

Oribatid mite diversity along an elevation gradient in a southeastern appalachian forest

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Summary. The abundance and diversity of oribatid mites in soil and litter was investigated at five sites along an elevation gradient of forest types at Coweeta Hydrologic Laboratory, Macon County, North Carolina, USA. A total of 135 species was collected from the five sites. Diversity indices (H' , J') suggested an increase in oribatid species diversity with increasing elevation. A single, very rich oribatid mite community was found over the entire elevation gradient, although the distribution of less abundant species differed between the sites. The two sites with lower abundances had higher species diversity indices. Lower abundance of soil oribatid mites may be characteristic of southeastern Appalachian sites which are mature or approaching maturity. The largest number of species was found for mixed oak communities, the predominant vegetation type at Coweeta.

Key words: Acarina, Oribatida, diversity, microarthropods, elevation gradient

Introduction

Soil microarthropods are abundant members of the forest floor fauna, widespread in occurrence, and implicated as being directly and indirectly important in decomposition processes and nutrient dynamics of forest ecosystems (Crossley 1977; Coleman and Crossley 1996). Microarthropod abundance, species distribution and community structure exhibit spatial variation at several hierarchic levels: latitudinally (Harding & Stuttard 1974), between local sites (Reeves 1969, 1973; McBrayer et al. 1977; Stanton 1979; Plowman 1981; Wauthy et al. 1989), and within sites at the microsite level (Metz & Farrier 1967; Usher 1975b; Anderson 1978; Luxton 1981a; 1981b; Schenker 1984; Stamou & Sgardelis 1989; Asikidis & Stamou 1991).

A multitude of studies have documented this variation and subsequently attempted to elucidate the biotic and abiotic factors responsible for it. Environmental variables are not independent of one another and community composition on a broad spatial scale may be determined by their combined effect. On smaller scales, soil microarthropods exhibit a contagious or aggregated distribution within sites (Usher 1976). This small-scale variation may be related to intraspecific relationships, food resources and oviposition sites (Butcher et al. 1971). Additionally, a number of studies have reported that microsite factors such as, soil temperature, soil moisture, soil organic matter, soil structure, C/N ratio, pH, and concentra-

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tion of nutrients, such as potassium, nitrogen, calcium, phosphorus, are important in explaining the variation in numbers and community composition of microarthropods (Mitchell 1978; Banerjee 1984; Schenker 1984; Tousignant & Coderre 1992). Temporal variation in microarthropod abundance has been attributed to factors such as temperature, precipitation, and litterfall (Usher 1975a; Luxton 1981b).

Among the soil microarthropods, oribatid mites are usually the numerically dominant group in temperate forest soils (Petersen & Luxton 1982, Wallwork 1983). Quantitative studies of oribatid mite communities – the diversity and abundance of species – require intensive sampling (Usher et al. 1982). There have been only a few studies which attempt to investigate the distribution and abundance these animals in relation to environmental gradients. Walter (1985) reported that as elevation increases on the Salmon Creek watershed, Oregon, the oribatid species inhabiting the litter layer decrease in both richness and similarity to the lower elevation species assemblages. Other elevation studies on different soil fauna have found groups to increase or decrease in importance as elevation increases (Atkin & Proctor 1988). Using principal component analysis, Stamou and Sgardelis (1989) recognized three zones of macrofauna abundance along a mountain gradient in Greece.

In research reported here, we postulated that oribatid mites would have different abundances at different elevations, because of changes in litter decomposition rates or other properties resulting from lower temperatures in high-elevation forest floors. We asked: Do oribatid mite species assemblages differ among the elevation gradient sites, as functions of changing climate or shifts in forest ecosystem structure or function (Whittaker 1956)? Do different species become dominant at different elevations? Do numbers of species change with elevation?

In the southern Appalachian mountains, any effects of climatic change may become manifest first at higher elevations. By documenting the nature of oribatid communities at this time, we provide background information against which future changes may be evaluated.

Materials and Methods

Research was conducted at The Coweeta Hydrologic Laboratory, located in the Nantahala Mountain Range of western North Carolina within the Blue Ridge Physiographic Province, latitude 35° 03' N, longitude 83° 25' W. Mean annual temperature is 12.6°C, and mean annual precipitation, 1821 mm (Swift et al. 1988). We sampled from five hardwood forest stands selected as part of a Long-Term Ecological Research (LTER) project (Hoover & Crossley 1995). These mixed hardwood stands (Table 1) are located on two control watersheds (WS-18 and WS-27), which have remained relatively undisturbed since 1934 (Swank & Crossley 1988).

Sampling of soil microarthropods was initiated in January 1992 and continued until December 1992. Three 1-m² subplots were established within each of the five LTER sites (see Table 1). Subplots were located well away from trees and woody debris in order to reduce local microhabitat effects on numbers and composition of microarthropods obtained at each site. Three cylindrical soil cores (5 cm diameter by 5 cm deep) were taken monthly within each of these subplots for a total of 9 samples per site per month. Soil cores were transported to the University of Georgia, refrigerated overnight, and extracted

Table 1. Site descriptions and leaf litter dynamics for Long-Term Ecological Research plots at Coweeta Hydrologic Laboratory for 1992. (Leaf litter decomposition rates from Hoover and Crossley 1995)

site	vegetation type	aspect	elevation	basal area m ² /ha	leaf litter decomp. rate (k)	leaf litterfall g/m ²	C/N ratio
118	pine-oak ridge	180°	782 m	21.4	-0.37	318	37
218	cove hardwoods	340°	795 m	30.0	-0.34	276	19
318	low elevation mixed oak	15°	865 m	30.4	-0.45	382	23
427	high elevation mixed oak	75°	1001 m	29.0	-0.41	378	30
527	northern hardwoods	20°	1347 m	23.4	-0.37	265	14

with the litter profile inverted for five days (Usher & Blair 1991). Fauna were collected by sieving through a 1.5 × 1.5 mm sieve and Pauropoda found in this area were collected. Microarthropod samples from only the oribatid mites were initially sorted and counted with a wide range of sieves sorted to suborder, and the remainder of the fauna sorted to species wherever possible. All adult oribatid mites were identified to genus and morphospecies. Specific identification to species wherever possible, specific identification.

Analysis of Data

The data for oribatid mites and total microarthropod abundance is usually found to follow a normal distribution, therefore, a natural log transformation was applied (Gerard & Berthet 1966). Significance of differences between each set of transformed data.

Community composition and relative species richness and similarity indices. For most data sets, the number of species was reduced by pooling similar species. Diversity indices were chosen for their ability to measure species richness (Hill 1973). Diversity was measured with Menhinicks's richness index (*R*), dominance index (*J'*). Similarity indices seek to estimate the degree of similarity between communities (Fujikawa 1974). Mountford's (1974) similarity index was used to compare assemblages and construct dendrograms.

