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Are there real endogeic species in temperate forest mites?

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Porosity

Summary

The determinants of mite diversity in soil and the reasons why so many species co-exist are poorly understood. There is evidence that niche differentiation (i.e. microhabitat complexity) in the litter layers of forest floors is important, however, little is known for deeper horizons since mite density and diversity in deeper soil layers have been rarely studied. In order to address this dearth of information, we collected microarthropods from both the forest floor and the mineral soil to a depth of 1 m in two deciduous forest locations. The density exceeded 8×10^5 microarthropods m^{-2} in one location, and a number of individuals were collected from deep in the soil. No species was exclusively living in mineral horizons. Measurements of porosity spectrum, pH, water content, total C and total N were made at each depth and related to mite diversity and species richness. Meso- and microporosity were strongly correlated with species distribution while macroporosity and pH were correlated to density and species richness.

Introduction

As Tilman (2000) noted, the co-existence of so many species on earth remains a mystery. In habitats where species appear to share similar resources, co-existence is not easily explained by niche segregation and potential competitive exclusion. This has reawakened interest in Hutchinson's 'paradox of the plankton' (Hutchinson, 1961), and the 'enigma of soil animal species diversity' (Anderson, 1975).

In terrestrial systems, the soil is considered a major reservoir of biodiversity (André et al., 1994) and hence, provides a good context for studying the determinants of species richness. Still, investigations of mite diversity have largely been limited to

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the litter and the top part of the hemiorganic horizon (see the review of André et al., 2002). Only two studies have looked at density and diversity of deep soil mites in temperate forest. In one, Moskacheva (1973) estimated 28–40 oribatids dm^{-3} for 6 species while Lebrun and Wauthy (1981) estimated 0.4 oribatids dm^{-3} for 32 species. We were unable to find comparable data for other mite orders.

The profile of vertical distribution of mites is known to be either unimodal or bimodal (André et al., 2002). Yet, local factors governing below-ground species richness remain uninvestigated for most taxonomic groups (Hooper et al., 2000; André et al., 2002; Wardle, 2002). Determinants of soil mite diversity and distribution have been extensively documented at the landscape scale (e.g. succession, deforestation, silvicultural practice, manuring, tillage; Paoletti, 1999; Usher, 1985). However, few data identify the key factors of species richness in situ—at the soil dweller's scale.

Only four studies (Anderson, 1978; Hansen and Coleman, 1998; Hansen, 2000; Kaneko and Salamanca, 1999) have specifically investigated the relationships between the diversity of adult oribatid mites and that of litter microhabitats (leaf fragments, roots, faeces, micro-organism clumps, etc.). Recently, Noti et al. (2003) showed that different factors acting at different scales influenced mite diversity, from the landscape level to in situ soil properties such as total nitrogen. However, all these studies were ecologically confined to the uppermost thin layer of soil (in most cases, the organic horizon) and systematically restricted to adults of a subgroup of hemiedaphic mites. Factors driving euedaphic (i.e. the hemiorganic and mineral horizons) biodiversity, are unknown even though euedaphic microarthropods may represent a large proportion of the total population of soil microarthropods (André et al., 2002).

In this study, we collected microarthropods in two forested sites at eight different depths ranging from the litter down to 1 m, in order to determine their vertical distribution. In addition, soil physical and chemical characteristics were measured as potential determinants of mite density and diversity.

Materials and methods

Study area

We collected microarthropods from two sites in the Lauzelle forest (50°40′00″N–4°38′40″E, Louvain-la-Neuve, Belgium), on a south-south-east 17° slope. Annual mean temperature and rainfall were 9.4°C and 816 mm, respectively. The samples were collected in November.

The first site (L for lower) was situated on the lower part of the slope (altitude: 88 m). The organic horizon (litter) was a 7-cm thick moder overlying silt that developed on colluvium. The tree cover was dominated by *Quercus petraea* and *Q. robur*. A single *Acer pseudoplatanus*, some *Carpinus betulus* individuals, *Athyrium filix femina*, *Pteridium aquilinum*, *Rubus* sp., *Oxalis acetosella*, and *Lamium galeobdolon* were also present at this site.

The second site (U for upper) was located on the upper part of the slope (altitude: 112 m). The organic horizon, 10-cm thick, was also a moder but the underlying soil was a silt-sand podzol. On this site, the tree cover was dominated by *Q. petraea* and *Q. robur* with some *Prunus serotina* and a single *Fagus sylvatica*.

