmai* and *L. queenslandicus* and undescribed species of *Cheiro-*

Taxa	Habitat <sup>b</sup>	Nematodes	Collembola	Small mites	Dead arthropods	Others	Source
<b>Gamasina</b>							
<b>Ascidae</b>							
<i>Asca aphidioides</i> (L.)	O	++					
<i>Asca garmani</i> Hurlbutt	CAN, RF, O, F	++					
<i>Gamasellodes adriannae</i> Walter	CAN, O	++		+			Walter, 2003b
<i>Iphidozercon</i> n. sp.	FG	++					Walter & Lindquist, 1995
<i>Zerconopsis</i> sp.	FG	++					Walter & Lindquist, 1995
<b>Blattisociidae</b>							
<i>Arrhenoseius gloriosus</i> Walter & Lindquist	CAN	++		(+)			Walter & Lindquist, 2000
<i>Cheiroseius</i> sp.	TH	++					
<i>Lasioseius boomsmai</i> Womersley	FG, RF, O	++	++	++			Walter & Lindquist, 1997
<i>Lasioseius queenslandicus</i> (Womersley)	FG, RF	++	++	++			Walter & Lindquist, 1995
<b>Laelapidae</b>							
<i>Cosmolaelaps</i> sp. nr <i>multisetosus</i> Domrow	CAN, RF	++	++		+		
<i>Androlaelaps laertes</i> (Domrow)	CAN, LG	(+)		++		blood	M. Shaw pers. comm., 2005
<i>Stratiolaelaps lamington</i> Walter & Campbell	CAN, TH	++	++				Walter & Campbell, 2002
<i>Stratiolaelaps lorna</i> Walter & Campbell	TH	++					Walter & Campbell, 2002
<i>Stratiolaelaps scimitus</i> Womersley	RF	++				thrips	Walter & Campbell, 2002; I. Vänninen, pers. comm.
<b>Leptolaelapidae</b>							
<i>Hunteracarus</i> sp.	RF				+		
Leptolaelapidae sp. 1	RF	++			++		
<b>Macrochelidae</b>							
<i>Macrocheles faveolus</i> Halliday	RF					fly eggs	Halliday, 1993
<i>Macrocheles novaezelandicae</i> Emberson	CAN, RF, D	+	+			fly eggs	Halliday, 1990
<i>Macrocheles spiculata</i> Halliday	CAN	++		+			
<b>Ologamasidae</b>							
<i>Acugamasus semipunctatus</i> (Womersley)	O				+		Lee, 1974
<i>Acugamasus</i> n. sp. 4	CAN, RF, O		(+)	(+)			
<i>Antennolaelaps</i> n. sp. 2	CAN, RF	+	++	+		thrips	
<i>Antennolaelaps</i> n. sp. 4	RF			(+)			
<i>Athiasella dentata</i> (Womersley)	O	+	++	++	+	organic matter	Lee, 1974
<i>Athiasella</i> n. sp. 3	RF	++	++	+			
<i>Athiasella</i> n. sp. 7	CAN	+					
<i>Athiasella</i> n. sp. 12	RF, O			+			
<i>Athiasella</i> n. sp. 18	RF	++	++	++	+		
<i>Caliphis novaezelandiae</i> Womersley	RF	+	+				
<i>Caliphis queenslandicus</i> Womersley	CAN, O, RF	++	++	+	+		
<i>Caliphis</i> n. sp. nr <i>queenslandicus</i>	RF	++	+	+			
<i>Euepicrius filamentosus</i> Womersley	O		++	++	+		Lee, 1974

