IJM 7: 62–91 (2012)
doi: 10.3897/ijm.7.3064
www.pensoft.net/journals/ijm

DATA PAPER

A peer-reviewed open-access journal
INTERNATIONAL JOURNAL OF
Myriapodology

Phoretic mite associates of millipedes (Diplopoda, Julidae) in the northern Atlantic region (North America, Europe)

Monica A. Farfan[1,2], Hans Klompen[2]

1 *Acarology Laboratory, Ohio State University, Columbus, Ohio, 43212, USA* **2** *Dept. of Biological Sciences, Univ. Illinois at Chicago, Chicago, Illinois, 60607, USA*

Corresponding author: *Monica Farfan* (mfarfa2@uic.edu)

Academic editor: *Pavel Stoev* | Received 10 March 2012 | Accepted 22 May 2012 | Published 5 June 2012

Citation: Farfan MA, Klompen H (2012) Phoretic mite associates of millipedes (Diplopoda, Julidae) in the northern Atlantic region (North America, Europe). International Journal of Myriapodology 7: 69–91. doi: 10.3897/ijm.7.3064

Abstract
Introduced millipede species in the family Julidae are common in the U.S. but little is known about how they interact with other organisms, such as mites. To start to determine the nature of the relationship, millipedes were sampled from across the eastern U.S.A. and the United Kingdom in 2008–2009. Sixteen morphospecies of mites (Acari: Astigmata, Mesostigmata) were collected from these millipedes, 12 of which from a total of 13 species of julid millipedes. None of these 12 species was restricted to a single host species. However, 12 of the 16 mite species collected were restricted to either the U.S.A. or the U.K. These results are consistent with locality, rather than host, specificity.

Keywords
Phoresy, host specificity, Astigmata, Mesostigmata

Introduction

Mites evolved relationships with other arthropods between 100–300 million years ago with the diversification of both plants and arthropods in the late Mesozoic era (Southwood 1973). As more niches became available mites developed a wide variety of well-known symbiotic relationships with many arthropods (Lindquist 1975) including many species of myriapods (Maes 1983; Southcott 1987; Bloszyk et al. 2006), especially members of the class Diplopoda, the millipedes. Notably, most available studies are limited to large mites associated with relatively large, tropical species of millipedes (generally length > 3 cm). Most of these mites belong to the suborder Mesostigmata (Table 1). Second, with some exceptions (Lawrence 1939a; Evans and Sheals 1959; Kethley 1978; Ishikawa 1986; Fain 1988; Gu et al. 1991; Fain 1994; Gerdeman and Klompen 2003; Uppstrom and Klompen 2005), most studies do not report a precise identification of the millipede host (even at the generic or familial level). This, of course, makes it difficult to recollect these species or to study their ecological relationships.

Most mites associated with small millipedes (length < 3 cm) are not Mesostigmata, but belong to the cohort Astigmata. Reported associations of astigmatid mite and millipedes are shown in Table 2. The relationships between astigmatid mites and small millipedes are suspected to be commensalistic (OConnor 2009) although little experimentation has been done to discern the exact nature of the relationship. The cohort Astigmata is characterized by having the second of the three ancestral nymphal instars, the deutonymph, highly modified for dispersal (the hypopus stage) (OConnor 2009). This instar is characterized by the absence of a mouth, a very flat venter and convex dorsum, strong sclerotization of both dorsum and venter, and modification of a number of posterior setae into a postero-ventral attachment organ. The astigmatid deutonymph is considered to be one of the best examples of a phoretic adaptation. A thorough definition of phoresy in mites is given in Houck and OConnor (1991). In broad terms, the deutonymph is a way for phoretic species to disperse from a suboptimal environment which it may not be able to escape on its own.

The focal taxon for this study are millipedes in the family Julidae. These millipedes, are relatively small (20–40mm), are primarily distributed in the Palaearctic region, and are now found in a variety of anthropogenic habitats in temperate regions. They have also been recorded from many countries in Europe and from Canada, the Tristan da Cunha Island group in the Atlantic Ocean, Mexico, Chile, Peru, New Zealand, South Africa, and Antarctica (Blower 1985). Currently, there are 19 species known from the U.K. (Blower 1985) and 10 from the U.S. (Hoffman 1999). They are assumed to be introduced to the New World from Europe by the deposition of ballast as part of colonial-era shipping (Lindroth 1957; Blower 1985; Shear 1999). Currently, julid millipedes are found in a wide variety of man-made habitats such as residential gardens and parks. Dispersal of these millipedes within North America was, and probably continues to be, mainly through landscape management and transport of plants by humans. This history makes them an ideal test group for examining the effects of recent long range dispersal and possible founder effects.

Between March 2008 and October 2009, millipedes of the family Julidae were collected for a population genetics study. This study allows us to present preliminary data on the following questions:

1. What species are present across the eastern U.S.?
2. What mites are associated with these species?
3. Are there strong indications of host and /or locality specificity?

Table 1. Literature records of mesostigmatid mites (Acari: Mesostigmata) associated with Diplopoda. Host names are given as in the original references.

Mite taxon	Millipede host	Country	Source
Gamasina			
Ascidae			
Asca aphidioides	*Parafontaria* sp.	Japan	Ishikawa 1986
Blattisociidae			
Lasioseius angustus	*"Phyodesmus" sublimbatus*	Indonesia	Evans and Sheals 1959
Lasioseius frontalis	*Platyrrhachus mirandus*	Indonesia	Evans and Sheals 1959
Lasioseius polydesmophilus	*Platyrrhachus mirandus*	Indonesia	Evans and Sheals 1959
Lasioseius sugawari	*Oxidus gracilis*	Japan	Ishikawa 1986
Iphiopsididae			
Iphiopsis mirabilis	millipede	Italy	Berlese 1882
Iphiolaelaps myriapoda	millipedes	Queensland (Australia)	Womersley 1956
Jacobsonia africanus	*Spirostrepta* sp.	Cameroon	Fain 1994
Jacobsonia andrei	*Spirostrepta* sp.	Cameroon	Fain 1994
Jacobsonia audyi	*Thyropygus* sp.	Malaya	Evans 1955
Jacobsonia berlesei	Indo-Malayan millipede	Java-Malaysia	Casanueva and Johnston 1992
Jacobsonia puylaerti	*Pachybolus macrosternus*	Dem. Rep. Congo	Fain 1994
Julolaelaps buensis	millipede	Cameroon	Maes 1983
Julolaelaps cameroonensis	millipede	Cameroon	Maes 1983
Julolaelaps celestiae	*Archispirostreptus gigas*	East Africa	Uppstrom and Klompen 2005
Julolaelaps dispar	juliform millipede	Somalia	Berlese 1916
Julolaelaps excavatus	large "julid"	Dem. Rep. Congo	Fain 1987b
Julolaelaps idjwiensis	large "julid"	Dem. Rep. Congo	Fain 1987b
Julolaelaps kilifiensis	spirostreptid millipede; *Archispirostreptus gigas*	Kenya; unknown	Kontschan 2005; Salmane and Telnov 2007
Julolaelaps lucator	juliform millipede	Somalia	Berlese 1916
	julid millipede	India	Vitzthum 1921 (as *J. indica*)
Julolaelaps madiakokoensis	large "julid"	Dem. Rep. Congo	Fain 1987b
Julolaelaps moseri	spirostreptid millipede; *Archispirostreptus gigas*	Trinidad; unknown	Hunter and Rosario 1986; Salmane and Telnov 2007
Julolaelaps myriapodalis	spirostreptid millipede	West Africa	Ryke 1959
Julolaelaps nishikawai	*Nedyopus patrioticus*	Japan	Ishikawa 1986
Julolaelaps pararotundatus	spirostreptid millipede	West Africa	Ryke 1959
	spirostreptid millipede	Kenya	Kontschan 2005
Julolaelaps parvitergalis	*Parafontaria* sp.	Japan	Ishikawa 1986
Julolaelaps parvunglatus	*Parafontaria* sp.	Japan	Ishikawa 1986
Julolaelaps paucipilis	large juliform millipede	Dem. Rep. Congo	Fain 1987b
Julolaelaps peritremalis	spirostreptid millipede	West Africa	Ryke 1959
Julolaelaps rotundatus	juliform millipede	Somalia	Berlese 1916
Julolaelaps serratus	millipede	Cameroon	Maes 1983
Julolaelaps spirostrepti	*"spirostreptus"* sp.	Tanzania	Oudemans 1914
Julolaelaps tritosternalis	*Ommatojulus caspius*	Iran	Moraza and Kazemi 2012
Julolaelaps vandaelensis	millipede	Cameroon	Maes 1983

