University of Alberta

Structure, composition and trophic ecology of forest floor predatory mites (Mesostigmata) from the boreal mixedwood forest of northwestern Alberta

by

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ABSTRACT

The forest floor, including the L, F and H horizons is the habitat for numerous soil fauna whose ecological relationships affect various soil processes. The forest floor is closely associated with stand development in boreal forests, creating distinct biochemical and physical characteristics within the different organic layers. Under the premise that forest floor soil communities are closely associated with, and characteristic of a particular stand type. I used predator mites (Mesostigmata) dwelling in forest floors to study the impact of forest stand type on the structure and composition of these mite assemblages.

Differences in species richness, dominance and assemblages were a consequence of forest stand type. Results further demonstrated the importance of coniferous trees in structuring mesostigmatan assemblages. Forest floor pH structured variation in mite assemblages and forest floor thickness were associated with habitat preferences. Thus, the variation in habitat changes from early seral stages to mature old-growth stands results in diverse predatory mite assemblages. A particularly interesting feature of the fauna was the great diversity of zerconid species of genus *Mixozercon* (Halašková, 1963), including *M. albertaensis*, *M. jasoniana* and *M. borealis*, species that are exclusively found in western boreal forests.

I used nitrogen isotope analysis ($\delta^{15}N$ values) to assess the trophic positions of mesostigmatan and some oribatid mites in relation to potential effects

of forest harvest on soil food webs in coniferous and deciduous stands. The differences in $\delta^{15}N$ separated the mites in three main trophic guilds: detritivores (only oribatid), omnivores (overlapping with predators) and predators. Each guild was further subdivided into subguilds based on feeding relationships. Isotopic nitrogen fractionation within the mites did not seem to be affected by their habitat (spruce vs aspen) or by clearcutting. Instead, the well-defined degree of isotopic fractionation observed within the food web may depend only on the predator-prey feeding relationships because the degree of isotopic enrichment (or depletion) of predator reflects its diet.

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My friends, which are the family that I chose

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CHAPTER 1

General introduction

1.1. The boreal mixedwood forest and its forest floor layers

The forest floor of the boreal mixedwood forest is a complex and dynamic biological system (Bonan and Shugart, 1989) in which vertebrates, macro-, meso-, and micro-invertebrates occur together with microorganisms and collectively influence soil development through the addition of organic matter and contibutions to soil forming processes (Jenny, 1941). There is variation in the litter added to the soil surface from vegetation of different stand types, including differences in litter quality such as the composition of carbohydrates, cutin, tannins and lignin (Preston et al., 2000). Decomposition of leaf litter influences the structural composition of the forest floor, providing highly diverse microhabitats. Microhabitat diversity can be determined for the litter (L), fermentation (F) and humus (H) horizons that are structurally heterogeneous (Aoki, 1967; Anderson, 1978). This structure is in turn related to the ecological characteristics of the soil fauna such as their richness, assemblage structure, distribution and activities (Emmerling et al., 2002). Characterization of organic horizons and the environment in which they occur shows that the soil fauna consists of communities that are closely associated with specific vegetation (Raw, 1967; Green et al., 1993; Ponge, 2003).

In the western boreal mixedwood forest of Alberta, the structure and composition of the native vegetation generated by wildfires and insect outbreaks (Bonan and Shugart, 1989) consist of a mixed tree species cover, representing different successional stages, in which aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) are dominant (Rowe, 1972). In general, deciduous forests (moder humus formation), and coniferous forests (mor humus formation) have an abundance of the most diverse group of microarthropods, i.e. the mesofauna (Green et al., 1993; Ponge, 2003). Two groups of mesofauna, mites (Acari) and springtails (Collembola), are predominant, accounting for about 85% of the microarthropods in forest soils (Hope, 2003).

The Acari are remarkably diverse and ecological studies of forest floor Acari require basic information relating to each order. Lindquist et al. (2009) divided the Acari into six main orders, of which one, Mesostigmata, is generally species-rich group in the forest floor mesofauna. An adequate understanding of the structure and function of mesostigmatan mite assemblages requires knowledge of the role of the canopy tree species (Sylvain and Buddle, 2010), which influence litter biochemistry (Hannam et al., 2004, 2006; Jerabkova et al., 2006). To this end, the forest floor must be considered as significant component of habitat structure influencing mesostigmatan assemblages, affecting their diversity and community composition as well as energy flow and nutrient cycling.