Results

Distribution of microarthropods

A total of 46,519 microarthropods were collected during the odd-numbered months of 1992 (Table 1). The majority of the total collected, comprising 74.8% of the total, were oribatid mites. The remainder of the arthropods were "Other arthropods". This category included Protocollinida, Chilopoda, Diplopoda, Coleoptera, and other groups. Other animals comprised only 7% of the total. Microarthropod abundance increased with elevation (Fig. 1). Abundance was lowest

Table 2. Microarthropod densities in soil at Coweeta Hydrologic Laboratory (variate are numbers per 5 cm diameter core)

Arthropod Group	individuals (n = 27)
Acarina	128.8 ± 12.1
Oribatida	86.9 ± 12.1
Prostigmata	26.1 ± 12.1
Mesostigmata	15.8 ± 12.1
Collembola	31.3 ± 12.1
Other microarthropods	12.1 ± 12.1
Total	172.2 ± 12.1

phosphorus, are important in extinction of microarthropods (Mitchell 1992). Temporal variation in such as temperature, precipitation,

the numerically dominant group (Proctor 1983). Quantitative studies of species – require intensive samplings which attempt to investigate the environmental gradients. Walter and Proctor (1989) recognized three zones of soil fauna in the lower part of the soil profile.

Soil fauna would have different abundances and composition rates or other properties in different floors. We asked: Do oribatid mite communities at sites, as functions of changing environmental conditions (Whittaker 1956)? Do different numbers of species change with elevational

change may become manifest in oribatid communities at this time, we can suggest that changes may be evaluated.

Study site, located in the Nantahala Mountain National Forest, North Carolina, is a temperate montane region with an annual precipitation, 1821 mm (Swift 1992). The site is part of a Long-Term Ecological Research (LTER) mixed hardwood stands (Table 1) and has remained relatively undisturbed since 1980.

Soil samples were collected in 1992 and continued until December 1992. The LTER sites (see Table 1). Subplots were established to evaluate local microhabitat effects on numbers of soil fauna. The cylindrical soil cores (5 cm diameter) were collected for a total of 9 samples per site per year, refrigerated overnight, and extracted

in the LTER Ecological Research plots at Coweeta National Forest (see Hoover and Crossley 1995)

Basal area (m ² /ha)	leaf litter decomp. rate (k)	leaf litterfall g/m ²	C/N ratio
11.4	-0.37	318	37
10.0	-0.34	276	19
10.4	-0.45	382	23
9.0	-0.41	378	30
13.4	-0.37	265	14

with the litter profile inverted for five days on a modified Tullgren-style high-gradient extractor (Crossley & Blair 1991). Fauna were collected in 95% ethyl alcohol. Microarthropods collected were those capable of passing through a 1.5 × 1.5 mm screen mesh. Most Acarina, Collembola, Protura, Symphyla and Paurodora found in this area were capable of passing through this mesh size.

Microarthropod samples from only the odd-numbered months were completely analyzed. Samples were initially sorted and counted with a wide-field binocular microscope at 70× magnification. Acari were sorted to suborder, and the remainder of the fauna were sorted to order. Oribatid mites were identified to species wherever possible. All adult oribatids were mounted on slides in CMC-10 medium and identified to genus and morphospecies. Specimens were ultimately sent to Dr. Roy A. Norton, State University College of Environmental Science and Forestry, Syracuse, New York, for corroboration and, where possible, specific identification.

Analysis of Data

The data for oribatid mites and total microarthropods were analyzed separately. Forest soil microarthropod abundance is usually found to fit a negative binomial distribution (Hartenstein 1961). Therefore, a natural log transformation was applied to normalize abundance for parametric statistical methods (Gerard & Berthet 1966). Significance of differences was tested by a one-way analysis of variance for each set of transformed data.

Community composition and relative species abundance of oribatid mites were investigated with diversity and similarity indices. For most data analyses the high variation in diversity and species composition among samples was reduced by pooling data from all 9 samples from each site on each date. Four diversity indices were chosen for their ability to measure diversity and discriminate richness and evenness (Hill 1973). Diversity was measured with the Shannon-Wiener index (H'), richness was measured with Menhinicks's richness index (R), dominance with Simpson's index (D) and evenness with Pielou's index (J'). Similarity indices seek to estimate inter-site or β -diversity. The Morisita-Horn ($C\lambda$) index utilizes quantitative data and measures the degree of overlap of component species between communities (Fujikawa 1974). Mountford's (1962) method was used to classify similarity of oribatid assemblages and construct dendrograms.

Results

Distribution of microarthropods

A total of 46,519 microarthropods was extracted from the 270 soil samples analyzed for the odd-numbered months of 1992 (Table 2). Acari were by far the most abundant order collected, comprising 74.8% of the total fauna. Collembola (18.2%) were the next most abundant group. The remainder of the arthropods were combined and designated "other microarthropods". This category included Protura, Paurodora, Symphyla, Arachnida, Psuedoscorpionida, Chilopoda, Diplopoda, Coleoptera, Homoptera, Hymenoptera and Diptera. These animals comprised only 7% of the total microarthropod fauna.

Microarthropod abundance increased at each site from January through November ($P < 0.001$, Fig. 1). Abundance was lowest and least variable over time for the cove and northern

Table 2. Microarthropod densities in soil samples from forested stands at Coweeta Hydrologic Laboratory (variates are numbers per 5 cm dia × 5 cm deep core samples)

Arthropod Group	individuals/sample ± se (n = 270)	10 ³ individuals/m ²
Acarina	128.8 ± 8.6	65.6
Oribatida	86.9 ± 6.7	44.2
Prostigmata	26.1 ± 1.6	13.3
Mesostigmata	15.8 ± 1.4	8.1
Collembola	31.3 ± 2.2	15.9
Other microarthropods	12.1 ± 1.0	6.2
Total	172.2 ± 11.1	87.7