Mite taxon	Millipede host	Country	Source
Narceolaelaps americanus	*Narceus americanus*	North Carolina (USA)	Kethley 1978
Narceolaelaps annularis	*Narceus annularis*	eastern USA	Kethley 1978
Narceolaelaps burdicki	*Tylobolus* sp	California (USA)	Kethley 1978
Narceolaelaps gordanus	*Narceus gordanus*	Florida (USA)	Kethley 1978
Scissuralaelaps bipartitus	millipede on orchid	Philippines	Ishikawa 1988
Scissuralaelaps breviseta	*Trigoniulus* sp.	Philippines	Ishikawa 1988
Scissuralaelaps grootaeri	unidentified "Iule"	New Guinea	Fain 1992
Scissuralaelaps hirschmanni	*Polyconoceras* sp.	New Guinea	Fain 1992
Scissuralaelaps irianensis	unidentified millipede	New Guinea	Fain 1992
Scissuralaelaps joliveti	*Polyconoceras* sp.	New Guinea	Fain 1992
Trichaspis julus	*Julus terrestris*	China	Gu et al. 1991
Laelapidae			
Cosmolaelaps hortensis	*Oxidus gracilis*	Japan	Ishikawa 1986
Hypoaspis polydesmoides	polydesmid millipede	Malaya	Evans 1955
Iphidolaelaps myriapoda	millipede	Australia	Womersley 1956
Macrochelidae			
Macrocheles muscaedomesticae	*Parafontaria* sp.	Japan	Ishikawa 1986
Ologamasidae			
Stylochyrus rarior	polydesmid millipede	Iowa & Missouri (USA)	Kethley 1983
	Xystodesmidae: *Apheloria*, *Appalachioria*, *Brachoria*, *Dixioria*, *Nannaria*, *Pleuroloma*, *Prionogonus*, *Sigmoria*	Appalachian Mtns. (USA)	Swafford and Bond 2009
Parholaspidae			
Holaspulus tenuipes	*Parafontaria sp.*	Japan	Ishikawa 1986
Sejina			
Heterozerconidae			
Afroheterozercon pachybolus	*Pachybolus macrosternus*	Dem. Rep. Congo	Fain 1988
Afroheterozercon spirostreptus	*Spirostreptus cornutus*	Dem. Rep. Congo	Fain 1988
Asioheterozercon audax	*Spirostreptus*	Java (Indonesia)	Berlese 1910
	millipede	Malaysia	Fain 1989
Allozercon sp.	Rhinocricidae	Philippines	Gerdeman and Garcia 2010
"*Heterozercon*" *elapsus*	*Thyropygus* sp.	Sumatra (Indonesia)	Vitzthum 1925; 1926
Heterozercon microsuctus	spirostreptid	Brazil	Fain 1989
Maracazercon joliveti	spirostreptid	Brazil	Fain 1989
Narceoheterozercon ohioensis	*Narceus annularis*	Ohio (USA)	Gerdeman et al. 2000; Gerdeman and Klompen 2003
Trigynaspida			
Costacaridae			
Costacarus reyesi	millipede	Mexico	Hunter 1993
Euzerconidae			
Neoeuzercon diplopodophilus	millipede	Panama	Funk 1980
Diplogyniidae			
Cryptometasternnum queenslandense	pill millipedes	Australia	Womersley 1958

Mite taxon	Millipede host	Country	Source
Diplogynium acuminatum	millipede	Brazil	Canestrini 1888
Neodiplogynium schubarti	*Sooretama aguirrei*	Brazil	Trägårdh 1950
Neotenogyniidae			
Neotenogynium malkini	*Orthoporus* sp.	Ecuador	Kethley 1973
Paramegistidae			
Meristomegistus vazquezi	*Aceratophallus* sp.	Mexico	Kim and Klompen 2002
Neomegistus julidicola	juliform millipede	South Africa	Trägårdh 1906; 1907
Neomegistus remus	*Proporobolus* sp.	Australia	Baker and Seeman 2008
Paramegistus confrater	juliform millipede	South Africa	Trägårdh 1906; 1907

Table 2. Literature reports of astigmatid mites (Acari: Astigmata) associated with Diplopoda. Host names are given as in the original references.

Mite taxon	Millipede host	Country	Source
Histiostomatidae			
Histiostoma feroniarum	*Ommatoiulus moreleti*	Australia	Baker 1985
Acaridae			
Caloglyphus julidicolus	*Doratogonus flavifilis*	South Africa	Lawrence 1939a
Schwiebea sp.	Xystodesmidae: *Apheloria*, *Appalachioria*, *Brachoria*, *Boraria*, *Dixioria*, *Nannaria*, *Rudiloria*, *Sigmoria*	Appalachian Mtns. (U.S.A.)	Swafford and Bond 2009
Schwiebea nova	*Cylindroiulus* sp.	Hungary	Mahunka 1962
Canestriniidae			
Diplopodocoptes transkeiensis	glomerid millipede	South Africa	Fain 1987a
	Odontopygidae	Kenya	Fain 1987a
Chetochelacaridae			
Chetochelacarus mamillatus	julid millipede	Dem. Rep. Congo	Fain 1987a
Lophonotacaridae			
Lophonotacarus minutus	glomerid millipede	South Africa	Fain 1987a
	Odontopygidae	Kenya	Fain 1987a
"Astigmata"	*Polydesmus inconstans*	Michigan (U.S.A.)	Snider 1984

Host specificity in relationships between the millipedes in the family Julidae and the phoretic mite would be indicated if particular mite species are consistently associated with specific millipede host species. If mites are host specific and there was a founder effect during colonization of the New World, diversity of specific mites in the U.S. is likely to be less than in Europe. Alternately, the presence of mites on a millipede may be based on locality, not host, specificity. This assumes that mites are specific to a certain area or type of off-host habitat. In this case a wide range of hosts occurring in the preferred habitat/ locality might be suitable as phoretic host. Predictions for the locality hypothesis are (1) individual mite species will be present on a number of different millipede host species but restricted to certain collection localities; (2) 'American', not European, mites will be present on U.S. representatives of European millipede species, and (3) there will be similar mite diversity on U.S. and European populations of the same millipede species.

Material and methods

Collection localities

Millipede specimens were collected from localities in the eastern United States from March through October in 2008 and 2009 and in the United Kingdom in April 2009. Sites in the U.S.A. were chosen to include geographic diversity and to include a number of cities used as colonial ports. While known to be found near such port cities, the current range of julid millipedes is more extensive.

Collection methods

Millipedes were collected by hand except in one instance (Whetstone Park, Columbus, OH) where litter was returned to the Ohio State University Acarology Laboratory (OSAL) for extraction by Berlese funnel. Hand collection was done from wood mulch, leaf litter, and soil. Much collecting was done at the soil/litter interface. Millipedes (with mites associates attached) were collected and placed individually into 1.5 mL vials containing 95% ethanol. Mites release their hold on immersion in alcohol, so individual host preservation is essential. Millipede and mite specimens used in this study are deposited at OSAL. Voucher numbers for representatives of all millipede host species and mite morphospecies, as well as species citations, are listed in Appendices 1 and 2.

Determinations

Millipedes were dissected and, in some cases, genitalia were slide mounted. Specimens were identified using the following keys: Blower (1985), Shear (unpublished key), and Shelley (1978, 1988, 2002). Hoffman's checklist (1999) was used as a reference for regional distributions.