1.2. Mesostigmatan mites

The forest floor contains remarkably diverse populations of free-living mites such as the Mesostigmata, which show great complexity and abundance in undisturbed habitats such as the western boreal mixedwood forests of Alberta. Mesostigmata are usually numerically less abundant than other Acari, comprising < 5 - 20% of the total Acari found in litter and soil (Petersen and Luxton, 1982). They are microscopic, spider-like invertebrates whose size ranges between 0.1 and 2 mm. Many of them are primarily predators and are distinguished essentially on the character of the respiratory system in which the stigmata (air breathing pore) is open laterally in the middle of the body in the region of the coxae III-IV (Evans, 1992). The mesostigmatan mites have mouthparts adapted for piercing, cutting, sucking and tearing (Wallwork, 1967; Lee, 1974; Evans, 1992; Walter and Proctor, 1999) and a conspicuous salivary stylet for external digestion (Lee, 1974; Evans, 1992). For their principal hunting strategies, they are considered to be pursuit and ambush predators (Walter et al., 1988; Karg, 1993). They are mainly fluid feeders rather than engulfers (Evans, 1992; Walter et al., 1988; Krantz, 2009); however, mites devouring whole nematodes have been observed (Muraoka and Ishibashi, 1976).

Their prey includes springtails, nematodes, enchytraeids, other mites, e.g. soft bodied Prostigmata and Astigmata, hard-bodied Oribatida and nymphs, larvae or eggs of insects as well as proturans and pauropods (Hurlbutt, 1965; Karg, 1993; Walter, 1988; Walter et al., 1988), including intraguild predation (Walter and Proctor, 1999; Scheu and Setälä, 2002). The feeding habits of mesostigmatan

mites provide the greatest contribution to their role in the population regulation of other soil organisms (Emmerling et al., 2002; Karg, 1993; Krantz, 2009); however, other direct or indirect ecological roles cannot be disregarded at this point.

1.2.1. Classification

Increased interest on soil acarine taxonomy has accelerated at an impressive rate during the last decades. Although notable acarine information is present on the World Wide Web (Walter and Proctor, 2010), much of this new information has not yet been able to facilitate species-level identification of all forest floor-inhabiting mesostigmatan species. In Canada, the boreal mixedwood forest may be an important reservoir of unknown species because it covers 35% of the land area and 77% of total of the forested land (Natural Resources Canada, 2009). However, systematics of Mesostigmata remain far less known than that of Oribatida (Walter and Latonas, 2011; Walter et al., 2011). The cohorts Uropodina and Gamasina still need to be explored in relation to their diversity and to be able to generate taxonomic information.

Among major families constituting the Gamasina, the family Zerconidae is an important component of the soil fauna in Northern Hemisphere forests and Neartic region (Halašková, 1977; Karg, 1993; Błaszak and Laniecka, 2007), ocurring in thick moss layer, leaf-litter, mor and moder humus (Karg, 1993). Many zerconid species may occur in mature and old coniferous forests, which are areas where forest management take place. New taxa of Canadian Zerconidae

from the boreal and temperate forests were first published by Halašková (1977), with new records not being reported since. It is therefore the intention of this work to document Mesostigmata diversity and apply that information in the creation of new tools for biodiversity conservation in northern forests.

1.3. Ecology of forest floor mesostigmatan mites

The importance of mesofauna in soil ecology is well recognized (Petersen and Luxton, 1982; Brussaard, 1997; Coleman et al., 2004) because of the dependence of soil processes on these organisms (Barot et al., 2007), which maintaining the equilibrium in the soil ecosystem. Nevertheless, they are still the least understood, and there remain major gaps in understanding of their biodiversity, community structure and food webs. Information about these topics is available for European forests, while in Canadian forests most previous studies have mainly focused on the most diverse and abundant soil mites, the Oribatida (Battigelli et al., 2004; Lindo and Visser, 2004; Lindo and Winchester, 2006; Lindo and Stevenson, 2007; Déchêne and Buddle, 2009; Sylvain and Buddle, 2010). Thus, the ecology of mesostigmatan mites is not well known for forest floor communities in Canadian boreal forest ecosystems.

The mixedwood boreal forest is among the largest regions in Alberta; it is formed of a mosaic of different seral stages created after wildfires (Chen and Popadiouk, 2002), with deciduous dominated forests representing early successional stages, and coniferous dominated forests representing later stages. Therefore, the area under study was part of the Ecosystem Management

Emulating Natural Disturbance (EMEND) project, which is an ecosystem-based research site that provides a framework for boreal forest management, located 90 km northwest of Peace River (Figure 1.1). The selected sites for the study of community structure of mesostigmatan mites were the unmanaged or control stands in the EMEND experiment to examine the native mesostigmatan communities in the area. From the standpoint of community dynamics, forest floor communities of mesotigmatan mites should have attributes similar to other arthropod communities (e.g., epigaeic spider and carabid beetle fauna; Work et al., 2004), except that within site variation could be greater due to the physicochemical and biological diversity and complexity of the forest floor (Setälä et al., 2000) at smaller scales.