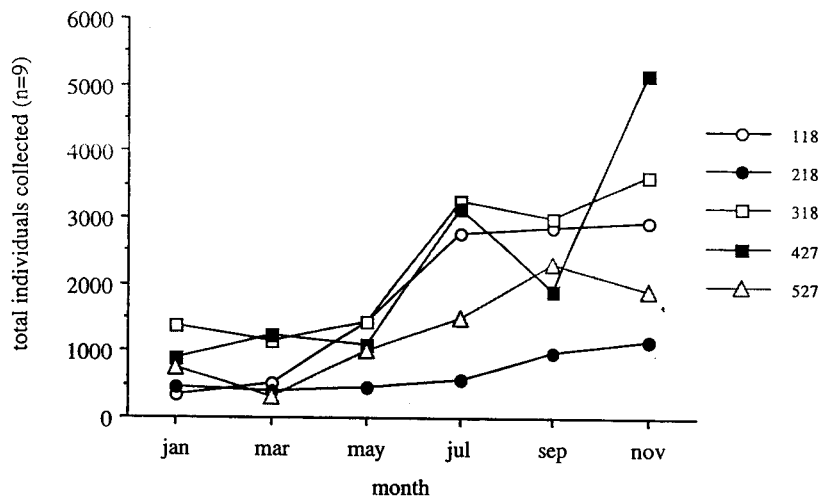


Fig. 1. Soil microarthropod abundance (all samples pooled) over time for each gradient site at Coweeta Hydrologic Laboratory, North Carolina, USA: Pine-oak ridge (118), Cove hardwoods (218), Low-elevation mixed oak (318), High-elevation mixed oak (427), Northern Hardwoods (527)

hardwoods sites, and highest and most variable in the high-elevation mixed oak. For all dates combined, differences in abundance between the sites were significant ($P < 0.001$). The cove hardwood site had the lowest densities, the northern hardwood site had intermediate densities, and the other three sites had highest densities.

Oribatid abundance

The suborder Oribatida comprised 68% of total Acari collected. A total of 8,644 adult oribatids was identified to morphospecies. Total abundance of adult oribatids increased during the sampling period (Fig. 2). Numbers remained fairly stable from January through July and

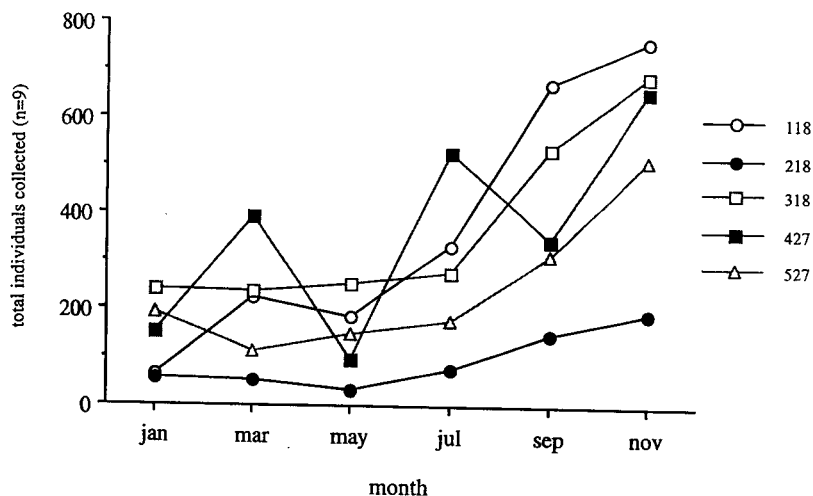


Fig. 2. Adult oribatid mites (all samples pooled) over time for each gradient site at Coweeta Hydrologic Laboratory, North Carolina, USA: Pine-oak ridge (118), Cove hardwoods (218), Low-elevation mixed oak (318), High-elevation mixed oak (427), Northern Hardwoods (527)

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 batid abundance varied least over
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 Abundance of oribatids at the site
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 northern hardwood site, and higher
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Table 3. Adult oribatid densities in 5 Coweeta Hydrologic Laboratory

Site (lowest to highest)

Pine-oak ridge (118)
Cove hardwoods (218)
Low-elevation mixed oak (318)
High-elevation mixed oak (427)
Northern hardwoods (527)

Diversity Measures of Oribatid Mites

In general, samples of oribatids from
 and low dominance. Diversity indices
 (N) and simple richness (number of s
 species collected per site ranged from
 the low-elevation mixed oak site. The
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 sity with increasing elevation (Table 4)
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 to be the most diverse site. But, except

Table 4. Diversity measures, individuals (N)

Site	Total	N
Pine-oak ridge (118)	2237	
jan	64	
mar	224	
may	185	
jul	331	
sep	674	
nov	758	

then showed a steady increase until November. As with all microarthropods combined, oribatid abundance varied least over time in the cove and northern hardwood sites, and fluctuated most widely at the high-elevation mixed oak site.

Abundance of oribatids at the sites did not show any trend associated with elevation. Total oribatid abundance was lowest in the cove hardwood site, intermediate at the high elevation northern hardwood site, and highest at the remaining sites (Table 3). For all dates combined, ANOVA for differences in mean population densities among the sites was highly significant ($P < 0.001$). Oribatid abundance at the cove hardwood site was significantly lower than all other sites, and the abundance of oribatids at the northern hardwood site was significantly lower than at the two intermediate elevation sites.

Table 3. Adult oribatid densities in 5×5 cm soil samples for each site in an elevational gradient at Coweeta Hydrologic Laboratory

Site (lowest to highest)	mean/sample \pm se (n = 54)	10^3 ind./m ²
Pine-oak ridge (118)	41.4 \pm 6.7	21.1
Cove hardwoods (218)	10.2 \pm 1.8	5.2
Low-elevation mixed oak (318)	41.4 \pm 5.9	21.1
High-elevation mixed oak (427)	40.2 \pm 6.2	20.4
Northern hardwoods (527)	26.9 \pm 4.5	13.7

Diversity Measures of Oribatid Mites

In general, samples of oribatids from all sites showed high diversity, richness and evenness, and low dominance. Diversity indices across sites and dates are shown in Table 4. Abundance (N) and simple richness (number of species, S) both increased over time. The total number of species collected per site ranged from a low of 64 in the cove hardwood site to a high of 96 in the low-elevation mixed oak site. The combination of diversity indices suggested species-rich assemblages, low in dominance. Simpson's dominance index (D) fluctuated irregularly over time, and was low for all sites, indicating low dominance. Values for Pielou's evenness index (J') were very high for all sites, again implying low dominance. Evenness varied less than other diversity indices. The Shannon diversity index (H') was high for all dates at all sites, but fluctuated a great deal between sites and across time. Lowest diversity measures for all sites were recorded in May with the exception of the northern hardwood site. Although S increased over time, Menhinick's richness index (R) declined over time at each site. This index was lowest for each sampling date at the pine-oak ridge and highest at the cove hardwood and northern hardwood sites.