Mites were sorted to morphospecies using a 12–110× Nikon SMZ dissecting microscope, and some individuals from each morphospecies (including a diversity of hosts and/or sites) were slide-mounted for final identification using a Zeiss Axioskop compound microscope at magnifications up to 1000×. Overall, 148 mites, approximately 11% of total mites collected, were slide mounted. Astigmatid mites were identified to genus using keys by OConnor (unpublished). Specific identification proved impossible as most mite species collected appear to be undescribed. Full description of these mites is beyond the scope of this study, but we do provide some of the characters on which discrimination into morphospecies was based. This should allow evaluation of the validity of those morphospecies concepts.

Prevalence and intensity

Prevalence of the identified mites was calculated for each host species and each locality. Prevalence is defined as: (number of hosts with a particular parasite species) / (number of hosts examined) (Margolis et al. 1982). Higher prevalence results from finding a high number of hosts that were examined are found to be carrying a parasite, or phoretic, species. Additionally, the intensity (average mites per infested host) for each host species was calculated (Margolis et al. 1982). Because not all mites were mounted for identification, prevalence calculations are imperfect. A relatively high percentage of associated mites was mounted for hosts collected < 20 times, and prevalence calculations for those hosts are relatively accurate, but these numbers are minimum estimates for millipedes species where N > 20.

Results

Millipede Collections

Twenty three species of millipedes were collected representing 9 different families (Table 3). Thirteen of these species belong to the family Julidae, the focus of this study. Six were collected in large numbers (> 100); *Brachyiulus pusillus*, *Cylindroiulus caeruleocinctus*, *Cylindroiulus latestriatus*, *Cylindroiulus punctatus*, *Cylindroiulus truncorum*, and *Ophyiulus pilosus*. Millipedes in the remaining 8 families (Abacionidae, Blaniulidae, Cleidogonidae, Euryuridae, Glomeridae, Parajulidae, Polydesmidae, and Spirobolellidae), with the exception of Blaniulidae, were collected in relatively low numbers.

Mite Collections

Representatives of 6 genera of mites were associated with millipedes collected in this study. These mites belong to two families in the cohort Astigmata; Acaridae and Histiostomatidae, and two families in the suborder Mesostigmata; Laelapidae and Uropodidae.

Astigmata

The astigmatid mites represented 13 morphospecies: *Rhizoglyphus* A and B (Figure 1a and 1c, respectively), *Sancassania* A and B (Figure 1b), *Schwiebea* A, C, D, E (Fig-

Table 3. Intensity (over all mite morphospecies) and prevalence (percentage by mite morphospecies) for mites associated with millipedes examined.

Family	Species	N (millipedes)	*Average intensity*	***Rhizoglyphus* A**	***Rhizoglyphus* B**	***Sancassania* A**	***Sancassania* B**	***Schwiebea* A**	***Schwiebea* C**	***Schwiebea* D**	***Schwiebea* E**	***Schwiebea* F**	***Schwiebea* G**	***Schwiebea* H**	***Thyreophagus* sp.**	***Histiostoma* sp.**	***Cosmolaelaps* sp.**	***Holostapis* sp.**	***Phaulodinychus* sp.**
Abacionidae	*Abacion lactarium*	8	3.0	13.0	13.0														
Blaniulidae	Blaniulid sp.	104	2.0						2.0	2.0		2.0				2.0			
	Blaniulus guttulatus	93	1.2						4.0							1.0			
	Choneiulus palmatus	8	2.4																
	Nopoiulus kochii	76	1.6																
Cleidogonidae	*Cleidogona caroliniana*	7	2.0																
Euryuridae	*Euryurus leachii*	14	11.3						7.0							7.0	7.0	14.0	14.0
Glomeridae	*Glomeris marginata*	4	2.7								5.0								
Julidae	*Brachyiulus lusitanus*	16	1.0																
	Brachyiulus pusillus	208	2.3	1.0					2.0										
	Cylindroiulus britannicus	35	2.0	3.0				3.0						3.0	3.0				
	Cylindroiulus caeruleocinctus	365	2.8	2.0		1.0	0.3			0.3					1.0				
	Cylindroiulus latestriatus	337	1.7	0.3					0.3							0.3			0.3
	Cylindroiulus londinensis	2	5.0	50.0												50			
	Cylindroiulus punctatus	109	3.3	1.0				4.0						1.0		1.0			
	Cylindroiulus truncorum	171	1.9	1.0			2.0			1.0						1.0			
	Cylindroiulus sp.	186	2.7	1.0		2.0										1.0			
	Julus scandinavicus	19	3.2					5.0	5.0										
	Ommatoiulus sabulosus	9	2.0												11.0				
	Ophyiulus pilosus	373	2.6	0.3					1.0										
	Tachypodoiulus niger	2	5.0										50.0						
Parajulidae	*Uroblaniulus carolinensis*	8	2.7						13.0							13.0			
Polydesmidae	*Polydesmus angustus*	6	6.0					17.0				17.0	17.0	17.0					
	Polydesmus sp.	8	1.0						13.0										
Spirobolellidae	*Paraspirobolus lucifugus*	5	2.9						20.0							40.0			

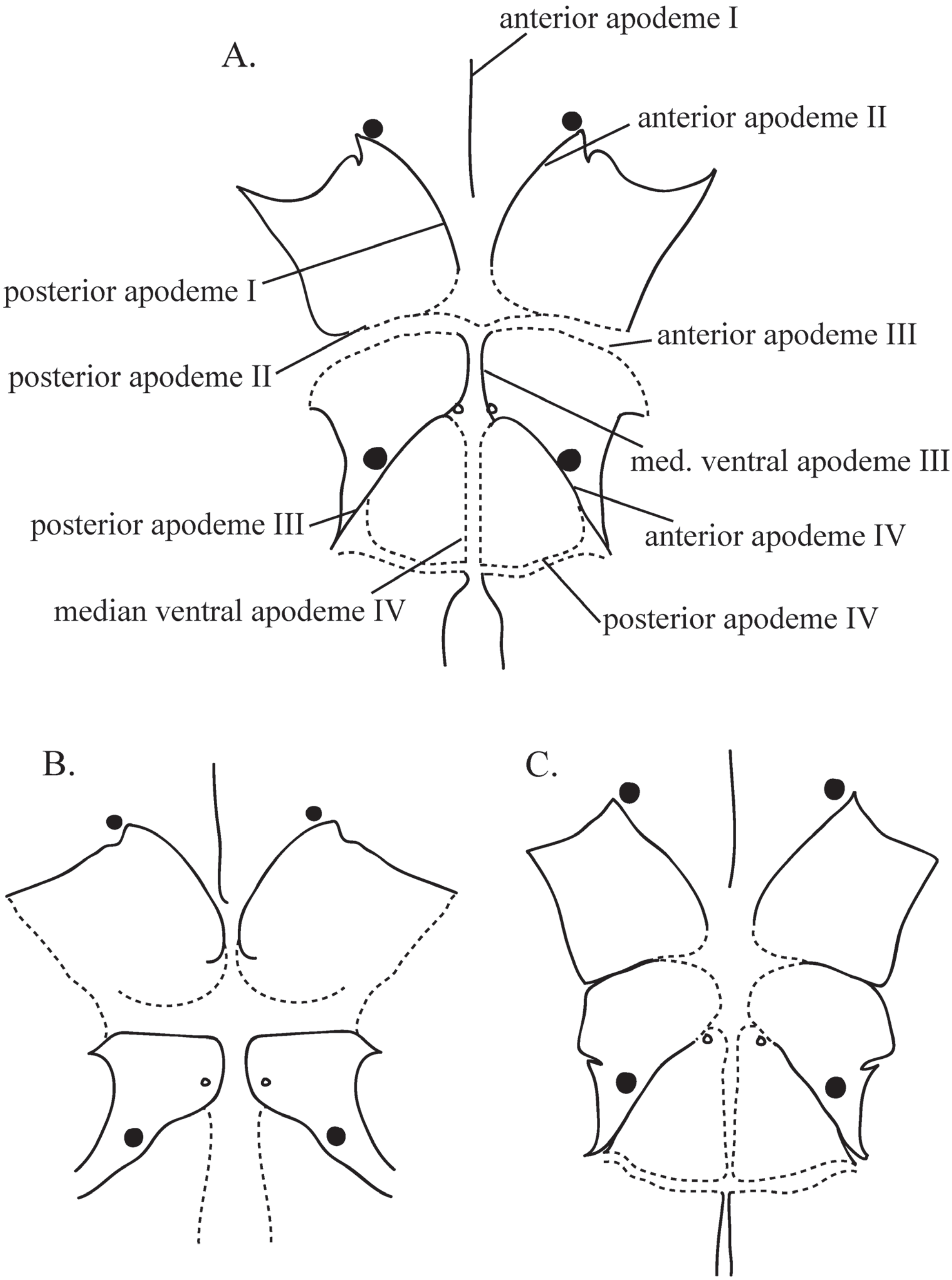

Figure 1. Diagram of the coxal fields and coxal apodemes of **a** *Rhizoglyphus* A **b** *Rhizoglyphus* B and **c** *Sancassania* B.