<i>Euepicrius</i> n. sp. 2	CAN, RF		+				
<i>Euepicrius</i> n. sp. 3	CAN, RF					+	
<i>Euepicrius</i> n. sp. 10	O	++					
<i>Gamasellus concinnus</i> (Womersley)	O		++	++			yeast Lee, 1974
<i>Gamasellus tragardhi</i> (Womersley)	O		+	++	+		yeast, organic matter Lee, 1974
<i>Gamasellus</i> n. sp. nr <i>discutatus</i> (Lee)	RF	++	++				
N. gen. nr <i>Gamasellus</i> sp.	RF	++	+	+			
<i>Gamasiphis fornicatus</i> Lee	O				++		Lee, 1974
<i>Gamasiphis</i> n. sp. nr <i>fornicatus</i>	RF, O	++	+	+			
<i>Gamasiphis saccus</i> Lee	O					+	Lee, 1974
<i>Gamasiphis</i> nr <i>australicus</i> Womersley n. sp. 1	RF	+	+				
<i>Gamasiphis</i> nr <i>australicus</i> Womersley n. sp. 5	RF	++	+				
<i>Gamasiphis</i> nr <i>australicus</i> Womersley n. sp. 6	RF	+			(+)		
<i>Gamasiphis</i> nr <i>australicus</i> Womersley n. sp. 10	RF		+				
<i>Gamasiphis</i> nr <i>australicus</i> Womersley n. sp.	RF		+				
<i>Gamasiphoides propinquus</i> (Womersley)	O					++	Lee, 1974
<i>Gamasiphoides</i> n. sp. 1	RF, wO		+				
<i>Gamasiphoides</i> n. sp. 2	RF		+				
<i>Geogamasus howardi</i> Lee	O		+				Lee, 1974
<i>Geogamasus minimus</i> Lee	O		+				Lee, 1974
<i>Geogamasus</i> n. sp. 3	RF	++	+				
<i>Laelaptiella anomala</i> Womersley	CAN, RF, O	+	+	+			
<i>Queenslandolaelaps</i> n. sp. 1	RF, wO	+					
Ologamasidae sp. 1	RF	+	++			+	
Podocinidae							
<i>Podocinum</i> sp. 1	O	+					
Microgyniina							
Nothogyniidae							
<i>Nothogynus klompeni</i> Walter & Krantz	TH, LG, RF	++					Walter & Krantz 1999
Sejina							
Sejidae							
<i>Epicroseius</i> n. sp. A	FG	++	+	+			Walter & Proctor, 1998
<i>Sejus</i> n. sp. A	CAN	+		(+)			
Trigynaspida							
Asternoseiidae							
N. gen. nr <i>Asternoseius</i> sp.	CAN, RF, O	++	++	++			enchytraeids Walter & Proctor, 1998
Davacaridae							
<i>Acanthodavacarus klompeni</i> Walter	CAN, RF	[+]					Walter, 2003a
Fedrizziidae							
<i>Fedrizzia grossipes</i> Canestrini	LG	++					Seeman, 2000
<i>Neofedrizzia camini</i> Womersley	LG	++				++	Seeman, 2000
Saltiseiidae							
<i>Saltiseius hunteri</i> Walter	LG, TH	++					Walter, 2000
Triplogyniidae							
<i>Funkotriplogynium iagobadius</i> Seeman & Walter	FG, LG, RF	++	++	++			maggots Seeman & Walter, 1997

Uropodina				
Polyaspididae				
<i>Polyaspis</i> sp. 1	RF	++	++	Walter & Proctor 1998
Unplaced				
Heatherellidae				
<i>Heatherella callimauros</i> Walter	RF	++		Walter, 1997
<i>Heatherella acanthocharis</i> Walter	RF	++		Walter, 1997

<sup>a</sup> + feeding observed at least once; ++ feeding observed repeatedly (on at least 4 individuals); (+) feeding not observed, but prey has been observed held by the mite's chelicerae; [ + ] feeding inferred from reproduction on food; blank: feeding not observed or have not been tested; symbols in bold ( + or ++ ) indicate that a culture was established for at least two generations.

<sup>b</sup>CAN, suspended soil in rainforest canopy; D, dung; F, foliage from rainforest tree; O, open forest floor; wO, floor of 'wet' open forest; RF, rainforest floor; LG: decaying logs; TH, rotting tree hollows.

TABLE 1. Degree of feeding of Mesostigmata on nematode and arthropod prey in laboratory arenas<sup>a</sup>. Species with no source indicated represent new observations.

*seius* (1 species), *Iphidozercon* (1 species) and *Zerconopsis* (1 species) were also reared on nematodes (WALTER & LINDQUIST, 1995, 1997; HALLIDAY *et al.*, 1998; TABLE 1). All *Lasioseius* species that have been observed in culture in Queensland also attacked small springtails and mites.