The trophic structure of predatory mites assemblages is determinated by competitive and predator -prey interactions. A first step in exploring their trophic structure is to elaborate the number of trophic guilds that are included in the species assemblages and relate this feature to energy flow. Because of the microscopic size of mites, they can be most easily studied with biochemical tools such as stable isotopes. This technique is now widely used to assess the trophic structure and the feeding strategies of mites in the soil food web (Post, 2002; Scheu and Falca, 2000; Scheu, 2002; Pollierer et al., 2009).

In an attempt to understand the complexity of feeding relationships of the mesostigmatan mites and explain the mechanisms of predator-prey interactions, I used stable isotopes as a tool to answer questions about trophic relationships. For instance, predator mites may be generalist feeders because of the high density of

potential prey and hidden habitats impeding the access to specific prey (Scheu and Falca, 2000). Thus, it is possible to answer this question using stable isotopes which can indicate the degree of enrichment or depletion reflecting inclusion of particular prey items in a predator's diet (Sulzman, 2007), and conclude whether predator mites are generalist or specialist feeders.

At the functional level, mesostigmatan mites are grouped in guilds according to their feeding preferences as indicated by Brussaard (1998) and the feeding experiments of Walter et al. (1988). To study the trophic ecology of mesostigmatan mites I studied uncut and clear-cut harvested stands both from coniferous and deciduous forests at EMEND. Clearcutting was used as a source of variation that may affect stable isotope ratios and the efficiency of isotope technique to construct the food web of predatory mites. My dissertation research outlines the structural components of taxonomy, community ecology and trophic structure of mesostigmatan mites in the northwestern boreal mixedwood forests in northwestern Alberta.

1.4. Thesis organization

This thesis consists of a general introduction, three chapters that comprise the main primary contributions of this dissertation, and a final chapter presenting conclusions and directions for future research. The introductory chapter provides a brief overview of the motivation for this research and lays out the theoretical framework for the study. The arrangement of the subsequent chapters reflects the sequence of the research. In the second chapter, I present the results of a scientific

paper produced in this study on new species described, mostly from the genus *Mixozercon*. The third chapter is related to community structure issues, especially on diversity, dominance and species composition, and how forest stand type affects the community composition of Mesostigmata. In the fourth chapter, I focus on trophic relations and the food web structure of mesostigmatan mites including how trophic organization may be affected by forest harvest. Finally, in the fifth chapter I provide the overall conclusions from my results identifying some limitations of the study and recommended directions for future research.

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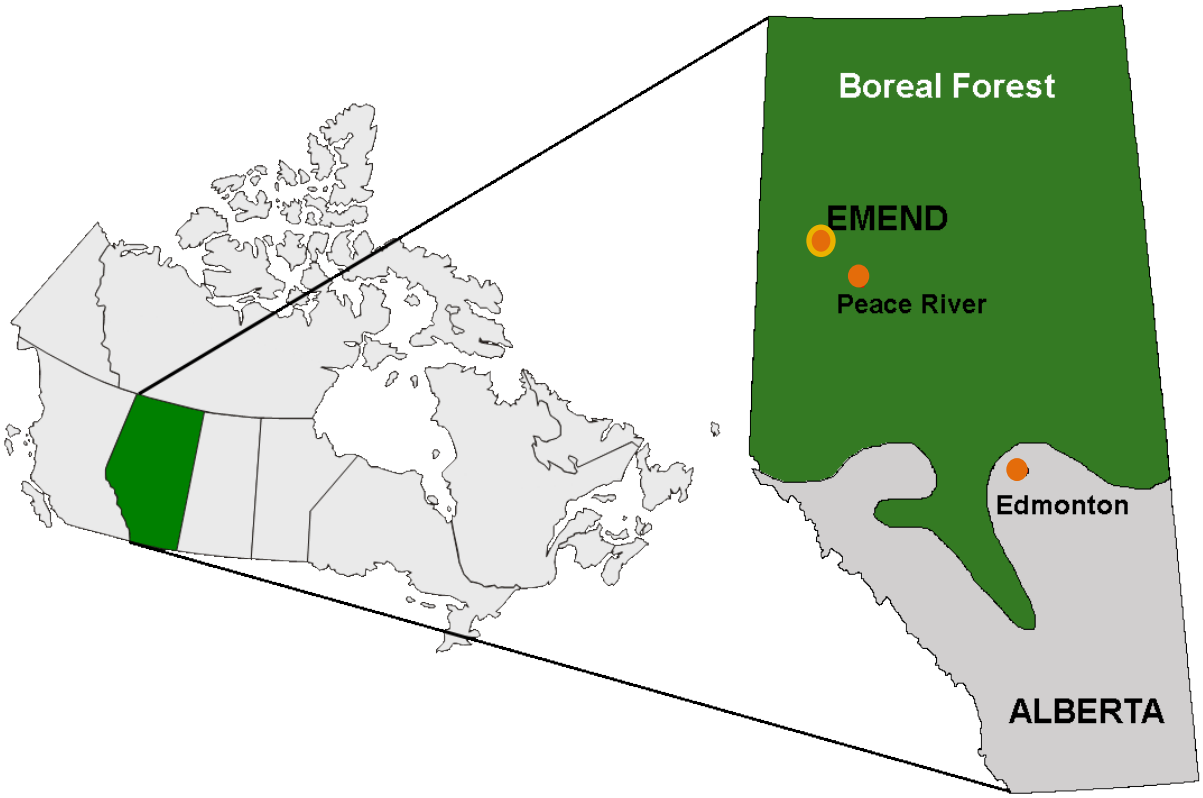