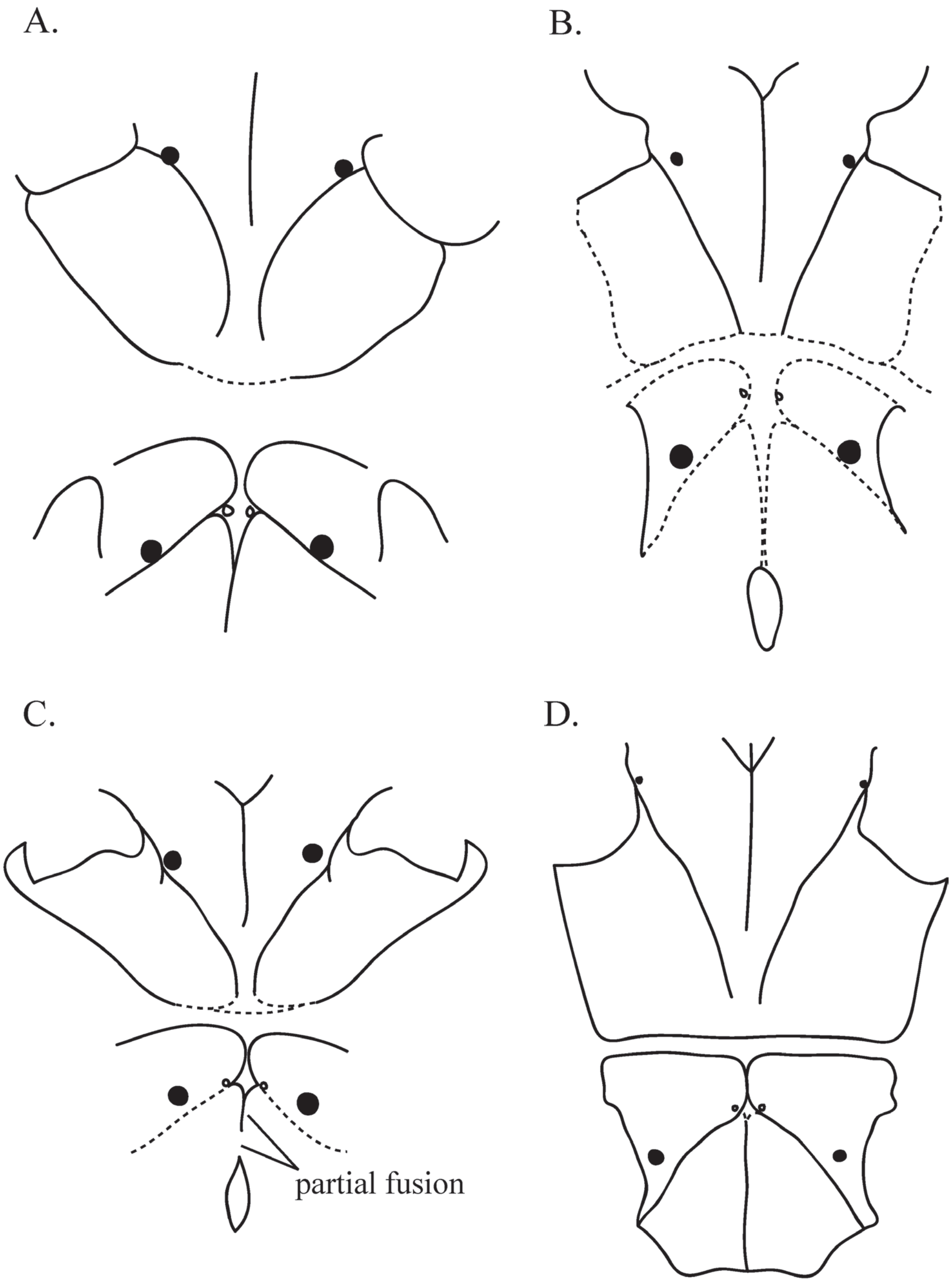

Figure 2. Diagram of the coxal fields and coxal apodemes of **a** *Schwiebea* A **b** *Schwiebea* C **c** *Schwiebea* D and **d** *Schwiebea* E.

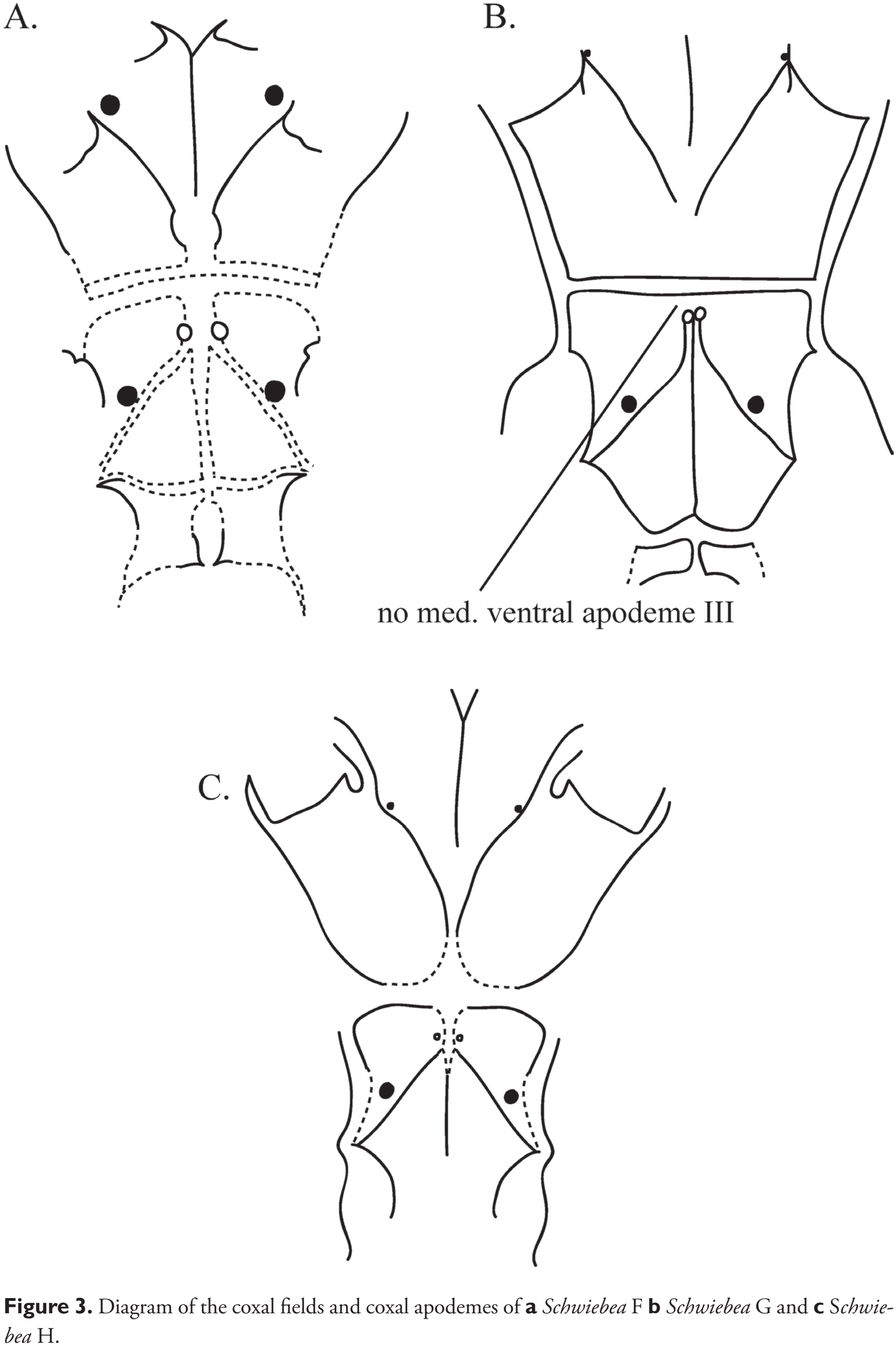

Figure 3. Diagram of the coxal fields and coxal apodemes of **a** *Schwiebea* F **b** *Schwiebea* G and **c** *Schwiebea* H.