Microarthropod sampling

Three 25-cm^2 samples were carefully cut out with a knife from both the O_l and O_h horizons at both sites. In addition, at least three 5-cm long cores were taken from the sides of dug trench with a steel corer (diameter 3.5 cm) at the following depths: underneath the litter ('h' samples), and then at 20-cm intervals from 20 to 100 cm depth (see Table 1). The two top series of cores (h and −20) were situated within the A_h layer and the remaining four (−40 to −100) within the mineral horizons. Microarthropods were extracted with two methods, Berlese–Tullgren funnels and DBE flotation (Ducarme et al., 1998). Berlese–Tullgren funnels were used for litter and five of the 'h' samples. Light bulbs (15 W), 10 cm above the intact samples, were turned on 1 week after the beginning of the extraction process. The extraction lasted for 3 weeks. The mean temperature in the extraction room was 20°C. The remaining 'h' and deeper samples were stored in Norvanol for about 4 months before extraction with the DBE flotation method (Ducarme et al., 1998).

Mites and springtails were counted. All mite stases from 'h' and deeper samples were identified to species level.

Physico-chemical measurements

Five major parameters were determined for every soil depth: pH, water content, C and N content, and the porosity spectrum. Only C and N content, however, were measured in litter horizons.

Table 1. Number of sampling units (*n*), physico-chemical characteristics, mite density (*D*) and richness (*S*) for each litter and soil depth

Site	Horizon	*n*	Depth (cm)	WC[a]	% Porosity[b]						pH	% C	% N	C/N	*D* (ind./dm^3)	*S*
					Total	A	B	C	D	E						
L	O_l	3	1.5	198								43.08	2.09	21	667	
	O_f	3	5	94								27.19	1.31	20	3430	
	A_h	10	9	33	68	38	2	3	13	12	3.5	5.91	0.30	19	782	48
	A_h	3	20	28	59	17	3	5	12	22	3.6	4.51	0.23	20	97	5
	B	3	40	25	53	13	2	3	6	29	3.9	1.95	0.08	26	35	3
	B	4	60	18	50	11	3	5	6	26	4.0	0.43	0.03	13	68	7
	B	3	80	18	48	7	3	5	6	27	4.1	0.21	0.02	9	0	0
	B	3	100	20	46	19	1	1	2	24	4.3	0.15	0.02	6	0	0
U	O_l	3	2.5	140								43.26	1.86	24	701	
	O_f	3	7.5	108								35.11	1.46	24	9827	
	A_h	9	14	27	67	36	4	12	9	7	3.5	3.03	0.13	23	931	36
	A_h	4	20	20	65	32	5	13	9	7	3.6	2.34	0.10	23	322	15
	E	3	40	20	52	16	3	25	7	2	3.7	0.28	0.01	23	166	7
	B_s	3	60	11	48	9	2	18	13	5	3.7	0.85	0.03	25	159	7
	C	3	80	4	44	7	3	20	12	2	4.1	0.40	0.02	24	14	1
	C	3	100	3	43	12	3	16	13	0	4.2	0.15	0.01	25	0	0

[a]Water content (%).
[b]Pore diameter: A: >200 μm; B: 200–100 μm; C: 100–50 μm; D: 50–20 μm; E: <20 μm.

Samples were oven-dried for 7 days at 100°C in order to determine water content and porosity (assuming a solid density of 2.6). Total C and N content were measured using combustion followed by gaseous chromatography. The pH was determined in water using an electrode.

Porosity was measured using mercury intrusion (Winslow-5000 porosimeter, American Instrument Company, Silver Spring, USA). Five porosity classes, expressed in volume units, were derived from the porosity spectrum: A (diameter >200 μm); B (200–100 μm); C (100–50 μm); D (50–20 μm); E (<20 μm).

Data analysis

We used the *k*-means method of the R-package (Legendre and Vaudor, 1991) for non-hiearchical partitioning. The principle of this method is to minimize the intra-group variance. In order to avoid an arch effect, detrended correspondence analysis (DCA) was performed with CANOCO (ter Braak and Smilauer, 1998). Ordination and partitioning techniques were used to analyze species profiles. For the latter analyses, samples below 50 cm were pooled due to low mite densities.

Correlation coefficients were calculated using the SAS Enterprise Guide software (SAS Institute, 2001). Only samples extracted with the flotation method were used in these analyses to avoid extraction method bias. Since the number of samples varied with sampling depth, the mean number of species collected in three samples was used as the richness variable.