Figure 1.1. Location of site of study at EMEND project in northwestern Alberta.

CHAPTER 2

New zerconid mites (Acari: Mesostigmata: Zerconidae) from Canada, with a review of the genus *Mixozercon* Halašková, 1963[1]

2.1. Introduction

Zerconid mites are an important component of the soil fauna of the Northern Hemisphere. Most of the faunistic and taxonomic research on this family has been carried out in the Palaearctic Region, and most of the described species are known from Eurasia. However, based on recent studies, the species-richness of the family is expected to be high in the Nearctic region as well (Sikora and Skoracki, 2008).

The first investigation of the North America fauna was by Sellnick (1958), who described four species of Zerconidae from Alaska and California, USA. Halašková (1969b) reported several new taxa of Zerconidae from South and North Carolina, USA. Later Błaszak (1976a) revised some of Sellnick's species, and described two new genera. Halašková (1977) enriched our knowledge of the Nearctic zerconid mite fauna by revising and describing nine new species and four new genera from Canada. During the 1980s the number of species and genera

[1] **A version of this chapter has been published as Diaz-Aguilar, I. and Ujvári, Z. 2010. New zerconid mites (Acari: Mesostigmata: Zerconidae) from Canada, with a review of the genus *Mixozercon* Halašková, 1963. Zootaxa 2555: 1–29.**

of Zerconidae described from the USA grew following the prolific work of Błaszak (1980, 1981a, 1981b, 1982, 1984), including the description of a fossil genus from a cave in New Mexico (Błaszak et al., 1995). Sikora and Skoracki (2008) then described the genus *Blaszakiella* Sikora and Skoracki, 2008. In spite of the relatively high number of taxonomic papers published, only a small proportion of North America's zerconid mites is known, with most of the genera represented by few records.

A total of 20 genera of Zerconidae is known from North America (Sikora and Skoracki, 2008), and only five of them (*Caurozercon* Halašková, 1977, *Echinozeron* Błaszak, 1976, *Mixozercon* Halašková, 1963, *Parazercon* Trägårdh, 1931 and *Zercon* C. L. Koch, 1836) are known from both the Palaearctic and Nearctic regions. *Zercon* is the most species-rich genus of the family, having representatives in both regions (Evans, 1955), but only very few species are common to the two regions. Most of the species of the genera *Caurozercon* and *Echinozercon* are distributed in the eastern part of Asia, with one species in each genus originally described from North America (Halašková, 1977; Błaszak, 1982). *Parazercon* appears to be widespread, with its species-richness lowest in the Holarctic region and highest in Southeast Asia. Only one species, *Parazercon radiatus* (Berlese, 1910), is distributed in the colder temperate zone and high mountains of North America, through Asia to Europe (Halašková, 1977). The presently known *Mixozercon* species show an interesting distribution pattern, with few records from the Far East (Aoki, 1964), northern and eastern Europe

(Schweizer, 1948; Halašková, 1969a; Balan, 1995), and western Canada (Halašková, 1977).

The present paper adds to the knowledge of the genus *Mixozercon* from northwestern Alberta, Canada, providing additional information on the distribution and morphology of the genus, with the description of three new species. In addition, one new species that represents a new genus is described.

2.2. Material and methods

Mites were collected in September 2006 from the forest floor of boreal mixedwood forests at the EMEND (Ecosystem Management Emulating Natural Disturbance) research study site of 1,000 ha, located in the Boreal Plains Ecozone, approximately 90 km northwest of Peace River, Alberta, Canada (56° 46' 13" N, 118° 22' 28" W). Three main forest stand types are represented in the area, with coniferous forests dominated by white spruce (*Picea glauca*), deciduous forests dominated by trembling aspen (*Populus tremuloides*), and mixed forests that consists of approximately of 35% *P. glauca* and 65% *P. tremuloides*. These forest stands were originated by fire between 80 and 140 years ago. Three random samples were collected throughout the stands of each type of forest and their three replications (N=27).