ures 2a, 2b, 2c, & 2d, respectively), F, G, and H (Figures 3a, 3b, & 3c, respectively), *Thyreophagus* (all Acaridae), and *Histiostoma* (Histiostomatidae). Specimens of *Rhizoglyphus*, *Sancassania*, and *Schwiebea* were separated into morphospecies by the shape and amount of fusion of the apodemes and the shape of the coxal fields on the venter. These characteristics were chosen because these features are unlikely to be artifacts of the slide-mounting process. The differences between the species can be subtle. Distinguishing characteristics of the morphospecies within the genera *Rhizoglyphus*, *Sancassania*, and *Schwiebea* are detailed in Table 4, and Figures 1–3. Figures show conoidal setae as filled-in circles and simple setae as open circles. The size of the filled-in circles in the diagram is indicative of the relative size of the conoidal setae. Broken lines indicate edges of apodemes with a greater degree of fusion. These edges appear not as distinct or "heavy" as non-fused apodemes. Apodemes and coxal fields are denoted with Roman numerals corresponding with the leg pair they are associates with (e.g., coxal fields II correspond with legs II).

Mesostigmata

Mites in the families Laelapidae and Uropodidae were determined to genus. Two genera of laelapids were identified as *Cosmolaelaps* and *Holostaspis*, the uropodid as *Phaulodinychus*.

Julidae - mite associations

Nearly all mite specimens collected from julid millipedes were astigmatid deutonymphs. Morphospecies of *Schwiebea* were the most commonly collected from these millipedes (Table 3). *Rhizoglyphus* A was collected from the highest number of julid species in this study (n = 9). This was followed by *Histiostoma* sp. (n = 6). *Thyreophagus* specimens were found on *Ommatoiulus sabulosus* and *Cylindroiulus britannicus* only. *Schwiebea* D, E, and G and *Phaulodinychus* sp. were also collected from one julid host species only. *Phaulodinychus* sp. was collected only once on a julid millipede, *C. latestriatus*. There were no laelapid mites collected from julid millipedes.

Cylindroiulus caeruleocinctus had five species of mite associates which was the highest diversity among julids. *Tachypodoiulus niger* and *O. sabulosus* had the fewest associate species (one species each).

Prevalences were found to range from 0.27%–50.0% (minimum estimates). Notable are the associations of *Schwiebea* H on *T. niger* (N=2), and *Rhizoglyphus* A and *Histiostoma* sp. on *Cylindroiulus londinensis* (N= 2), each with the highest prevalence of 50.0%. The lowest prevalence was calculated for *Rhizoglyphus* A on *O. pilosus* (0.27%) (but see comments in Material and Methods). Intensity also tends to be low. The average intensities for the six most common julid species ranged from 1.66–3.32 mites per host with an average of 2.43. This is probably close to the average intensity for all Julidae.

Table 4. Comparative characters for *Schwiebea* (Acari, Astigmata, Acaridae) species associated with millipedes (Diplopoda).

	***Schwiebea* A (Fig. 2A)**	***Schwiebea* C (Fig. 2B)**	***Schwiebea* D (Fig. 2C)**	***Schwiebea* E (Fig. 2D)**	***Schwiebea* F (Fig. 3A)**	***Schwiebea* G (Fig. 3B)**	***Schwiebea* H (Fig. 3C)**
Coxal fields II	oval, well-developed	quadrilateral; apodemes straight, well-developed	oval, widened distally, mostly well-developed	quadrilateral; coxal fields I & II contiguous, well-developed	quadrilateral; anterior apodemes II end in distinct curve medially	quadrilateral; fields I & II contiguous, well-developed	oval, well-developed
Posterior edge of coxal fields II	convex, poorly developed medially	concave, poorly developed	convex, poorly developed medially	straight, horizontal, well-developed	slightly concave, quadrilateral edge poorly developed	straight, horizontal, well-developed	median section of posterior curve poorly developed
Anterior edge of coxal fields III	roughly concave, well-developed	concave, poorly developed	slightly concave, well-developed	straight, horizontal, well-developed	slightly concave, poorly developed	straight, horizontal, well-developed	slightly concave at lateral edges, well-developed
Coxal fields III	rounded medially	rounded medially	rounded medially, almost touching	triangular, separated medially	triangular, not touching	connected, quadrilateral	triangular, not touching
Coxal fields IV	triangular	triangular	triangular	deltoid	triangular	deltoid; acutely tapering medially	arrow-shaped
Apodemes III & IV	well-developed	poorly developed	anterior III and median ventral apodemes well-developed; others poorly developed	well-developed	poorly developed	well-developed	mostly well-developed
Median ventral apodemes III	not fused	not fused	almost fused	fused	not fused	not present	not fused, poorly developed
Median ventral apodemes IV	fused, extending to genital opening	not fused, extending to genital opening	fused, terminates half-way to genital opening	fused, extending to genital opening	not fused, extending to genital opening	fused, extending to genital opening	fused, terminates half-way to genital opening
Conoidal setae on coxal field I	medium	medium	large	small	large	very small	very small

Non-julid millipede collections

Schwiebea C was collected from the highest number of non-julid hosts (n = 5). *Polydesmus angustus* was associated with 4 morphospecies of *Schwiebea*, all collected from one host individual. *Histiostoma* sp. and three species of *Schwiebea* have been collected from the combined specimens in the family Blaniulidae. The two taxa collected from *Uroblaniulus carolinenesis* and *Paraspirobolus lucifugus* were *Histiostoma* sp. and *Schwiebea* C. *Abacion lactarium* was the only species, julid or non-julid, to have *Rhizoglyphus* B as an associate. The euryurid *Euryurus leachii* was the only millipede host to have mite associates in the family Laelapidae. Representatives of two genera, *Cosmolaelaps* and *Holostaspis*, were collected. Consistent with the general association pattern of Laelapidae, these mites were collected as adults, not deutonymphs. Additionally, a considerable number of deutonymphs of the uropodine *Phaulodinychus* sp. were collected from this millipede. *Euryurus leachii* was the millipede with the highest intensity (11.27) and the largest number of mite species among the non-julids with five mite morphospecies.

The prevalence of mites found on non-julid millipedes was generally high. This may be associated with the fact that the numbers of non-julids collected were relatively low, with the exception of blaniulids. For example, 50.0% of the *Glomeris marginata* (N = 4) carried *Schwiebea* E. Blaniulids were collected most commonly, and showed prevalences between 0.94–3.77% for their mite associates *Schwiebea* D, E, and F, and *Histiostoma* sp.

Mite taxa and telation to locality

Only four mite species were collected from localities in both the U.S.A. and in the U.K., *Rhizoglyphus* A, *Schwiebea* C, *Schwiebea* F, and *Histiostoma* sp. (Table 5). Mite taxa that were found exclusively in the U.S.A. are *Rhizoglyphus* B, *Sancassania* A, *Sancassania* B,

Table 5. Prevalence (percentage) of mites on millipedes (all species combined) by collecting locality.