With the exception of the cove hardwood site, the indices indicated a slight increase in diversity with increasing elevation (Table 4). The cove hardwood site had the highest total richness (R) and evenness (J') and by far the lowest dominance (D), which combine to make it appear to be the most diverse site. But, except for the cove hardwood site, the diversity index H' in-

Table 4. Diversity measures, individuals (N), and species (S) at each elevation gradient site

Site		N	S	Richness (R)	Diversity (H')	Evenness (J')	Dominance (D)
Pine-oak ridge (118)	Total	2237	78	1.649	3.276	.752	.057
	jan	64	19	2.375	2662	.904	.072
	mar	224	37	2.472	3.024	.838	.067
	may	185	24	1.765	2.597	.817	.092
	jul	331	37	2.034	2.953	.818	.071
	sep	674	46	1.772	2.818	.736	.095
	nov	758	41	1.489	2.907	.783	.082

Table 4. continue

Site		N	S	Richness (R)	Diversity (H')	Evenness (J')	Dominance (D)
Cove Hardwoods (218)	Total	570	64	2.680	3.643	.876	.034
	jan	54	26	3.583	2.762	.848	.099
	mar	53	21	2.885	2.658	.873	.081
	may	31	17	3.053	2.684	.948	.047
	jul	75	33	3.811	3.292	.942	.032
	sep	149	30	2.458	2.944	.866	.062
	nov	190	36	2.680	3.643	.888	.051
Low-elevation oak (318)	Total	2234	96	2.031	3.406	.746	.060
	jan	241	44	2.834	3.006	.794	.079
	mar	237	41	2.663	3.024	.814	.073
	may	252	33	2.079	2.745	.785	.098
	jul	277	51	3.065	3.339	.849	.050
	sep	537	58	2.503	3.342	.823	.055
	nov	690	55	2.094	2.990	.746	.083
High-elevation oak (427)	Total	2192	92	1.965	3.440	.761	.066
	jan	152	39	3.163	3.234	.8883	.047
	mar	392	49	2.475	3.216	.826	.060
	may	97	28	2.843	2.751	.826	.106
	jul	528	59	2.568	3.285	.806	.060
	sep	345	44	2.369	3.001	.793	.094
	nov	657	57	2.224	3.151	.779	.088
Northern hardwoods (527)	Total	1454	81	2.124	3.483	.793	.053
	jan	193	45	3.239	3.281	.862	.050
	mar	113	31	2.916	3.165	.992	.042
	may	148	38	3.124	3.211	.883	.053
	jul	176	38	2.864	3.186	.876	.054
	sep	310	40	2.272	2.875	.779	.088
	nov	511	51	2.256	3.022	.769	.083

creased with increasing elevation. Dominance showed no clear trend. No clear patterns emerge from the diversity measures over time, making it difficult to make any assumptions about seasonal changes in diversity of oribatid mite communities.

Similarity of Assemblages

A dendrogram, constructed according to Mountford (1962) from the Morisita-Horn similarity measure, suggested that the oribatid assemblages at all sites were essentially similar to one another. The two mixed oak sites were most similar in species composition, while the pine-oak ridge and cove hardwood were most dissimilar (Fig. 3). Furthermore, there was no clear pattern of similarity along the elevation gradient. The fact that the two intermediate elevation sites (318 and 427) demonstrated high similarity is probably due to similarity in vegetation type (Table 1) rather than proximity in elevation.

Species Composition of Oribatid Assemblages

A total of 135 species from 52 families and 87 genera were identified (Appendix I). Many of the adult oribatids could be identified only to morphospecies. Some evidently are unnamed. We are continuing efforts to compile a more complete species list for oribatids of the southern Appalachians.

The species composition of the assemblages varied between the five sites, but the same dominant species occurred in all sites. Table 5 shows the abundance of each species at each

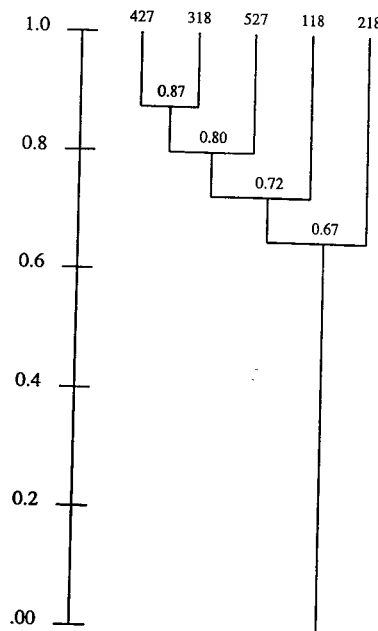


Table 5. Percent representation of the mon at all sites to species common at o elevation mixed oak (318), high-elevati

Species

- Suctobelbella* spp
- Oppiella* spp
- Tectocephus* sp. nr. *velatus*
- Quadroppia* sp a
- Atropacarus striculus*
- Ceratozetes angustus*
- Carabodes falcatus*
- Micropopia minus*
- Nanhermannia dorsalis*
- Eniochthonius* sp a
- Eremobodes* sp. nr. *pectinatus*
- Xylobates robustior*
- Epilomannoides terrae*
- Malaconothrus* sp a
- Lasiobelba rigida*
- Pergalumma curva*
- Eohypochthonius* sp a
- Parachipteria* sp a
- Scheloribates lanceoliger*
- Oppia parviaures*
- Carabodes spiniformes*
- Insculptoppia* sp a
- Ceratozetes* sp. nr. *mediocris*
- Xylobates capucinus*
- Caleremaeus* sp a

* represented by less than 3.0 %

Diversity (H')	Evenness (J')	Dominance (D)
3.643	.876	.034
2.762	.848	.099
2.658	.873	.081
2.684	.948	.047
3.292	.942	.032
2.944	.866	.062
3.643	.888	.051
3.406	.746	.060
3.006	.794	.079
3.024	.814	.073
2.745	.785	.098
3.339	.849	.050
3.342	.823	.055
2.990	.746	.083
3.440	.761	.066
3.234	.8883	.047
3.216	.826	.060
2.751	.826	.106
3.285	.806	.060
3.001	.793	.094
3.151	.779	.088
3.483	.793	.053
3.281	.862	.050
3.165	.992	.042
3.211	.883	.053
3.186	.876	.054
2.875	.779	.088
3.022	.769	.083

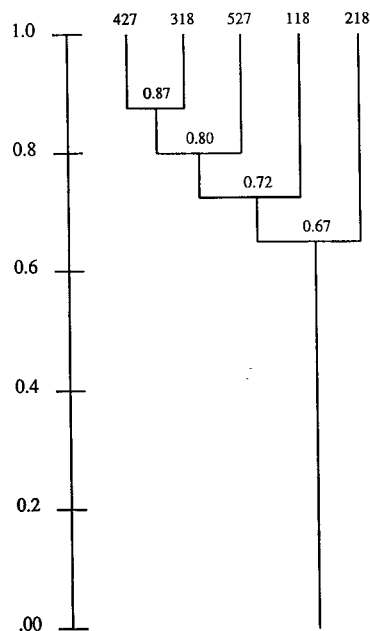


Fig. 3. Similarity of oribatid mite assemblages between LTER gradient sites at Coweeta Hydrological Laboratory, North Carolina

Table 5. Percent representation of the most common species in each site. Arranged from species common at all sites to species common at only one site. Pine-oak ridge(118), cove hardwoods (218), low-elevation mixed oak (318), high-elevation mixed oak (427) and northern hardwoods (527).