The forest floor of the sampled coniferous forest consists of needle leaf-litter and mosses, of which the more abundant species are stair-step moss (*Hylocomiun splendens*), knight's plume (*Ptilium crista-castrensis*) and feather moss (*Pleurozium schreberi*). In the deciduous forest, the forest floor contained

broadleaf-litter and small twigs, and the understory consisted of diverse shrubs such as green alder (*Alnus crispa*), low bush-cranberry (*Viburnum edule*), prickly rose (*Rosa acicularis*), and buffaloberry (*Shepherdia canadensis*), and understory vascular plants such as dewberry (*Rubus pubescens*), bunchberry (*Cornus canadensis*), twinflower (*Linnaea borealis*), fireweed (*Chamerion angustifolium*), tall bluebells (*Mertensia paniculata*) and bluejoint grass (*Calamagrostis canadensis*). The floor of the mixed forest also included mainly broadleaf-litter and small twigs, and the understory consisted of almost the same vascular plants as deciduous forest but observed with a higher frecuency of lingonberry (*Vaccinium vitis-idaea*).

Specimens were extracted using Tullgren funnels, sorted under a stereomicroscope, cleared in lactic acid and mounted in slides with PVA (polyvinyl alcohol). Preparations were examined using light microscopy, and drawings were made with a drawing tube attached to a compound microscope. SEM images were taken in the Hungarian Natural History Museum with a HITACHI SN 2600 scanning electron microscope. Holotypes and paratypes of the new species are deposited in the Canadian National Collection of Insects, Arachnids and Nematodes (CNC), at Agriculture and Agri-Food Canada, Ottawa, Canada. Paratypes of the new species are also in the Collection of Soil Zoology of the Hungarian Natural History Museum, Budapest, Hungary (HNHM), and Ohio State University Acarology Collection, Columbus, Ohio, USA (OSAL). Terminology of setae follows Sellnick (1958), adapted by Błaszak (1974) and Mašán and Fenďa (2004), except that the i and I setal nomenclature were replaced

by j and J as proposed by Lindquist and Evans (1965) and Lindquist and Moraza (1998). Measurements are given in micrometres (μm) and presented as range and average for body sizes. Abbreviations used are: DN=deutonymph, PN=protonymph, CD=coniferous dominant forest, DD=deciduous dominant forest, MX=mixed forest and CC=clear cut.

2.3. Systematics

Genus *Mixozercon* Halašková, 1963

Mixozercon Halašková, 1963: 206; 1969a: 343; Błaszak, 1974: 49; 1976a: 565; 1979: 85; Mašán and Fenďa, 2004: 56; Blaszak et al., 2007: 104.

Parazercon (in part).— Schweizer, 1948: 23.

Zercon (in part).— Sellnick, 1958: 337.

Type species: *Parazercon sellnicki* Schweizer, 1948: 23; by original designation.

Diagnosis. Peritrematal shield bearing two setae: p1 short and smooth, p2 elongate and pilose; projecting beyond the lateral margin of idiosoma, situated in the anterior half of the shield. Small cuticular knobs present near p2. Peritrematal shield separated from podonotal shield by a narrow strip of interscutal membranous cuticle; in the female, shield truncate behind the fourth pair of coxae, in the male, its posterolateral end fused to ventri-anal shield. Peritremes short, straight or slightly bent. Adgenital sclerites absent, only a single pair of gland openings (gv2) present posterolateral to the genital shield. A pair of narrow post-genital sclerites may be present. Anterior margin of ventri-anal shield typically with two pairs of setae. Anterior ends of peritrematal shields fused

together, and fused to the anterior margin of the dorsal shield to form a ventral extension of the vertex of the dorsal shield. Lateral margin of opisthonotum with 7–8 pairs of R-series setae. Dorsal cavities small and conspicuous. Epistome with a bifurcate medial process.

Remarks. Apart from the narrow separation of the peritrematal shield from the body margin and the absence of adgenital sclerites, Halašková (1963) mentioned the less conspicuous dentation of the margin of idiosoma as a differential character to separate Mixozercon from *Zercon*. She also drew attention to the different length and type of pilosity of the dorsal setae (as in the genus *Prozercon* Sellnick, 1943). However, these differences are useless for distinguishing genera, because of the large interspecific variation within species of the same genus. As a result of the many intermediate character states (between *Zercon* and *Prozercon* species) combined in the single species, she gave the name *Mixozercon* to the newly established genus. Later the diagnosis of the genus was amended by inclusion of the posterior end of the peritrematal shield, which is generally truncate posteriorly, and the number of setae on the anterior margin of the ventri-anal shield (Halašková, 1969a; Błaszak, 1974, 1979). Very little information can be found about those characters in the males of *Mixozercon* species. In our opinion, the other specific character of the genus, besides the setation, the marginal separation of the peritrematal shield, the shape of its posterior end, and the absence of adgenital sclerites, and the presence of setae V11, is the lateral fusion of the ventri-anal and peritrematal shields in males

(however, this phenomenon characterises other species of different Zerconidae genera as well).