Locality	(millipedes) N	*Rhizoglyphus* A	*Rhizoglyphus* B	*Sancassania* A	*Sancassania* B	*Schwiebea* A	*Schwiebea* C	*Schwiebea* D	*Schwiebea* E	*Schwiebea* F	*Schwiebea* G	*Schwiebea* H	*Thyreophagus* sp.	*Histiostoma* sp.	*Cosmolaelaps* sp.	*Holostapis* sp.	*Phaulodinychus* sp.
North Kingstown, RI	175	1		3			1			1				2			
Chicago, IL	452													1			
Lakewood, OH	61						2										
Cleveland, OH	119	2												1			
Delaware, OH	23	9	4				4										
Columbus, OH	1054						1										
Southern Ohio	7														14	29	33

Locality	**(millipedes) N**	***Rhizoglyphus* A**	***Rhizoglyphus* B**	***Sancassania* A**	***Sancassania* B**	***Schwiebea* A**	***Schwiebea* C**	***Schwiebea* D**	***Schwiebea* E**	***Schwiebea* F**	***Schwiebea* G**	***Schwiebea* H**	***Thyreophagus* sp.**	***Histiostoma* sp.**	***Cosmolaelaps* sp.**	***Holostapis* sp.**	***Phaulodinychus* sp.**
Baltimore, MD	102	8		1	3									2			
Charlotte, NC	161				1		1	1						1			
Fort Mill, SC	15						7							7			7
Cornwall, UK	59	2				2	2		2		2	2	2	2			
Eden Project, UK	56					2	4					2	2	5			
Slough, UK	27	7				19			7	4	4	4		4			

Schwiebea D, *Cosmoglyphus* sp., *Holostapis* sp. and *Phaulodinychus* sp. Taxa found only in the U.K. *Schwiebea* A, *Schwiebea* E, *Schwiebea* G, *Schwiebea* H, and *Thyreophagus* sp. The highest diversity of mite taxa by locality was found in Cornwall, U.K. Only one mite taxon each was collected in Chicago, IL, Columbus, OH, and Lakewood, OH.

Of the seven millipede species collected in both the U.S.A. and the U.K. only *Cylindroiulus caeruleocinctus* had the same mite associates in both countries, *Rhizoglyphus* A and *Histiostoma* sp. (Table 5). Mite associates of the other six species of millipedes did not appear in both countries on the same julid host species.

Discussion

The current study does not suggest strong host specificity of mite species for julid hosts. The only species that were collected from only one host, *Rhizoglyphus* B, *Cosmolaelaps* sp. and *Holostaspis* sp. are rare, and (so far) exclusively associated with non-julid hosts. This result supports the view of OConnor (1998) who noted that acarids are (1) often associates of a wide variety of hosts and (2) are often cosmopolitan. There is precedent for this in terms of millipede-associated Mesostigmata. While most Heterozerconidae are associated with large millipedes, one genus, *Amheterozercon* (Fain 1989), is associated with snakes and amphisbaenids (Flechtmann and Johnston 1990). Similarly, most Paramegistidae are associates of carabid beetles or millipedes, except for the genus *Ophiomegistus* (Banks 1914) which is associated with skinks and snakes (Klompen and Austin 2005). These records suggest that these mites may favor a host with a specific type of locomotion, general distance from the ground, or habitat preference, at best a modified host specificity.

Neither is there strong overlap of the mite fauna of specific julid millipedes collected both in the U.S.A. and the U.K., another prediction of the host specificity hypothesis. Only one millipede species (*C. caeruleocinctus*) carried the same mite species in both the U.S.A. and the U.K. In a comparison of mite associates found on millipedes and the locality in which they were found (Table 5), 12 of the 16 taxa were collected in either the U.S.A. or the U.K. Only four were collected from both countries. This is an indication that the mites are most likely not associated with specific hosts but, instead, are favoring hosts associated with specific habitats.

An unusual finding regarding mite associates was the collection of a species in the genus *Thyreophagus* collected in the U. K. Past reports of *Thyreophagus* sp. are mostly from the U.S.A. *Thyreophagus* is a mite thought to be associated only with subcortical insects (OConnor 1982) with often high host specificity (OConnor 1984). This is very different from the lifestyles of the other acarids collected in this study that seem to be very general in their host choice. *O. sabulosus* and *C. britannicus* were the hosts of this mite. They were collected from an outdoor garden and a greenhouse/conservatory in Cornwall, U.K., sites which were a good distance from each other. A further survey of ground arthropods in Cornwall could help clarify the degree of specificity of this genus in the area.

Acknowledgements

Thanks to Helen J. Read, and the British Myriapod and Isopod Group for their help in the collection of specimens, and to Barry OConnor for permission to use his unpublished keys to Astigmatid genera. Thanks to John W. Wenzel, currently Carnegie Mellon University, and Andrew P. Michel, OSU Department of Entomology, for their kind review of earlier drafts of this publication.

References

Baker GH (1985) Parasites of the millipede *Ommatoiulus moreleti* (Lucas) (Diplopoda: Iulidae) in Portugal, and their potential as biological control agents in Australia. Australian Journal of Zoology 33: 23–32. doi: 10.1071/ZO9850023

Baker MR, Seeman OD (2008) Mites and millipedes: a new *Neomegistus* (Acari: Mesostigmata: Paramegistidae) from Australia. Systematic and Applied Acarology 13 (3–4): 204–213.

Berlese A (1916) Centuria prima di Acari nuovi. Redia 12: 31–32.

Bloszyk J, Klimczak J, Lesniewska M (2006) Phoretic relationships between Uropodina (Acari: Mesostigmata) and centipedes (Chilopoda) as an example of evolutionary adaptation of mites to temporary microhabitats. European Journal of Entomology 103 (3): 699–707.

Blower JG (1985) Millipedes: Keys and notes for the identification of the species. E. J. Brill/Dr. W. Backhuys, London, 242 pp.

Canestrini G (1888) Intorno ad alcuni Acari ed Opilionidi dell America. Atti della Società Veneto-Trentina di Scienze Naturali 11 (1): 100–111.

Casanueva ME, Johnston DE (1992) Systematic studies on *Jacobsonia* (Acari, Mesostigmata), a mite associated with Indo-Malaysian millipedes. Boletin de la Sociedad de Biologia de Concepcion 63: 55–63.

Causey NB (1953) On five new North American millipeds and records of some established species. American Midland Naturalist 50 (1): 152–158. doi: 10.2307/2422160

Corente C, Knülle W (2003) Trophic determinants of hypopus induction in the stored-product mite *Lepidoglyphus destructor* (Acari: Astigmata). Experimental and Applied Acarology 29: 89–107. doi: 10.1023/A:1024230517969

Eickwort GC (1990) Associations of mites with social insects. Annual Review of Entomology 35: 469–488. doi: 10.1146/annurev.en.35.010190.002345

Eisner T, Alsop D, Hicks K, Meinwald J (1978) Defensive secretions of Millipeds. In: S. Bettini (Ed) Handbook of Experimental Pharmacology: Arthropod Venoms. Springer-Verlag, New York, 41–72.

Evans GO (1955) A review of the laelaptid paraphages of the Myriapoda with descriptions of three new species (Acarina: Laelaptidae). Parasitology 45 (3–4): 352–368. doi: 10.1017/S0031182000027694

Evans GO, Sheals JG (1959) Three new mesostigmatic mites associated with millipedes in Indonesia. Entomologische Berichten, Amsterdam 19: 107–111.

Fain A (1987a) Notes on mites associated with Myriapoda. I. Three new astigmatic mites from Afrotropical Myriapoda (Acari, Astigmata). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 57: 161–172.

Fain A (1987b) Notes on mites associated with Myriapoda: II. Four new species of the genus *Julolaelaps* Berlese, 1916 (Acari, Laelapidae). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 57: 203–208.

Fain A (1988) Notes on mites associated with Myriapoda. III. Two new species of the genus *Heterozercon* Berlese, 1888 (Acari, Mesostigmata) from Afrotropical Myriapods. Bulletin et Annales de la Société royale belge d'Entomologie 124: 237–242.