Species	Sites				
	118	218	318	427	527
<i>Suctobelbella</i> spp	10.9	11.0	10.8	7.6	14.9
<i>Oppiella</i> spp	11.0	6.8	15.4	20.4	10.4
<i>Tectocephus</i> sp. nr. <i>velatus</i>	4.6	4.0	9.8	3.3	*
<i>Quadroppia</i> sp a	*	5.4	4.5	*	7.4
<i>Atropacarus striculus</i>	8.3	3.9	5.3	*	*
<i>Ceratozetes angustus</i>	7.3	*	*	3.5	*
<i>Carabodes falcatus</i>	*	*	5.3	5.2	*
<i>Microppia minus</i>	3.8	*	3.5	*	*
<i>Nanhermannia dorsalis</i>	8.7	*	*	*	4.1
<i>Eniochthonius</i> sp a	*	5.4	*	*	4.1
<i>Eremobodes</i> sp. nr. <i>pectinatus</i>	4.9	*	*	*	*
<i>Xylobates robustior</i>	3.5	*	*	*	*
<i>Epilomannoides terrae</i>	3.4	*	*	*	*
<i>Malaconothrus</i> sp a	3.6	*	*	*	*
<i>Lasiobelba rigida</i>	*	5.4	*	*	*
<i>Pergalumma curva</i>	*	3.3	*	*	*
<i>Eohypochthonius</i> sp a	*	5.8	*	*	*
<i>Parachipteria</i> sp a	*	*	3.6	*	*
<i>Scheloribates lanceoliger</i>	*	*	*	5.1	*
<i>Oppia parviaures</i>	*	*	*	3.6	*
<i>Carabodes spiniformes</i>	*	*	*	3.8	*
<i>Insculptoppia</i> sp a	*	*	*	3.1	*
<i>Ceratozetes</i> sp. nr. <i>mediocris</i>	*	*	*	3.3	*
<i>Xylobates capucinus</i>	*	*	*	*	4.8
<i>Caleremaeus</i> sp a	*	*	*	*	6.5

* represented by less than 3.0%

no clear trend. No clear patterns difficult to make any assumptions on.

from the Morisita-Horn similarity sites were essentially similar to one in species composition, while the (Fig. 3). Furthermore, there was no The fact that the two intermediate is probably due to similarity in on.

re identified (Appendix I). Many of species. Some evidently are unnamed. species list for oribatids of the southern

between the five sites, but the same abundance of each species at each

site, expressed as a percentage. The ubiquitous *Suctobelbella* and *Oppiella* species complexes dominated the oribatid assemblages at all sites. No other species comprised more than 10% of the individuals at any site (Table 5). *Oppiella* spp. were most numerous in the two mixed oak sites, and *Suctobelbella* most numerous in cove and northern hardwood sites. Eight other species of moderate abundance (3%–10% of total individuals) were found at more than one site. Among these, the common species *Tectocephus velatus* was collected from all sites (although at low numbers in the northern hardwood site). *Atropacarus striculus* was common in the three lower elevation sites.

Fifteen moderately abundant oribatid species (3%–7%) were restricted to a single site on the elevation gradient. Many of the remaining species were found at more than one site, some at all five sites, but with low relative abundances (Appendix I).

Discussion

The soil microarthropod community of aggrading hardwood forest sites at Coweeta appears to be dominated by oribatid mite species, at all five sites in the elevation gradient and during all seasons of the year. Variations in numbers of total microarthropods generally mirrored variations in oribatid mite numbers. Our sampling methods (Tullgren extraction) may have underestimated populations of onychiurid collembolans (Edwards 1991). The depth of our samples (5 cm) doubtless missed some species which occur further down in the soil profile, but Seastedt and Crossley (1981) reported that over 90% of microarthropods were found in the top 5 cm of soil in undisturbed Coweeta watersheds.

Samples from the elevation gradient revealed a species-rich oribatid community. Few comparable data exist for this region. A previous listing of oribatid species at Coweeta (Abbott et al. 1980) contained only one-third as many species. Crossley & Bohnsack (1960) found 59 oribatid species from an aggrading mixed pine stand in east Tennessee, compared with the 135 species reported here from Coweeta watersheds (Appendix I). It is likely that the productive mixed hardwood forest stands, the temperate climate, and the year-long pattern of adequate rainfall provide an optimum habitat for these soil mites (Swank & Crossley 1988). The forest floors evidently contain a wide variety of resources and microhabitats, but it is not clear how oribatid species may be subdividing them (Siepel and Ruiten-Dijkman 1993).

Only subtle differences appeared between oribatid mite communities at the different sites. All sites were found to have a diverse assemblage of oribatid species with low dominance. The most abundant species groups were the same at each site. The two mixed oak sites shared a number of species in common, and were similar in that *Oppiella* spp. outnumbered *Suctobelbella* spp. Mixed oak is the predominant vegetation type at Coweeta. The two mixed oak sites contained the greatest number of oribatid mite species (92 and 96). The low elevation cove hardwoods had the smallest number of species (64). Since sampling effort was equal at all sites, these differences indicate that the cove hardwood site was relatively depauperate.

The differences in elevation between the sites along the gradient were confounded by other, independent variables. The pine-oak ridge and the cove hardwood sites were not duplicated at other elevations. The patterns of oribatid mite distribution among the five sites did not display any evidence of the effect of elevation, per se, although some diversity indices did show an effect. The most unique site was the cove hardwood stand where abundance of oribatids was significantly lower than any other site. Perhaps as a result of this depression of numbers, diversity indices indicate that the cove hardwood stand contained the most diverse oribatid community, despite the low number of species collected. Aside from the cove hardwood site, the diversity indices H' and J' increased with elevation.