2.3.1. *Mixozercon heterosetosus* (Balan, 1995)

Mixozercon heterosetosus Balan, 1995: 76; Mašán and Fenďa, 2004: 56.

Diagnosis. Central and submarginal setae of podonotum smooth, except j1. Setae J1-J4 and Z1-Z2 short, smooth, other J-, Z- and S-setae elongate, brush-like, plumose. R- setae uniform in length, R1 pilose, others smooth and thorn-like. Setae J5 situated in front of dorsal cavities. None of the setae on the dorsal shield reaching the bases of the following seta. Setae S1 situated posterolaterally to Z1. Pores Po2 situated on a line connecting Z2 and S2. Podonotum and opisthonotum without sculpturing pattern. Dorsal cavities well-sclerotised, saddle-like, with undulate anterior margin.

Distribution. Ukraine.

2.3.2. *Mixozercon sellnicki* (Schweizer, 1948)

Parazercon sellnicki Schweizer, 1948: 23.

Zercon sellnicki.— Sellnick, 1958: 337; Schweizer, 1961: 166; Karg, 1971: 309; Petrova, 1977: 591.

Mixozercon sellnicki.— Halašková, 1963: 206; 1969a: 343; Błaszak, 1974: 49; Karg, 1993: 329; Mašán and Fenďa, 2004: 56; Błaszak et al., 2007: 104.

Diagnosis. Central and submarginal setae of podonotum smooth, except j1 and j2 longer and pilose. Setae J1-J2 and Z1 short, smooth, J3-J5 and Z2-Z3 short,

pilose, other J-, Z- and S-setae elongate, brush-like, plumose. Setae R1 pilose, longer than other R-setae, which are smooth and thorn-like. Setae J5 situated between dorsal cavities. No dorsal seta long enough to reach the base of the following seta. Setae S1 situated lateral to Z1. Pores Po2 situated on a line connecting Z2 and S1. Podonotum covered by tile-like pattern; distinct punctation present on whole opisthonotum. Dorsal cavities well-sclerotised, saddle-like, with smooth anterior margin. Adgenital and post-genital sclerites absent.

Distribution. Iceland, Sweden, Switzerland, Germany, Latvia, Poland, Slovakia and Romania.

Remarks. We examined the type material of the species deposited in the Natural History Museum of Basel (syntypes on slides He 159, He 170 and He 176). On the slides labelled as "*Parazercon sellnicki*" there are also other mesostigmatid mite species, which might be confusing. Schweizer (1948) designated five females and two males as syntypes, but we found no male specimens on the slides. In Slovakian specimens found by Halašková (1963), setae j2 are short and smooth, and J2 are pilose, which was insufficient for establishing a new taxon, perhaps as a result of intraspecific variation. In a later diagnosis of Halašková (1969a), J2 is described as smooth. In Halašková's drawing there is only one pair of setae on the anterior margin of the ventri-anal shield, but Błaszak (1974), Halašková (1969a) and Błaszak (1979) indicated that there are two pairs of setae in that position. The second pair of ventri-anal setae on the anterior margin of ventri-anal shield was probably present but not clearly visible, according to the diagnosis in Halašková (1969a).

2.3.3. *Mixozercon stellifer* (Aoki, 1964)

Prozercon stellifer Aoki, 1964: 489.

Mixozercon stellifer.— Halašková, 1977: 67; Błaszak, 1979: 85.

Diagnosis. Central and submarginal setae of podonotum smooth, except j1-j2, z2 and s6 pilose. Setae J1-J4, Z1-Z3 and S1 short, pilose, other J-, Z- and S-setae longer, densely pilose. Setae R1 pilose, markedly longer than the others, which are smooth and thorn-like. Setae J5 situated between dorsal cavities. Opisthonotal setae do not reach the bases of the following setae. Setae S1 situated posterolaterally to Z1. Pores Po2 situated inside the line connecting Z1 and Z2. Podonotum covered by circular, squamous pattern, the area between J setal-rows densely ornamented by triangular protuberances forming stellar pattern. Dorsal cavities weakly sclerotised, with undulate anterior margin. Post-genital sclerites absent.

Distribution. Japan and possibly Canada.