Fain A (1989) Notes on mites associated with Myriapoda. IV. New taxa in the Heterozerconidae (Acari, Mesostigmata). Bulletin de l'Institut royal des Sciences Naturelles de Belgique, Entomologie 59: 145–156.

Fain A (1992) Notes on mites associated with Myriapoda: V. The genus *Scissuralaelaps* Womersley, 1945 (Acari, Mesostigmata): Description of four new species from New Guinea. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 62: 109–116.

Fain A (1994) Notes on mites associated with Myriapoda: VI. The genus *Jacobsonia* Berlese, 1910 (Acari, Laelapidae): Description of four new species from New Guinea. Journal of African Zoology 108: 585–595.

Flechtmann CHW, Johnston DE (1990) *Zeterohercon*, a new genus of Heterozerconidae (Acari: Mesostigmata) and the description of *Zeterohercon amphisbaene* n sp. from Brasil. International Journal of Acarology 16 (3):143–148. doi: 10.1080/01647959008683526

Funk RC (1980 (1981)) Generic revision of the family Euzerconidae (Mesostigmata: Celaenopsoidea) with description of seven new genera. International Journal of Acarology 6 (4): 313–349. doi: 10.1080/01647958008683236

Gerdeman BS (2002) The biology of the Heterozerconidae. Columbus, OH, Ohio State University, 105pp.

Gerdeman BS, Garcia R (2010) Heterozerconidae: A comparison between a temperate and a tropical species. Trends in Acarology, Proceedings of the 12th International Congress. Sabelis MW, Bruin J. Dordrecht, Springer Science: 93–96.

Gerdeman BS, Klompen H (2003) A new North American heterozerconid, *Narceoheterozercon ohioensis*, n. gen., n. sp., with first description of immatures of heterozerconidae (Acari: Mesostigmata). International Journal of Acarology 29 (4): 351–370. doi: 10.1080/01647950308684352

Gerdeman BS, Klompen H, Tanigoshi L (2000) Insights into the biology of a mite-millipede association. Fragmenta Faunistica, Warszawa Supplement 43: 223–227.

Gu Y, Wang C, Li J (1991) A new genus and species of Gamasides off *Julus terrestris* and a new family proposed (Acari: Dermanyssoidea). Acta Zootaxonomica Sinica 16: 428–431.

Hoffman RL (1999) Checklist of the millipeds of North and Middle America. Virginia Museum of Natural History, Martinsville, VA, 581 pp.

Hoffman RL, Payne JA (1969) Diplopods as carnivores. Molecular Ecology Resources 50 (6): 1096–1098.

Hopkin SP, Read HJ (1992) The Biology of Millipedes. Oxford University Press, Oxford, England, 233 pp.

Houck MA, OConnor BM (1991) Ecological and evolutionary significance of phoresy in the Astigmata. Annual Review of Entomology 36: 611–636. doi: 10.1146/annurev.en.36.010191.003143

Hunter PE (1993) A new family of mites, Costacaridae (Mesostigmata: Trigynaspida: Celaenopsoidea), associated with millipedes in Mexico. Israel Journal of Zoology 39 (2): 185–191.

Hunter PE, Rosario RMT (1986) A new species of *Julolaelaps* Berlese (Acari: Laelapidae). International Journal of Acarology 12 (2): 63–67. doi: 10.1080/01647958608683442

Ishikawa K (1986) Gamasid mites (Acarina) associated with Japanese millipeds. Reports of Research Matsuyama Shinonome Jr. College 17: 165–177.

Ishikawa K (1988) Two new species of *Scissurolaelaps* (Acarina, Laelapidae) associated with Philippine millipeds. Bulletin of the National Science Museum, Tokyo, Serie A14 (4): 173–178.

Kethley JB (1973) Developmental chaetotaxy of a paedomorphic celaenopsoid, *Neotenogynium malkini* n. g., n. sp. (Acari: Parasitiformes: Neotenogyniidae, n. fam.) associated with millipedes. Annals of the Entomological Society of America 67 (4): 571–579.

Kethley JB (1978) *Narceolaelaps* n. g., (Acari: Laelapidae) with four new species parasitizing spirobolid millipedes. International Journal of Acarology 4 (3): 195–210. doi: 10.1080/01647957808683117

Kethley JB (1983) The deutonymph of *Epiphis rarior* Berlese, 1916 (Epiphidinae n. subfam., Rhodacaridae, Rhodacaroidea). Canadian Journal of Zoology 61 (11): 2598–2611. doi: 10.1139/z83-341

Kim C, Klompen H (2002) A new genus and species of Paramegistidae (Mesostigmata: Trigynaspida) asociated with millipedes from Mexico. Acarologia, Paris 42 (1): 39–52.

Klompen H, Austin CC (2007) A new species of *Ophiomegistus* Banks (Acari: Paramegistidae) from Papua New Guinea. Zootaxa 1387: 47–57.

Kontschan J (2005) Two species of *Julolaelaps* Berlese, 1916 (Acari : Mesostigmata : Laelapidae) associated with millipedes from Kenya. Annales Historico-Naturales Musei Nationalis Hungarici 97: 257–260.

Lawrence RF (1939a) A new mite attached to the Sex Organs of South African Millipedes. Transactions of the Royal Society of South Africa 27: 226–231. doi: 10.1080/00359193909519792

Lawrence RF (1939b) Notes on the habits of the two mites living on South African millipeds. Transactions of the Royal Society of South Africa 27: 233–239. doi: 10.1080/00359193909519793

Lindquist EE (1975) Associations between mites and other arthropods in forest floor habitats. The Canadian Entomologist 107: 425–437. doi: 10.4039/Ent107425-4

Lindroth CH (1957) The Faunal Connections between Europe and North America. Almqvist & Wiksell, Stockholm, 344 pp.

Maes K (1983) Scientific reports of the Belgian Mount Cameroon expedition 1981. VIII. Description of four new species of the genus *Julolaelaps (*Acarina: Laelapidae). Revue de Zoologie africaines 97 (1): 211–220.

Mahunka S (1962) Neue Beiträge zur Kenntnis der einheimischen Acariden-Fauna (Acari). Opuscula Zoologica (Budapest) 4 (2–4): 97–103.

Mahunka S (1992) New and interesting mites from the Geneva Museum. XXXVII. New mites from the Pacific Islands (Acari: Anoetidae, Scutacaridae). Revue Suisse de Zoologie 99 (2): 395–403.

Marek P, Shelley RM (2005) Expert Burrowers. http://www.myriapoda.org/diplopoda/millipede_general_info.html [accessed 18 March 2010]

Margolis L, Esch GW, Holmes JC, Kuris AM, Schad GA (1982) The use of ecological terms in parasitology (Report of an ad hoc committee of the American Society of Parasitologists). Journal of Parasitology 68 (1): 131–133. doi: 10.2307/3281335

Moraza ML, Kazemi S (2012) “Description of a new millipede-associated species (Acari: Mesostigmata: Laelapidae) from Iran and a key to species of *Julolaelaps* Berlese.” International Journal of Acarology 38(1): 6–17. doi: 10.1080/01647954.2011.583273

OConnor BM (1982) Evolutionary Ecology of Astigmatid Mites. Annual Review of Entomology 27: 385–409. doi: 10.1146/annurev.en.27.010182.002125

OConnor BM (1994) Life history modifications in astigmatid mites. In: Houck MA (Ed) Mites: Ecological and Evolutionary Analyses of Life-History Patterns. Chapman & Hall, New York, 136–159.

OConnor BM (2009) Cohort Astigmata. In: Krantz GW, Walter DE (Eds) A Manual of Acarology. Texas Tech University Press, Lubbock, Texas, 565–658.

Olynyk JE, Freitag R (1979) Some Phoretic Associations of Ground Beetles (Coleoptera: Carabidae) and Mites (Acarina). The Canadian Entomologist 111: 333–335. doi: 10.4039/Ent111333-3

Oudemans AC (1914) Acarologische Aanteekeningen LII. Entomologische Berichten 4, 65–73.