— Laelapidae: Two species in the genus *Stratiolaelaps* (*S. lorna* and *S. scimitus*) have been cultured on nematodes and one also fed on thrips pupae (WALTER & CAMPBELL, 2003; I. VÄNNINEN, AgriFood Research Finland, pers. comm.; TABLE 1). The rainforest canopy soil specialist *Stratiolaelaps lamington* also fed on nematodes, and readily attacked springtails and developed from eggs to adults on this food source alone (TABLE 1). Adults and nymphs of *Cosmolaelaps* sp. nr *multisetosus*, also fed on nematodes and springtails. One adult was observed feeding on the haemolymph of a crushed caterpillar of *Helicoverpa armigera* (Hübner) (TABLE 1). *Androlaelaps laertes* voraciously consumed mesostigmatic mites, including adults of *Stratiolaelaps* sp. (M. SHAW, University of Queensland, pers. comm.; TABLE 1). An adult was also observed picking at a nematode but there was no evidence of feeding. This mite is also associated with bush rats and feeds readily on blood in laboratory conditions (M. SHAW, pers. comm.). Its presence in suspended soil and decaying logs is in concordance with its association with small mammals.

— Ologamasidae: Ologamasid mites are one of the two dominant mesostigmatan families in Australian forest soils (BEAULIEU, 2005). Nematodes were attacked by virtually all species tested, most of which appear to be aggressive nematophages, recognizing nematodes as prey and often seizing them immediately upon contact. The rather small *Laelaptiella anomala* (408  $\mu$ m), however, did not feed on nematodes as readily, and over 10 minutes elapsed before the mite seized one and started feeding. Three other individuals of this species did not attack the nematodes during the 10 minute observation period. We attempted to rear *Athiasella* n. sp. 3 and sp. 18 on nematodes but they did not lay eggs.

Ologamasids also readily fed on collembolans. Larger species of ologamasids (*Antennolaelaps* n. sp. 2, *Gamasellus* n. sp., Ologamasidae sp. 1) (850-900  $\mu$ m) were particularly voracious towards the springtail *F. candida* and they were very efficient at pursuing and grabbing a prey in the container. Feeding rates have been estimated for two species of *Athiasella* (sp. 3 and sp. 18), through a period of 5-6 days, and  $1.4 \pm 0.4$  ( $n = 5$ ) and  $1.2 \pm 0.15$  ( $n = 4$ ) immature springtails were consumed per day, respectively. Although these two species are intermediate in body size (500-640  $\mu$ m), they were aggressive towards springtails and were observed ( $n = 1$  and  $n = 2$ , respectively) grabbing another prey while still holding a partially consumed springtail by the chelicerae.

Ologamasids (10 species in total) usually accepted the small, lightly sclerotized, and slow moving adults and juveniles of *G. adriannae*. The nymphs of other Mesostigmata were often seen being carried in the chelicerae of several species (*Acugamasus* n. sp. 4, *Athiasella* spp., *Antennolaelaps* n. sp. 2, *Caliphis* spp., *Euepicrius* n. sp. 3, N. gen. nr *Gamasellus* sp., *Gamasiphis* n. sp. 6). *Antennolaelaps* n. sp. 2 was one of the swiftest ologamasids studied. It was seen running with a variety of Mesostigmata (*Acugamasus*, *Athiasella*, *Dendrolaelaspis*, *Hunteracarus*) in its chelicerae, as well as the adult of a thrips. Eggs of a moth that were preserved in the freezer were offered to some species and indirect observations (shrivelled eggs) suggested feeding by *Athiasella* and *Gamasiphis* spp. The exposed haemolymph from crushed caterpillars, oribatid mites, maggots or springtails was fed upon by *Athiasella* n. sp. 18 ( $n = 3$ ) and *Caliphis queenslandicus* ( $n = 2$ ).

LEE (1974) studied in the laboratory ten species of ologamasids belonging to seven genera (*Acugamasus*, *Athiasella*, *Euepicrius*, *Gamasellus*, *Gamasiphis*, *Gamasiphoides*, *Geogamasus*; TABLE 1) collected from soil and litter of temperate open (eucalypt) forest. All were observed at least once feeding on juveniles of other mites, especially *Tyrophagus putrescentiae* (Schrank) but also of mesostigmatic mites and oribatid mite in one case (*Athiasella dentata*). *Athiasella dentata* was also reported feeding on the adult stage of the small *Geogamasus howardi* and to cannibalize its own eggs and larvae. Three species, *A. dentata*, *Gamasellus concinnus* and *G. tragardi*, consumed eggs of *T. putrescentiae*. Only one species fed on nematodes (*A. dentata*) and three fed on various Collembola species. However, Lee did not indicate if nematodes and springtails were offered to the other species. Three species were observed consuming yeast globules from the surface of currant fruits and two on moist organic matter. Three species were also seen feeding on decomposing mites or springtail juveniles (TABLE 1).