Results

Physico-chemical profiles

Few vertical trends in physico-chemical factors were evident at either the U or the L site (Table 1). Microporosity, for instance, showed no consistent depth pattern across the sites. At the L-site, microporosity skewed to high values at −40 cm whereas the reverse distortion occurred at the U-site. In contrast, total porosity at both the sites and pH values at the L-site showed a consistent trend with depth.

Given that few linear relationships were observed, a matrix of Spearman rank correlation coefficients was calculated between physico-chemical factors (Table 2). The factors that showed the best correlations with depth were total porosity, pH, C and N content.

Extraction methods

The DBE extraction method collected 2.9 times more microarthropods than the Berlese–Tullgren funnels from the 'h' samples (paired *t*-test,

Table 2. Spearman correlation coefficients between physico-chemical factors

	WC[a]	Porosity[b]						pH	C	N	C/N
		Total	A	B	C	D	E				
Poro T	0.81	1.00									
Poro A	0.78	0.75	1.00								
Poro B	−0.18	0.14	0.02	1.00							
Poro C	−0.55	−0.27	−0.39	0.48	1.00						
Poro D	−0.13	0.08	0.07	0.24	0.41	1.00					
Poro E	0.41	0.25	0.04	−0.32	−0.81	−0.66	1.00				
pH	−0.60	−0.90	−0.61	−0.28	−0.07	−0.41	0.09	1.00			
C	0.69	0.88	0.56	0.18	−0.20	0.32	0.20	−0.91	1.00		
N	0.77	0.85	0.65	0.06	−0.46	0.17	0.39	−0.80	0.94	1.00	
C/N	−0.30	−0.10	−0.20	0.23	0.50	0.38	−0.43	−0.14	0.08	−0.10	1.00
Depth	−0.74	−0.97	−0.68	−0.21	0.09	−0.26	−0.08	0.96	−0.92	−0.83	−0.04

[a]Water content (%).
[b]Pore diameter: A: >200 μm; B: 200–100 μm; C: 100–50 μm; D: 50–20 μm; E: <20 μm.

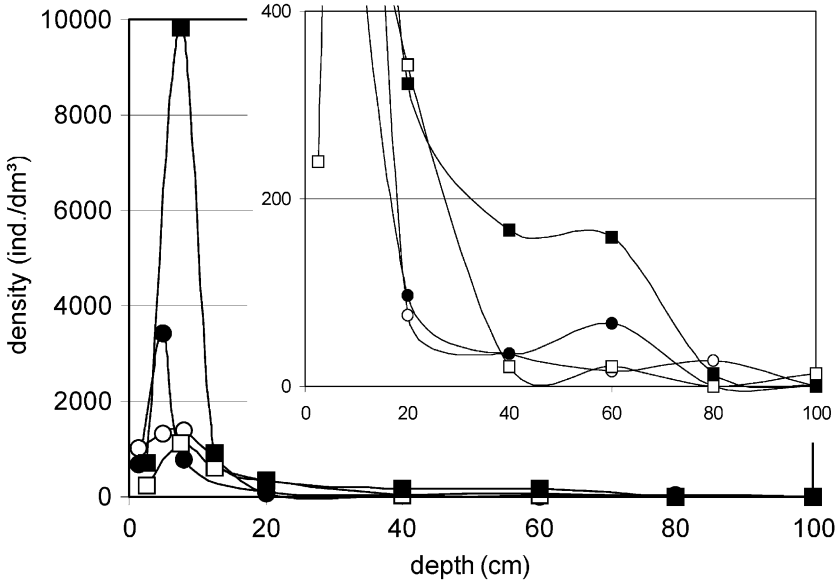

Figure 1. Vertical density profile of Acari (black) and Collembola (white) in sites L (circles) and U (squares). Insert: zoom on low densities.

$t = -2.13^*$, $n = 9$). However, the number of mite species was similar with 47 and 50 species for Berlese–Tullgren funnels and DBE extractions, respectively.

Microarthropod vertical distribution

Overall, 1139 springtails and 5127 mite specimens were collected from the litter, compared to 161 springtails and 773 mite specimens from the hemiorganic and mineral soil below. Specimens collected from the hemiorganic and mineral horizons represented 64 species of which 10 were Mesostigmata, 15 Prostigmata, 3 Endeostigmata, 33 Oribatida and 3 Astigmata (list of species is given in Appendix A).