It is unlikely that altitude, by itself, is responsible for any relationships between elevation and oribatid mite assemblages found in this study. The five sites differ in ways other than elevation (Table 1). Plant communities, temperature and moisture regimes change with increased elevation. Other investigators have observed that moisture, soil type, pH, SOM, C:N ratio, nutrient concentrations and various other factors can be implicated in increased abundance or

compositional changes in oribatid and lowest abundance of oribatid litter inputs (Crossley, unpublished 1995). Mature stages in forest succession primary production, slower decomposition in cove and northern hardwood (crossing) approaching respiration and are associated with climax communities? These communities are variable seasonally, and with high diversity at high elevation sites. Species richness may increase with stages but perhaps evenness increases with variable. Plant communities on mature forest, xeric communities may approach a asymptote late in succession. These results suggest that oribatid mite communities increase in species diversity indicate undisturbed watersheds at Coweeta. The abundance of oribatids and more s

Acknowledgments

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a and *Oppiella* species complexes species comprised more than 10% most numerous in the two mixed northern hardwood sites. Eight other mites were found at more than one site. *Suctobellicosus* was collected from all sites and *Tropacarus striculus* was common

was restricted to a single site on the elevation gradient and during microarthropods generally mirrored the pattern of soil microarthropods (Tullgren extraction) may have been found at more than one site, some at low elevations.

of forest sites at Coweeta appears to be the elevation gradient and during microarthropods generally mirrored the pattern of soil microarthropods (Tullgren extraction) may have been found at more than one site, some at low elevations.

of oribatid community. Few oribatid species at Coweeta (Abbott et al. 1960) found 59 species at Coweeta, compared with the pattern of soil microarthropods (Appendix I). It is likely that the pattern of soil microarthropods, and the year-long pattern of soil mites (Swank & Crossley 1988). species and microhabitats, but it is not clear if the pattern of soil microarthropods and Ruiten-Dijkman 1993).

communities at the different sites. All oribatid species with low dominance. The pattern of soil microarthropods. The two mixed oak sites shared a pattern of soil microarthropods. *Oppiella* spp. outnumbered *Suctobellicosus* at Coweeta. The two mixed oak sites (1992 and 1996). The low elevation cove sites had a relatively depauperate pattern of soil microarthropods.

of the elevation gradient were confounded by other factors. The two mixed oak sites were not duplicated in the pattern of soil microarthropods among the five sites did not distinguish some diversity indices did show that abundance of oribatids result of this depression of numbers, contained the most diverse oribatid community. Aside from the cove hardwood site,

relationships between elevation and oribatid diversity differ in ways other than elevation. Soil moisture regimes change with increased elevation, soil type, pH, SOM, C:N ratio, and are implicated in increased abundance or

compositional changes in oribatid communities. The two sites with highest diversity indices and lowest abundance of oribatids (cove hardwoods, northern hardwoods) also had lower leaf litter inputs (Crossley, unpublished) and slower decomposition rates (Hoover & Crossley 1995). Mature stages in forest succession are characterized by respiration which approaches net primary production, slower decomposition rates, and higher biomass. Do measures for the cove and northern hardwood (decomposition rates, litterfall) indicate that production is approaching respiration and are these two sites displaying ecosystem properties associated with climax communities? These are the sites in which oribatid abundance is lower and less variable seasonally, and with higher oribatid species diversity measures than the other gradient sites. Species richness may or may not increase with advancing successional forest stages but perhaps evenness increases, dominance decreases and population sizes are less variable. Plant communities on mesic sites decline in diversity from late successional to equilibrium forest, xeric communities increase in diversity through time, and intermediate sites approach an asymptote late in succession according to Auclair and Goff (1971). Our measurements suggest that oribatid mite communities may decline in abundance of individuals but increase in species diversity indices as forest ecosystems approach equilibrium. Most of the undisturbed watersheds at Coweeta are in an aggrading phase, and thus tend to support larger abundance of oribatids and more species, with somewhat lower diversity indices.

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Appendix I. Species distribution with site number: Pine-oak ridge (118), Cove oak (427) and Northern hard

Species

PALEOSOMATA

Zachvatkinella sp a

ENARTHRONOTA

Eohypochthonius sp a

Hypochthonius rufulus carolinicus Jacot

Liochthonius fimbriatus (Jacot, 1936)

Eniochthonius sp a

Brachychthonius jugatus (Jacot, 1938)

Eobrachychthonius sp a

Liochthonius sp a

Liochthonius sp b

Poecilochthonius sp a

Sellnickochthonius zelawaiensis (Sellnick)

Pterochthonius sp a

Atopochthonius sp a

MIXONOMATA

Atropacarus striculus (C. L. Koch, 1835)

Archiphthiracarus sp a

Phthiracarus sp a

Phthiracarus sp b

Mesotritia sp. nr. *glabrata* (Say)

Eupthiracarus sp a

Microtritia sp a

Rhysotritia spp.

Synichotritia sp a

Mixacarus brevipes (Banks, 1947)

Epilomannoides terrae (Jacot, 1936)

Epilomannoides jacoti (Norton, Metz & S)

Nehypochthonius porosus (Norton and M)

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 different microhabitats in forest floors.
 tion of Oribatei (Acari). II. The trans-
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Appendix I. Species distribution within each site arranged phylogenetically according to Marshall et al. (1994). Pine-oak ridge (118), Cove hardwoods (218), Low-elevation mixed oak (318), High-elevation mixed oak (427) and Northern hardwoods (527).

Species	Sites					Total
	118	218	318	427	527	
PALEOSOMATA						
<i>Zachvatkinella</i> sp a	0	0	1	5	0	6
ENARTHRONOTA						
<i>Eohypochthonius</i> sp a	2	33	2	23	11	71
<i>Hypochthonius rufulus carolinicus</i> Jacot, 1936	7	9	9	6	14	45
<i>Liochthonius fimbriatus</i> (Jacot, 1936)	0	1	0	0	0	1
<i>Eniochthonius</i> sp a	0	31	8	12	60	111
<i>Brachychthonius jugatus</i> (Jacot, 1938)	1	0	0	1	0	2
<i>Eobrachychthonius</i> sp a	0	0	3	3	1	7
<i>Liochthonius</i> sp a	0	1	2	1	6	10
<i>Liochthonius</i> sp b	4	0	2	7	2	15
<i>Poecilochthonius</i> sp a	1	0	0	1	2	4
<i>Sellnickochthonius zelawaiensis</i> (Sellnick, 1928)	0	0	2	1	0	3
<i>Pterochthonius</i> sp a	13	7	4	2	3	29
<i>Atopochthonius</i> sp a	0	0	0	4	1	5
MIXONOMATA						
<i>Atropacarus striculus</i> (C. L. Koch, 1835)	185	22	119	35	24	385
<i>Archiphthiracarus</i> sp a	4	2	4	3	8	21
<i>Phthiracarus</i> sp a	15	7	11	11	13	57
<i>Phthiracarus</i> sp b	2	0	0	1	0	3
<i>Mesotritia</i> sp. nr. <i>glabrata</i> (Say)	8	1	2	3	0	14
<i>Eupthiracarus</i> sp a	9	4	12	3	3	31
<i>Microtritia</i> sp a	72	6	56	41	7	182
<i>Rhysotritia</i> spp.	58	12	30	11	15	126
<i>Synichotritia</i> sp a	0	0	8	17	30	55
<i>Mixacarus brevipes</i> (Banks, 1947)	0	10	0	0	0	10
<i>Epilomannoides terrae</i> (Jacot, 1936)	75	6	42	16	1	140
<i>Epilomannoides jacoti</i> (Norton, Metz & Sharma, 1978)	7	1	2	0	1	11
<i>Nehypochthonius porosus</i> (Norton and Metz)	1	0	0	1	0	2