Nearly all Ologamasidae studied were cruise or pursuit predators. *Euepicrius* spp. are relatively fast moving predators. *Euepicrius* n. sp. 3 was observed doing a nearly 180° turn in a fraction of a second when approached from behind. Their long forelegs appear to be used for mechanical contact detection of

prey and also to ensnare the prey and push it towards the mouthparts. The larger ologamasid species are generally the fastest (especially *Antennolaelaps* n. sp. 2, Ologamasidae sp. 1) and the smaller ones were relatively slow. LEE (1974) noted that some ologamasids (*A. dentata*, *G. concinnus*) rapidly charged collembolan or mite prey. However, one large mite, that appears to represent a new genus near *Gamasellus* (870 µm body length), is an ambush predator. The shields of this mite bear setae with complex, brushy extremities which accumulated a layer of soil particles that may act as protective armour and/or perhaps as camouflage. Attacks by this sluggish predator were surprisingly successful against the fast jumping collembolans.

— Other Gamasina: An undetermined genus of Leptolaelapidae ( $n = 4$ ) and *Hunteracarus* sp. ( $n = 1$ ) scavenged on the haemolymph of a crushed caterpillar for several minutes. When not feeding on the haemolymph, individuals of Leptolaelapidae sp. 1 repeatedly palpated the caterpillar carcass. Three individuals of that species were also observed feeding actively on nematodes. *Macrocheles spiculata* is a suspended soil specialist; it fed readily on nematodes ( $n = 5$ ), and also on immature Mesostigmata ( $n = 1$ ). *Macrocheles novaezelandiae* is associated with suspended and ground litter in rainforest, as well as wallaby and cattle dung and was observed feeding on nematodes and collembolans. HALLIDAY (1990) reared the species on a substrate of cow dung and a diet of eggs and larvae of the bushfly, *Musca vetustissima* Walker. He also reared *M. faveolus* on the same diet (HALLIDAY, 1993). Two individuals of *Podocinum* sp. 1 fed on nematodes.

— Microgyniina: Nothogyniidae are early derivative mesostigmatans associated with tree holes and rotting logs (WALTER & KRANTZ, 1999). One of the two known species, *Nothogynus klompeni*, was observed feeding repeatedly on nematodes (WALTER, 2001).

— Sejina-Uropodina: An undescribed species of *Sejus* confined to suspended soil in rainforest canopy was observed feeding vigorously on nematodes ( $n = 2$ ) and seizing springtails in their chelicerae ( $n = 3$ ), although no feeding on the latter was observed. Another sejid, *Epicroseius* n. sp. A, collected from a fungal sporocarp, was reared on a diet of nematodes, but

also fed on small mites and springtails (WALTER & PROCTOR, 1998). Collembolans were attacked and consumed by the uropodine *Polyaspis* sp. 1 (WALTER & PROCTOR, 1998).

— Trigynaspida: Members of the Trigynaspida are among the most plesiotypic of mesostigmatans and their feeding behaviour is of special interest for understanding the evolution of feeding strategies in the Mesostigmata (WALTER & PROCTOR, 1999). A species of an undescribed genus near *Asternoseius* was observed feeding aggressively on enchytraeids, nematodes as well as soft-bodied arthropods, including springtails and small mites (WALTER & PROCTOR, 1998; TABLE 1). *Acanthodavacarus klompeni*, a common inhabitant of rainforest suspended soil and forest floor litter, was cultured through several generations with only nematodes provided as prey; however, we were not able to determine if they fed on live nematodes or on their rotting bodies and microbial decomposers (WALTER, 2003b). The jumping mite *Saltiseius hunteri* and the passalid beetle associates *Neofedrizzia camini* and *Fedrizzia grossipes* are primarily associated with decaying logs. The three species fed readily on nematodes (SEEMAN, 2000; WALTER, 2000). *Neofedrizzia camini* went through several generations on a nematode diet and was also observed feeding on the haemolymph of dead conspecifics in cultures and on crushed maggots (SEEMAN, 2000). The triplogyniid *Funkotriplogynium iagobadius* preyed aggressively on nematodes, springtails, mites (astigmatans and immature Mesostigmata), and small and large maggots. It was cultured mainly on nematodes (SEEMAN & WALTER, 1997).