A strong litter effect was observed on microarthropod vertical distribution (Fig. 1). Nevertheless animals were still present deeper in the profile. Collembola were found down to 1 m but mites only to 0.8 m. The estimated microarthropod density for the entire soil profile was 870 467 and 495 481 individuals m^{-2} at the U- and L-site, respectively.

No mite species was found to be restricted to the mineral horizons, except *Nanhermannia elegantula* (2 specimens) and *Suctobelbella acutidens* (1 specimen).

The ratio Brachypilina/total oribatids decreased with depth: 64% and 80% in O_l, 42% and 46% in O_f, 30% and 41% in A_h and 25% and 38% in deeper soil horizons, at the L- and U-site, respectively.

Species composition

The species richness of the two sites was similar (40 vs. 50 species), but their community composition was very different (Fig. 2a). At both sites, the 40-cm samples were distinct from all others. These samples occupied extreme locations along DCA axis 1, which discriminated the two sites (Fig. 2b). While axis 2 related to soil depth, axis 1 correlated with meso- and microporosity (positive correlation with porosity class E, $r^2 = 0.86$***; negative correlation with porosity class C, $r^2 = 0.82$**).

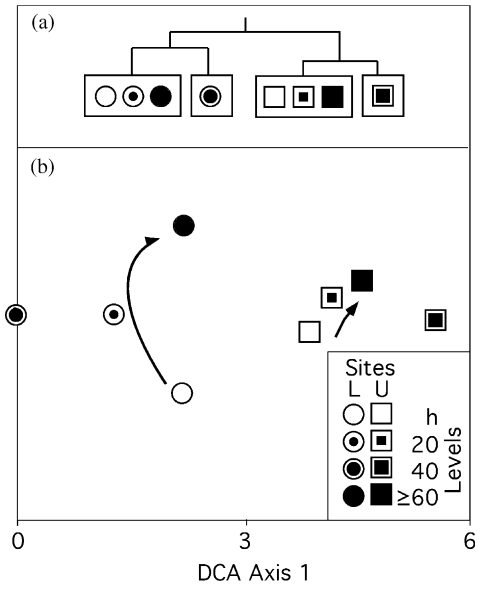

Figure 2. Partitioning (a) and DCA ordination (b) of relevés following mite communities in both sites. Arrows indicate increasing depth.

Correlation with mite density

Mite density correlated best with pH (logarithmic negative relationship, $r^2 = 0.89$***) and porosity class A (positive relationship, $r^2 = 0.78$***). The best multiple linear regression was given by these two variables and depth ($R^2 = 0.84$**).

When depth (*d*) was selected as a control variable, porosity class A and pH were still correlated with mite density (partial correlation, linear $r^2 = 0.58$** and logarithmic $r^2 = 0.41$* for poroA and pH, respectively).

Correlation with mite species richness

Species richness (*S*) was strongly related to mite density (linear relationship, $r^2 = 0.98$***). As a result, environmental variables best correlating with *S* were the same as those correlating with density: porosity class A ($r^2 = 0.79$***; Fig. 3a) and pH (logarithmic $r^2 = 0.89$***; Fig. 3b).

To clarify the ways in which physico-chemical factors influenced mite richness, partial correlation analyses were performed, using mite density as a control variable. The pH was still significantly correlated (logarithmic $r^2 = 0.74$***), while the correlation with porosity class A was no longer significant.

Discussion

Publications dealing with soil microarthropods in the lower soil horizons are rare with only 19 papers studying the soil fauna at depths equal to or greater than 30 cm (André et al., 2002). None of these papers considered soil porosity and few measured other physico-chemical factors. Still rarer are the studies which identified mite species (André et al., 2002) even though soil mites offer a high diversity of ecological niches and life-history tactics (Siepel,

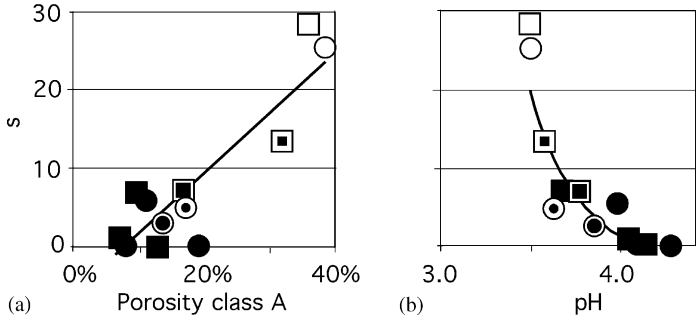

Figure 3. Species richness (*S*) related to porosity class A (linear $r^2 = 0.79$) and pH (logarithmic $r^2 = 0.89$). Symbols as in Fig. 2.