Oudemans AC (1915) Notizen über Acari. XXII. - Archiv für Naturgeschichte 81: 131–134.

Pherson DA, Beattie AJ (1979) Fungal loads of invertebrates in beech leaf litter. Revue d Ecologie et de Biologie du Sol 16: 325–335.

Rossi W, Weir A (1998) *Triainomyces*, a new genus of Laboulbeniales on the pill-millipede *Procyliosoma tuberculatum* from New Zealand. Mycologia 90 (2): 282–289. doi: 10.2307/3761304

Ryke PAJ (1959) A revision of the hypoaspid mites associated with Myriapoda with descriptions of three new species of the subgenus *Julolaelaps* Berl. (Acarina: Laelaptidae). Parasitology 49 (1–2): 6–22. doi: 10.1017/S0031182000026676

Salmane I, Telnov D (2007) "Laelaptidae mites (Parasitiformes, Mesostigmata) of east African millipedes (Diplopoda)." Latvijas Entomologs 44: 121.

Schmidt-Rhaesa A, Farfan MA, Bernard EC (2009) First Record of Millipedes as Hosts for Horsehair Worms (Nematomorpha) in North America. Northeastern Naturalist 16 (1): 125–130. doi: 10.1656/045.016.0110

Shear WA. Key to Milliped Families of the Eastern United States. unpublished key. 22 pp.

Shelley RM (1978) Millipeds of the eastern Piedmont region of North Carolina, U. S. A. (Diplopoda). Journal of Natural History 12: 37–79. doi: 10.1080/00222937800770051a

Shelley RM (1984) A synopsis of the millipede genus *Abacion* Rafinesque (Callipodida: Caspiopetalidae). Canadian Journal of Zoology 62: 980–988. doi: 10.1139/z84-137

Shelley RM (1988) The millipeds of eastern Canada (Arthropoda: Diplopoda). Canadian Journal of Zoology 66: 1638–1663. doi: 10.1139/z88-239

Shelley RM (2002) The millipeds of central Canada (Arthropoda: Diplopoda), with reviews of the Canadian fauna and diplopod faunistic studies. Canadian Journal of Zoology 80: 1863–1875. doi: 10.1139/z02-170

Snider RM (1984) The ecology of *Polydesmus inconstans* (Diplopoda: Polydesmidae) in Michigan wood lots. Pedobiologia 26: 185–196.

Southcott RV (1987) A new larval mite (Acarina: Trombidioidea) ectoparasitic on an Australian centipede, and the Trombidiidae reclassified. Transactions of the royal Society of South Australia 3 (1): 43–52.

Southwood TRE (1973) The insect/plant relationship - an evolutionary perspective. In: Van Emden HF (Ed) Insect/Plant Relationships. Halsted Press, London, p. 3–30.

Swafford L, Bond JE (2009) The symbiotic mites of some Appalachian Xystodesmidae (Diplopoda: Polydesmida) and the complete mitochondrial genome sequence of the mite *Stylochyrus rarior* (Berlese) (Acari : Mesostigmata : Ologamasidae). Invertebrate Systematics 23 (5): 445–451. doi: 10.1071/IS09036

Szabo IM, Nasser EGA, Striganova BR, Rakhmo YR, Jäger K, Heydrich M (1992) Interactions among Millipedes (Diplopoda) and their Intestinal Bacteria. Berichte des Naturwissenschaftlich-medizinischen Vereins in Innsbruck, Supplementum 10: 289–296.

Trägårdh I (1906) Neue Acariden aus Natal und Zululand. Zoologischer Anzeiger 30 (26): 870–877.

Trägårdh I (1907) Description of two myriopodophilous genera of Antennophorinae, with notes on their development and biology. Arkiv för Zoologi 3 (28): 1–35.

Trägårdh I (1950) Studies on the Celaenopsidae, Diplogyniidae and Schziogyniidae. Arkiv för Zoologi 1 (25): 361–449.

Uppstrom K, Klompen H (2005) A new species of *Julolaelaps* (Acari: Iphiopsididae) from African millipedes. International Journal of Acarology 31 (2): 143–147. doi: 10.1080/01647950508683666

Vitzthum HG (1925) Fauna sumatrensis (Beitrag No. 5) Acarinae. Supplementa Entomologica 11: 37–48.

Vitzthum HG (1921) Acarologische Beobachtungen. Archiv für Naturgeschichte 86: 14–22.
Walter DE, Krantz GW (2009) Oviposition and Life Stages. In: Krantz GW, Walter DE (Eds) A Manual of Acarology. Texas Tech University Press, Lubbock, Texas, p. 57–63.
Womersley H (1956) On some new Acarina-Mesostigmata from Australia, New Zealand and New Guinea. Linnean Society's Journal-Zoology 42 (No. 288): 505–599.
Womersley H (1958) Some Acarina from Australia and New Guinea paraphagic upon millipedes and cockroaches, and on beetles of the family Passalidae. Pt 2. The family Diplogyniidae (Mesostigmata-Trigynaspida). Transactions of the Royal Society of South Australia 81: 13–29.

Appendix I

Voucher numbers for millipede hosts.

Millipede species	Author, year	Accession number
Abacion lactarium	(Say, 1821)	N/A
Blaniulus guttulatus	(Fabricius, 1789)	OSAL0100704 ♂
Brachyiulus lusitanus	Verhoeff, 1898	OSAL0100959 ♂
		*OSAL006951 ♂
Brachyiulus pusillus	(Leach, 1815)	OSAL0100593 ♂
Choneiulus palmatus	(Nemec, 1895)	OSAL0100811 ♂
Cleidogona caroliniana	Causey, 1957	OSAL0100283 ♂
Cylindroiulus britannicus	(Verhoeff, 1891)	OSAL0100455 ♀
		OSAL0100394 ♂
		*OSAL006949 ♀
		*OSAL006950 ♂
Cylindroiulus caeruleocinctus	(Wood, 1864)	OSAL0100759 ♂
		*OSAL006948 ♂
Cylindroiulus latestriatus	(Curtis, 1845)	OSAL0100650 ♂
		*OSAL006947 ♂
Cylindroiulus londinensis	(Leach, 1815)	OSAL0100375 ♂
		*OSAL006955 ♂
Cylindroiulus punctatus	(Leach, 1815)	OSAL0100417 ♂
Cylindroiulus truncorum	(Silvestri, 1896)	OSAL0100935 ♀
		OSAL0100536 ♂
		*OSAL006952 ♂
Euryurus leachii	(Gray, 1832)	OSAL0100840 ♂
Glomeris marginata	(Villers, 1789)	OSAL0100376 ♂
Julus scandinavicus	Latzel, 1884	OSAL0100358 ♂
Nopoiulus kochii	(Gervais, 1836)	OSAL0100282 ♂
Ommatoiulus sabulosus	(Linné, 1815)	OSAL0100403 ♂
Ophyiulus pilosus	(Newport, 1843)	OSAL0100423 ♀
		OSAL0100613 ♂
		*OSAL006954 ♀
		*OSAL006953 ♂
Paraspirobolus lucifugus	(Gervais, 1836)	OSAL0100386 ♂
Polydesmus angustus	(Latzel 1884)	OSAL0100439 ♂
Tachypodoiulus niger	(Leach, 1815)	OSAL0100384 ♂
Uroblaniulus carolinensis	Causey, 1953	OSAL0100882 ♂

* denotes slide of genitalia

Appendix 2

Voucher numbers for associated mite morphospecies.

Mite morphospecies	Accession number
Holostapis sp.	OSAL0006958
Phaulodinychus sp.	OSAL0006790
Rhizoglyphus A	OSAL0083451
Rhizoglyphus B	OSAL0006896
Sancassania A	OSAL0006911
Sancassania B	OSAL0083471
Schwiebea A	OSAL0000697
Schwiebea C	OSAL0006942
Schwiebea D	OSAL0083456
Schwiebea E	OSAL0083474
Schwiebea F	OSAL0006853
Schwiebea G	OSAL0083448
Schwiebea H	OSAL0006939
Thyreophagus sp.	OSAL0006843