Remarks. On the basis of the figures and descriptions of Aoki (1964) and Halašková (1977), the Japanese and Canadian specimens differ in some characters; for example, the body shape, the shape and length of setae R1 and some podonotal setae; specially j2, which is smooth for Canadian specimens, and the J and Z setal rows inserted in bigger setal bases. Therefore, we have some doubt that the Palaearctic and Nearctic specimens are conspecific; however, further investigation is necessary.

2.3.4. *Mixozercon albertaensis* sp. nov.

(Figures 2.1–6, 21, 25, 29, 33)

Material examined. Holotype: female collected in stand 867-MX, plot 2 (56° 44' 36.370" N, 118° 22' 35.480" W) at EMEND research study site, southern area, from understory vascular plants and leaf-litter on forest floor, 8.09.2006, leg. Díaz-Aguilar, I. (deposited in CNC). Paratypes: stand 867-MX, plot 4, southern area, from understory vascular plants and leaf-litter on forest floor, 8.09.2006, leg. Díaz-Aguilar, I. (1 female deposited in HNHM); stand 852-DD, plot 1, southeastern area, from understory vascular plants and broadleaf-litter on forest floor, 11.09.2006, leg. Díaz-Aguilar, I. (1 female, 1 male deposited in CNC); stand 864-DD-CC, southern area, from grassed forest floor, 7 years after harvested, 10.09.2006, leg. Díaz-Aguilar, I. (1 female deposited in HNHM); stand 889-CD, plot 6, southwestern area, from mosses and needle leaf-litter on forest floor, 9.09.2006, leg. Díaz-Aguilar, I. (1 female, 1 male deposited in CNC, 1 female, 1 male deposited in HNHM); stand 862-DD, plots 2, 4 and 5, and stand 852-DD, plots 1, 2 and 6, southern and southeastern areas, from understory vascular plants and broadleaf-litter on forest floor, 10–11.09.2006, leg. Díaz-Aguilar, I. (43 females, 14 males, 7 PN, 16 larvae); stand 867-MX, plots 1, 2 and 4, and stand 902-MX, plots 1, 3 and 6, southern and southwestern areas, from understory vascular plants and leaf-litter on forest floor, 8–10.09.2006, leg. Díaz-Aguilar, I. (35 females, 7 males, 1 PN, 17 larvae); stand 889-CD, plot 6, southwestern area, from mosses and needle leaf-litter on forest floor, 9.09.2006, leg. Díaz-Aguilar, I. (6 females, 7 males); stand 864-DD-CC, southern area, from

grassed forest floor, 7 years after harvested, 10.09.2006, leg. Díaz-Aguilar, I. (1 female, 1 male).

Diagnosis. Adult female. Central and submarginal setae of podonotum smooth, except j1 and j2. Setae J1, Z1, S1 and marginal setae R1-8 smooth, other opisthonotal setae pilose to varying degrees. Central members of J and Z setal row inserted in enlarged setal bases. Setae J5 situated above the line of dorsal cavities. Z3 not reaching the bases of Z4. Setae S1 situated lateral to Z1. Pores Po2 situated on a line connecting Z1 and Z2. Medial part of podonotum covered by tile-like pattern, the area between J setal rows densely ornamented by small, irregular depressions. Dorsal cavities weakly sclerotised, with undulate anterior margin. Posterior ending of peritrematal shield straight, reaching beyond the level of setae R1. Post-genital sclerites present.

Description. Female. Length of idiosoma 335–360μm (mean 350); width 240–260μm (mean 250) (n = 6).

Dorsum (Figures 2.1, 2.21). Podonotum with 22 pairs of setae: j-row with six pairs, z-row with two pairs, s-row with six pairs, r-row with six pairs, p-row with two pairs. Setae j1 densely pilose, j2 lightly pilose, s3 elongate, pilose. Other j-, z- and s-setae short, smooth and needle-like. Marginal seta r1 short and smooth, r3 and r6 elongate and plumose, others shorter and densely pilose. Pores po1 situated above the line connecting the insertions of j2 and s1, po2 lying on a line connecting j4 and s4, po3 on a line connecting s5 and s6. Peritrematal seta p1 short and smooth, and p2 elongate and pilose; both visible in dorsal view. Lateral parts of podonotum covered by small, circular, squamous ornamentation; central