1994). Stase identification is also very infrequent in spite of their importance for the co-existence of species (André, 1989) and the bias introduced in richness estimates when immatures are disregarded (André et al., 2002).

The estimated high microarthropod density observed in the U site has not been paralleled in other forest soil studies, with the notable exception of Forsslund (1948) who collected 2.0–2.9 million microarthropods m^{-2} in spruce litter. There could be two explanations for the high numbers found in the present study. First, the vertical extent of the sampled profile provided an estimation of mite density 45% higher than what would have been calculated from litter data only. Second, the method used for extracting microarthropods from soil samples (i.e. DBE flotation) is more efficient than the classical Berlese–Tullgren funnels used in most studies (André et al., 2002).

Our results question the definition of endogeic (or euedaphic) species. It has never been clearly stated if this term was intended for mineral horizon-dwellers only, or if animals living in the hemiorganic horizon had to be included (e.g. Lebrun and Wauthy, 1981). In the present study, two species were found only in mineral horizons although these species have been collected previously from humus (Strenzke, 1951; van der Hammen, 1952). Since species defined as 'hypogeic' (Lebrun et al., 1989), such as *Palaeacarus hystricinus*, *Gehypochthonius rhadamanthus*, *Microtritia minima* or *Suctobelbella tuberculata*, occur in the hemiorganic horizon, we suggest that the terms 'endogeic' or 'hypogeic' be reserved for species that live exclusively in the hemiorganic or mineral horizons of the soil. This also implies that organic matter concentration, which is the main physico-chemical difference between hemiorganic and mineral horizons, is not an excluding factor for endogeic mites. This was confirmed by the fact that C and N content were weakly correlated with both density and species richness of mites.

The decrease in the dominance of Brachypilina with depth complements the data of Lebrun (1971), which documented a decline in this group from tree bark to the hemiorganic horizon of soils. Lebrun explained this decrease by the parallel increase in humidity that allowed species less adapted to drought, such as soft-bodied Palaeosomata, to colonize these habitats.

As early as 1955, Haarlov (1955) speculated that the vertical distribution of Collembola and mites depended on a set of factors of which the most important, presumably, were the size and shape of soil pores, their relative humidity and presence or absence of food. Surprisingly, no evidence has been found since Haarlov's publication to support his statement and to evaluate the relative importance of the different factors.

Since several physico-chemical factors in the present study did not follow a regular vertical gradient and since profiles were site dependent, it was possible to separate the effects of these factors from that of depth using a series of partial correlation analyses. Density was directly correlated with macroporosity and pH, independent of depth. Furthermore, since richness correlated strongly with mite density, macroporosity and pH were, in turn correlated to richness. However, soil pH was also correlated with richness independently of density.

Porosity is a key factor in explaining the density, species distribution and richness of soil mites in temperate forests. The soil may be perceived as a two-phase mosaic comprised of empty spaces (pores and crevices)—potentially colonized by microarthropods depending on the mosaic grain—and the solid elements (mineral and organic particles) that separate them.

The macroporosity (porosity class A) is a measure of the space available to soil microarthropods and was correlated to their density and richness in this study. Therefore, the available space could be considered a potential causal factor that influences the species richness of deep soil mites. Our findings differ from previous studies on litter (Anderson, 1978; Hansen and Coleman, 1998; Hansen, 2000; Kaneko and Salamanca, 1999) in two respects. First, the soil here is perceived as a simple two-phase mosaic (pores vs. solid elements) while in previous studies the litter was regarded as an *n*-phase mosaic composed of various microhabitats (leaf fragments, roots, faeces, micro-organism clumps, etc.). Second, the determinant of mite richness was not the number of phases as in litter (i.e. its heterogeneity) but simply the grain of the mosaic (i.e. the soil porosity as defined in pedology).

The relationship between species richness and porosity, however, further confounds rather than resolves the problems of niche differentiation. In contrast to herbivore communities, there is little evidence of trophic specialization in most soils with large number of species apparently co-existing while utilizing similar food resources (Anderson, 1975; Ghilarov, 1977). The meso- and microporosity determine the distribution of individual species, probably through size selection and food availability. For example, larger species cannot invade small pores where fungi are more abundant (Elliott et al., 1980; Vreeken-Buijs et al., 1998).