— Other Mesostigmata: The family Heatherellidae was proposed to accommodate the species *Heatherella acanthocharis* and *H. callimaulos*, for which the phylogenetic relationships are unclear (WALTER, 1997). Both species attacked and consumed nematodes in the laboratory.

#### DISCUSSION

External digestion and imbibing of digested fluids or blood (fluid-feeding) is the dominant method of feeding in three orders of Parasitiformes (Holothyrida, Ixodida, and Mesostigmata). Ticks (Ixodida) are well known obligate hematophages. Holothyrida

is the least studied of these orders, but Australian representatives are known to scavenge on dead animal tissues (WALTER & PROCTOR, 1998). Within the largest parasitiform order, Mesostigmata, some lineages are known to feed on fungi or pollen and nectar (KRANTZ & LINDQUIST, 1979; OCONNOR, 1984; SEEMAN & WALTER, 1995; NASKRECKI & COLWELL, 1998), others are vertebrate hematophages (RADOVSKY, 1994), and others are parasites or symbionts of arthropods with unknown feeding habits (HUNTER & ROSARIO, 1988). Active predation, however, is the predominant life-style among the Mesostigmata that have been studied both within Australia and overseas (KRANTZ, 1978; KARG, 1983; WALTER & PROCTOR, 1998; this study).

The present results corroborate prior observations that nematodes represent a widely accepted food by mesostigmatic mites (MURAOKA & ISHIBASHI, 1976; KARG, 1983; WALTER, 1988). Nematodes may be consumed by a variety of mites traditionally viewed as fungivorous or detritivorous (many Oribatida (including Astigmata) and Prostigmata), and also by springtails, symphylans and earthworms (MURAOKA & ISHIBASHI, 1976; WALTER, 1988; WALTER & IKONEN, 1989). Nematodes appear as a nutritionally superior food source, resulting in faster development and better reproductive output than microarthropod prey in several Mesostigmata (WALTER *et al.*, 1987). The extremely high densities of nematodes observed in soil and litter layers (BONGERS & BONGERS, 1998) combined with the avidity with which most mites attacked nematodes in containers leaves little doubt that they constitute a natural prey for them. The same can be said for Collembola, which are ubiquitous, locally abundant soil-dwellers and are commonly recognized prey for mesostigmatic mites and predaceous Prostigmata (KARG, 1961; SARDAR & MURPHY, 1987; WALTER, 1988; WALTER & KAPLAN, 1991). LEE (1974) classified *Gamasiphis* (2 spp.), *Gamasiphoides* (1 sp.) and *Geogamasus* (2 spp.) as non-collembolan feeders. Our study indicates that species in these genera may feed readily on springtails.

Our study supports previous findings (WALTER, 1988) that most soil Mesostigmata are generalist predators, feeding on worm-like invertebrates and soft-bodied arthropods. Virtually all species tested responded positively to the prey offered, including