Species	Sites					Total
	118	218	318	427	527	
DESNOMONATA						
<i>Nothrus silvestris bistilis</i> Jacot, 1937	15	0	12	3	0	30
<i>Nothrus silvicus</i> Jacot, 1937	27	1	30	9	0	67
<i>Heminothrus ornatissimus</i> (Berlese, 1910)	12	1	9	7	7	36
<i>Platynothis peltifer</i> (C. L. Koch, 1839)	51	0	7	7	3	68
<i>Platynothis bicarinatus</i> Jacot, 1938	0	0	0	0	10	10
<i>Trhypochthonius silvestris</i> Jacot, 1937	4	0	11	10	0	25
<i>Malacothis sp a</i>	81	1	6	0	1	89
<i>Trimalacanthrus crinitus</i> (Berlese, 1908)	2	0	3	5	1	11
<i>Nanhermannia dorsalis</i> (Banks, 1896)	194	0	36	46	60	336
PYCNONOTA						
<i>Hermaniella</i> sp a	21	6	2	3	1	33
<i>Hermaniella</i> sp b	1	2	2	0	2	7
<i>Jacotella quadricaudicula</i> (Jacot, 1937)	2	0	2	6	1	11
gen nr <i>Hungarobelba</i>	0	0	0	0	22	22
<i>Dyobelba</i> sp. nr. <i>tectopediosa</i>	27	1	37	30	23	118
<i>Epidamaeus</i> sp a	0	0	8	0	3	11
<i>Epidamaeus canadensis</i>	0	1	0	0	0	1
<i>Belba</i> sp a	0	0	0	1	6	7
<i>Cepheus</i> sp. nr. <i>corae</i> Jacot 1928	0	2	1	3	0	6
<i>Cepheus</i> sp a	0	0	1	0	0	1
<i>Polypterozetes</i> sp a	0	16	4	4	29	53
<i>Gymnodampia setata</i> (Berlese 1916)	2	0	6	15	19	42
<i>Epiemulus geometricus</i> (Berlese, 1916)	1	0	0	0	1	2
<i>Fosseremus americanus</i> Jacot, 1938)	0	1	15	2	9	27
<i>Eremobelba gracilior</i> Berlese, 1908	26	13	57	32	15	143
<i>Eremobelba leporoides</i> Jacot, 1938	0	0	4	0	0	4
<i>Dorycranosus</i> sp a	0	0	0	0	3	3
<i>Liacarus detosus</i> Woolley, 1968	9	1	5	9	2	26
<i>Liacarus latus</i> Ewing, 1909	0	0	0	0	6	6
<i>Stonyxenillus spilatus</i> Woolley and Higgins, 1966	0	0	2	2	0	4
<i>Cultoribula</i> sp. nr. <i>vtouri</i>	0	1	1	0	0	2
<i>Cultoribula bicultrata</i> (Berlese, 1905)	2	0	0	3	0	5
<i>Ceratoppia</i> sp. nr. <i>bipilus</i> (Nicolet)	5	4	17	11	10	47
<i>Metrioppia</i> nr <i>Paenoppia</i>	1	0	2	3	6	12
<i>Metrioppia atlantica</i> Jacot, 1938	4	6	4	3	6	23
<i>Parapyroppia</i> sp a	0	0	0	0	3	3
<i>Carabodes pentasetosis</i> Reeves, 1992	16	1	0	0	0	17
<i>Carabodes niger</i> Banks, 1885	1	0	1	0	0	2
<i>Carabodes falcatus</i> Jacot, 1937	37	6	121	114	13	291
<i>Carabodes clavatus</i> Jacot, 1938	6	1	3	1	0	11
<i>Carabodes cherokee</i> Reeves, 1993	8	1	9	3	9	30
<i>Carabodes phylliformis</i> Reeves, 1993	0	0	9	2	2	13
<i>Carabodes spiniformes</i> Reeves	8	0	23	84	7	122
<i>Carabodes granulatus</i> Banks 1885	1	0	1	1	0	3
<i>Carabodes erectus</i> Reeves 1992	1	0	0	0	0	1
<i>Carabodes chandleri</i> Reeves, 1992	1	0	1	2	0	4
<i>Carabodes nantahalensis</i> Reeves 1993	2	0	2	0	0	4
<i>Odontocephus</i> sp a	0	0	1	0	0	1
<i>Odontocephus</i> sp b	3	0	1	4	0	8
<i>Tectocephus</i> sp. nr. <i>velatus</i>	104	23	219	72	33	451
<i>Suctobelbella</i> spp.	245	63	241	166	217	932
<i>Microppia minus</i> (Paoli, 1908)	85	0	77	54	0	216

Species	
Astegistidae genus	
<i>Oppiella</i> spp.	
<i>Oppiella</i> sp a	
<i>Oppia durhamensis</i> Metz and Sharn	
<i>Oppia parviaures</i> Jacot, 1939	
<i>Lasiobelba rigida</i> (Ewing)	
<i>Quadroppia</i> sp a	
<i>Quadroppia</i> sp b	
<i>Rectoppia</i> sp a	
<i>Ramusella</i> sp a	
<i>Insculptoppia</i> sp a	
<i>Insculptoppia</i> sp b	
<i>Allosuctobelba</i> sp a	
<i>Eremobodes</i> sp. nr. <i>pectinatus</i>	
<i>Caleremaeus</i> sp a	
<i>Caleremaeus</i> sp b	
<i>Gemmatetes crosbyi</i> (Berlese, 1908)	
<i>Dolicheremaeus rubripedes</i> Jacot, 1938	
PORONOTA	
<i>Kalyptozetes</i> sp a	
<i>Kalyptozetes harpezus</i> (Higgins, 1966)	
<i>Xylobates robustior</i> Jacot	
<i>Xylobates capucinus</i> (Berlese, 1908)	
<i>Haplozetes</i> sp a	
<i>Rostrazetes ovulum</i> (Berlese)	
<i>Oripodidae</i> sp a	
<i>Hemileius</i> sp. nr. <i>quadripilis</i>	
<i>Schelorbates cf lanceoliger</i> (Berlese, 1908)	
<i>Schelorbates</i> sp c	
<i>Haplozetes</i> sp b	
<i>Eupelops silvestris</i> (Jacot, 1937)	
<i>Propelops minnesotensis</i> (Ewing)	
<i>Diapterobates humeralis</i> (Banks)	
<i>Ceratozetes</i> sp. nr. <i>mediocris</i> (Banks)	
<i>Ceratozetes virginicus</i> (Banks, 1906)	
<i>Ceratozetes angustus</i> (Banks, 1947)	
<i>Chamobates</i> sp a	
<i>Chamobates</i> sp b	
<i>Lepidozetes</i> sp a	
<i>Parachipteria</i> sp a	
<i>Parachipteria</i> sp b	
<i>Oribatella</i> sp a	
<i>Oribatella</i> sp c	
<i>Ferolocella tessellata</i> (Berlese)	
<i>Anachipteria australoides</i> Jacot	
<i>Oribatella brevicornuta</i> Jacot, 1935	
<i>Ophidiotrichus</i> sp a	
<i>Galumna ithacensis</i> (Jacot, 1929)	
<i>Pergalumna curva</i> (Ewing, 1907)	
<i>Cultrobates quadricuspidatus</i> (Ewing, 1907)	
<i>Protokalumna pterora</i> (Banks, 1910)	
N	
S	