Presumably, soil pH is also a major correlate of mite richness, both indirectly through its influence on mite density and independent of mite density, as deduced from the partial correlations. On a global scale, it is known that acidic conifer litter supports high population densities of mites (e.g. Petersen and Luxton, 1982; Walter and Proctor, 1999). However, a correlation between pH and mite richness that is independent of density had not been observed to date.

Our results differ from those of Noti et al. (2003) who noted that water content was a key factor for oribatid mite density in the tropics. In the same study, oribatid mite species richness was season-dependent and was explained, independent of density, by the organic matter, C/N ratio and total nitrogen. The C/N ratio was also a key factor for the microathropod (mite and Collembola) richness in the Namib Desert (André et al., 1997). Clearly, different key determinants appear to explain soil mesofauna richness in different climates (temperate vs. tropical vs. arid).

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Appendix A

See Table 3 for details.

Table 3. List and abundance of mite species collected from the hemiorganic (A_h) and mineral horizons of the soil

Taxa	A_h	Deeper
Mesostigmata		
Pachylaelaps multidentatus Evans & Hyatt[a]	3	3
Rhodacarus agrestis Karg[a]	48	1
Rhodacarus cf aequalis Karg[a]	1	4
Rhodacarus coronatus Berlese[a]	34	—
Leptogamasus suecicus (Trägardh)	2	—
Paragamasus sp.	1	—
Veigaia exigua (Berlese)[a]	3	1
Veigaia nemorensis (C.L. Koch)	3	—
Polyaspidoidea (undet. gen.)	3	—
Uropodoidea (undet. gen.)	10	—
Prostigmata		
Cocceupodes sp. 1[a]	14	—
Cocceupodes sp. 2	4	—
Eupodes sp. 1[a]	46	3
Eupodes sp. 2	2	—
Eupodes sp. 3	1	—
Eupodidae (undet. gen.)	2	—
Brevipalpia sp.[a]	12	2
Crassocheles sp. 1	1	—
Crassocheles sp. 2	4	—
Latoempodia sp.	1	—
Metatydaeolus sp.	5	—
Microtydeus sp.	1	—
Tydeus sp.	1	—
Gymnereynetes sp.	5	—
Scutacaridae (undet. gen.)	1	—
Endeostigmata		
Alicorhagia sp.[a]	119	2
Bimichaelia sp.	12	—
Nanorchestes sp.[a]	7	3

Table 3. (*continued*)

Taxa	A_h	Deeper
Oribatida		
Adelphacarus sellnicki Grandjean	1	—
Palaeacarus hystricinus Trägårdh[a]	4	2
Hypochthonius rufulus Koch	5	—
Sellnickochthonius cricoides (Weis-Fogh)[a]	7	—
Sellnickochthonius honustus (Moritz)	38	—
Sellnickochthonius zelawaiensis (Sellnick)	2	—
Liochthonius simplex (Forsslund)	4	—
Mixochthonius pilososetosus (Forsslund)	2	—
Gehypochthonius rhadamanthus Jacot[a]	28	12
Microtritia minima (Berlese)[a]	14	6
Rhysotritia duplicata (Grandjean)[a]	3	—
Nothrus palustris Koch	1	—
Nothrus silvestris Nicolet[a]	30	1
Nanhermannia cf. nana (Nicolet)	8	—
Nanhermannia elegantula Berlese[a]	—	2
Malaconothrus sp.	1	—
Damaeobelba minutissima (Sellnick)	1	—
Metabelba papillipes (Nicolet)	6	—
Xenillus tegeocranus (Hermann)	1	—
Quadroppia sp.[a]	11	—
Medioppia obsoleta (Paoli)[a]	7	1
Microppia minus (Paoli)[a]	6	17
Neotrichoppia confinis (Paoli)	1	—
Oppiella nova (Oudemans)[a]	17	1
Suctobelbella acutidens (Forsslund)[a]	—	1
Suctobelbella falcata (Forsslund)[a]	11	—
Suctobelbella hamata Moritz	3	—
Suctobelbella sarekensis (Forsslund)	3	—
Suctobelbella subcornigera (Forsslund)	32	—
Suctobelbella subcornigera (Forsslund) ssp. 1	3	—
Suctobelbella tuberculata (Strenzke)[a]	14	1
Tectocepheus minor Berlese	1	—
Oribatula tibialis (Nicolet)	1	—
Astigmata		
Astigmata sp. 1	3	—
Astigmata sp. 2	12	—
Schwiebea sp.	6	—

[a]Species collected below 15 cm depth.

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