species living in suspended soil (22 species, including seven largely restricted to litter in epiphytes and/or tree holes). Nevertheless, the diet of a generalist predator must still have limits and will be restricted by prey vulnerability (a function of body size, speed, cuticle thickness, etc.), spatial/temporal distribution, and defence mechanisms, including behavioural and physiological aspects (WALTER *et al.*, 1988; WALTER & KAPLAN, 1991; TOFT & WISE, 1999; SYMONDSON *et al.*, 2002). In our study, large springtails were successfully attacked only by the large, rapid mites (e.g., laelapids, a few large ologamasids). Adults of oribatid and mesostigmatic mites are usually well sclerotized and are avoided by nearly all but the most aggressive mesostigmatans (KARG, 1961; PESCHEL *et al.* in press). In this study, small, lightly sclerotized adults of *Gamasellodes* and *Geogamasus* were preyed upon by various Mesostigmata; but the adult of larger species was only attacked and consumed by the large laelapid *Androlaelaps laertes*. Such voraciousness towards adult mesostigmatic mites is also observed in other Laelapidae (e.g., *Geolaelaps aculeifer* (Canestrini); F.B., unpublished data) and large Parasitidae (HARTENSTEIN, 1962). Compared to most other groups of soil microarthropods, the adults of strongly sclerotized oribatids appear to be relatively difficult to kill for Mesostigmata (PESCHEL *et al.* in press). The eggs of mites and insects are also seldom reported as food for soil-dwelling Mesostigmata, presumably because of the thick, protective cuticle that is often present, and also immobile prey such as eggs may be unappealing to many predators. However, some species have lightly sclerotized eggs and some laelapids, macrochelids and parasitids do feed on insect eggs (HALLIDAY, 1990, 1993; SARDAR & MURPHY, 1987). Some ologamasids fed on *T. putrescentiae* eggs and cannibalized their own eggs (LEE, 1974). Some Sejidae have been reared on (pre-frozen and therefore softened) moth eggs (D.E.W., unpublished data) and we have weak evidence that ologamasids may feed on moth eggs (this study).

These observations were obtained in laboratory arenas with sympatric prey extracted from the same samples as the predators or from similar general prey types in culture. As such they provide only a rough indication of the range of organisms that are attacked in the field. For example, preferred prey in the

laboratory may not be the most targeted prey in the field. MCKEMEY *et al.* (2003) found that the carabid beetle *Pterostichus melanarius* (Illiger) preferred small slugs of *Deroceras reticulatum* (Müller) in laboratory conditions, but did not show preference for any size class in field experiments. They attributed these results to the higher accessibility of refugia for smaller slugs in natural conditions. Successfully culturing of mites on a given food, present in the same habitat, can provide a stronger indication that this food is consumed in the field (WALTER *et al.*, 1988; WALTER & KAPLAN, 1991). Microscopic analysis of gut contents, or detection of protein for specific prey using electrophoresis or monoclonal antibodies, or DNA using PCR-techniques from field-collected specimens (e.g., SUNDERLAND *et al.*, 1987; CALDER *et al.*, 2005) can provide more accurate data on the diet of arthropods. However, except for some fungivorous forms which can swallow fungal spores and hyphae, the traditional study of gut contents is of limited use because most Mesostigmata are fluid-feeders. PCR-based approaches screening for multiple prey at once is a promising avenue (HARPER *et al.*, 2005).

Scavenging of dead arthropods has sometimes been observed in Mesostigmata. The adults and immature instars of four species of phytoseiid mites accepted dead mites as food, and the immatures of parasitid mites fed on artificially (freshly) killed mesostigmatans (HARTENSTEIN, 1962; CROFT & CROFT, 1993, 1996). Some uropodine mites fed on freshly dead insects, and others on dead earthworms that have been colonized by fungi (ATHIAS-BINCHE, 1981). Although its actual food is uncertain, the laelapid *Hypoaspis johnieae* Hunter & Glover was found associated with decomposing carcasses of grasshoppers (in a field experiment) and authors suggested it may be feeding on liquids from the rotting arthropods (SEASTEDT *et al.*, 1981). Some beetle associates belonging to Megisthanidae and Euzerconidae have been reported to be predators as well as fungivores and scavengers of small arthropods and eggs (SEEMAN, 2000). Many traditionally considered predators do scavenge to a varying degree. Several wolf spiders readily consumed dead arthropods in the laboratory (KNOST & ROVNER, 1975) and the brown recluse spider, *Loxosceles reclusa* Gertsch & Mulaik, feeds primarily on dead prey (SANDIDGE, 2003). Many carabid

beetles include dead invertebrates in their diet (CALDER *et al.*, 2005). In the present study, most records of necrophagy involved freshly dead arthropods. Predators may react differently to aged carcasses heavily colonized by bacteria or fungi.

Although choice experiments and observations in semi-natural situations would clarify the question, our study suggests that some soil Mesostigmata are opportunistic scavengers of dead invertebrates. It also supports the hypothesis that many soil Mesostigmata are generalist predators that feed on nematodes and a variety of arthropod prey, and that canopy species have essentially similar feeding habits to forest floor dwellers.

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