Appendix I. continue

			Total	Species					Total	
318	427	527		Sites						
				118	218	318	427	527		
				Astegistidae genus	10	1	5	8	0	24
12	3	0	30	<i>Oppiella</i> spp.	247	39	345	448	151	1230
30	9	0	67	<i>Oppiella</i> sp a	11	13	18	9	0	51
9	7	7	36	<i>Oppia durhamensis</i> Metz and Sharma, 1975	10	9	21	21	19	80
7	7	3	68	<i>Oppia parviaures</i> Jacot, 1939	0	15	12	79	20	126
0	0	10	10	<i>Lasiobelba rigida</i> (Ewing)	2	31	11	13	17	74
11	10	0	25	<i>Quadroppia</i> sp a	3	31	90	46	88	258
6	0	1	89	<i>Quadroppia</i> sp b	0	0	11	16	20	47
3	5	1	11	<i>Rectoppia</i> sp a	0	0	0	2	1	3
36	46	60	336	<i>Ramusella</i> sp a	1	2	1	26	6	36
				<i>Insculptoppia</i> sp a	1	0	5	68	2	76
2	3	1	33	<i>Insculptoppia</i> sp b	0	0	1	3	0	4
2	0	2	7	<i>Allosuctobelba</i> sp a	1	0	4	0	1	6
2	6	1	11	<i>Eremobodes</i> sp. nr. <i>pectinatus</i>	110	6	57	1	0	174
0	0	22	22	<i>Caleremaeus</i> sp a	0	0	1	0	95	96
37	30	23	118	<i>Caleremaeus</i> sp b	0	0	0	1	0	1
8	0	3	11	<i>Gemmazetes crosbyi</i> (Berlese, 1908)	0	12	0	0	1	13
0	0	0	1	<i>Dolichere-maeus rubripedes</i> Jacot, 1938	0	0	2	0	9	11
0	1	6	7	PORONOTA						
1	3	0	6	<i>Kalyptrazetes</i> sp a	0	1	0	0	27	28
1	0	0	1	<i>Kalyptrazetes harpezus</i> (Higgins, 1965)	0	1	0	0	0	1
4	4	29	53	<i>Xylobates robustior</i> Jacot	78	8	21	18	26	151
6	15	19	42	<i>Xylobates capucinus</i> (Berlese, 1908)	4	16	2	2	70	94
0	0	1	2	<i>Haplozetes</i> sp a	9	2	3	3	0	17
15	2	9	27	<i>Rostrazetes ovulum</i> (Berlese)	9	0	0	0	0	9
57	32	15	143	<i>Oripodidae</i> sp a	0	0	0	0	1	1
4	0	0	4	<i>Hemileius</i> sp. nr. <i>quadripilis</i>	0	0	0	1	0	1
0	0	3	3	<i>Scheloribates cf lanceoliger</i> (Berlese, 1908)	17	3	64	111	3	198
5	9	2	26	<i>Scheloribates</i> sp c	0	1	13	4	5	23
0	0	6	6	<i>Haplozetes</i> sp b	2	0	1	2	0	5
2	2	0	4	<i>Eupelops silvestris</i> (Jacot, 1937)	23	0	35	12	9	79
1	0	0	2	<i>Propelops minnesotensis</i> (Ewing)	0	1	0	0	1	2
0	3	0	5	<i>Diapterobates humeralis</i> (Banks)	2	0	0	0	0	2
17	11	10	47	<i>Ceratozetes</i> sp. nr. <i>mediocris</i> (Banks)	3	4	2	72	0	81
2	3	6	12	<i>Ceratozetes virginicus</i> (Banks, 1906)	0	5	0	0	0	5
4	3	6	23	<i>Ceratozetes angustus</i> (Banks, 1947)	164	0	51	77	0	292
0	0	3	3	<i>Chamobates</i> sp a	0	0	7	5	0	12
0	0	0	17	<i>Chamobates</i> sp b	1	0	0	1	0	2
1	0	0	2	<i>Lepidozetes</i> sp a	0	12	6	0	23	41
121	114	13	291	<i>Parachipteria</i> sp a	10	5	80	30	8	133
3	1	0	11	<i>Parachipteria</i> sp b	0	1	8	48	38	95
9	3	9	30	<i>Oribatella</i> sp a	40	4	20	44	60	168
9	2	2	13	<i>Oribatella</i> sp c	7	0	17	26	4	54
23	84	7	122	<i>Ferolocella tessellata</i> (Berlese)	0	0	1	6	0	7
1	1	0	3	<i>Anachipteria australoides</i> Jacot	0	4	0	0	2	6
0	0	0	1	<i>Oribatella brevicornuta</i> Jacot, 1935	0	0	0	0	3	3
1	2	0	4	<i>Ophidiotrichus</i> sp a	0	0	0	29	1	30
2	0	0	4	<i>Galumna ithacensis</i> (Jacot, 1929)	0	1	3	11	7	22
1	0	0	1	<i>Pergalumna curva</i> (Ewing, 1907)	1	19	2	1	1	24
1	4	0	8	<i>Cultrobates quadricuspidatus</i> (Ewing, 1909)	0	0	1	0	0	1
219	72	33	451	<i>Protokalumma pterora</i> (Banks, 1910)	1	0	0	2	0	3
241	166	217	932	N	2237	570	2233	2192	1454	8644
77	54	0	216	S	78	64	95	92	81	134