parts with irregular, tile-like pattern (Figure 2.33). Ornamentation between setae z1 weakly developed. Opisthonotum with 23 pairs of setae (Figures 2.25, 2.29): J-row with six pairs, Z-row with five pairs, S-row with four pairs and R-row with eight pairs. Setae J1 short, smooth, distance between their bases 41 μm. Setae J2-J5 similar in shape and length, pilose and pointed, J5 situated above the line of dorsal cavities, J6 elongate and plumose. Setae Z1 similar in shape and length to J1, Z2-Z3 delicately pilose. Z4 elongate, brush-like, distally expanded, Z5 short, delicately pilose. Setae S1 smooth, simple, situated laterally to Z1, the distance between their insertions 23 μm. Setae S2-S4 elongate, densely plumose, extending beyond the lateral margin of opisthonotum. Setae S2 situated posterolateral to Z2. J-, Z- and S- setae not reaching the bases of the following setae. Setal bases of J2-J5 and Z2-Z4 prominently enlarged. Marginal setae R short, smooth, thorn-like. Pores Po1 situated anterolateral to Z1, Po2 on a line connecting the insertions of Z1 and Z2, Po3 enlarged, on a line connecting J4 and Z4, Po4 inside the bases of setae S4. Lateral and posterior parts of opisthonotum densely covered by large, distinct, bulging spots. Central area between J setae with irregular depressions (foveolate) forming circles of 6-7. Dorsal cavities weakly sclerotised, uniform, with undulate anterior margin and with axes parallel to that of the body. Length of opisthonotal setae and the distances between their insertions as in Table 2.1.

Venter (Figure 2.2). Slit between peritrematal shield and body margin relatively narrow. Posterior ends of peritrematal shield truncated, straight, reaching beyond the level of R1. Peritremes straight, with curved anterior section.

One pair of narrow post-genital sclerites present. Anterior margin of ventri-anal shield with two pairs of setae. Pre-anal setae short simple, post-anal seta elongate, distally pilose. Ventri-anal pores situated anterolateral to adanal setae. Sternal shield with reticulate ornamentation, ventri-anal shield covered by squamous pattern.

Male. Length of idiosoma 270–278μm (mean 275); width 192–200μm (mean 195) (n = 3). Chaetotaxy, poroidotaxy and sculpturing pattern of dorsal shield (Figure 2.3) similar to those of female, except setae j2 and Z5 smooth. Sternogenital shield weakly sclerotised, posteriorly rounded, bearing five pairs of setae. Post-genital sclerites oblong, situated between adgenital gland openings. Peritrematal shield and ventri-anal shield fused laterally, between level of setae R2 and R3, not separated from the body margin (Figure 2.4). Anterior margin of ventri-anal shield with two pairs of setae. Length of opisthonotal setae and the distances between their insertions are as in Table 2.1.

Deutonymph. Unknown.

Protonymph (Figure 2.5). Length of idiosoma 220–225 μm (mean 223); width 147–152 μm (mean 150) (n = 3). Podonotal setae s4-s5 and r3 elongate, brush-like, plumose, others short, smooth and needle-like. Opisthonotal setae J1, J2, J3, J5 short, smooth or barely pilose, J4 distinctly pilose. Setae Z1-Z2 similar to short J-setae, needle-like. Setae Z3 longer, delicately pilose, other members of J, Z and S setal-rows elongate, brush-like, densely plumose. Setae R1 short, smooth, thorn-like. Pores Po3 situated on a line connecting the bases of J4 and Z4. Dorsal cavities as in adult stages. Surface of podonotum smooth, opisthonotal

shield with some irregular posterolateral pits, irregular depressions between J and Z rows weakly developed. Length of J, Z and S setae and distances between their insertions are as in Table 2.1.

Larva (Figure 2.6). Length of idiosoma 208–230μm (mean 220); width 170–182μm (mean 178) (n = 4). Podonotal setae elongate, densely plumose. Opisthonotal setae J2, J3, J5, Z2 and S2 short and simple, others elongate, densely plumose. Well-sclerotised parts of dorsal idiosoma with a reticulate pattern, surface of opisthonotum covered by small cavities lying at intersections of a reticulate ornamentation. Dorsal cavities situated in a row, the medial pair fused.

Etymology. The species is named after the Canadian province of Alberta where it was collected.

Remarks. *Mixozercon albertaensis* is closely related to *M. jasoniana* sp. nov., and *M. borealis* sp. nov. by the shape of dorsal cavities and the presence of enlarged setal bases, but these species can easily be distinguished according to the features given in Table 2.4.

2.3.5. *Mixozercon jasoniana* sp. nov.

(Figures 2.7–11, 22, 26, 30, 34)

Material examined. Holotype: female collected in stand 940-DD, plot 6 (56° 49' 5.753" N, 118° 21' 38.284" W) at EMEND research study site, northern area, from understory vascular plants and broadleaf-litter on forest floor, 8.09.2006, leg. Díaz-Aguilar, I. (deposited in CNC). Paratypes: stand 940-DD, plot 6, northern area, from understory vascular plants and broadleaf-litter on

forest floor, 8.09.2006., leg. Diaz-Aguilar, I. (3 females, 1 DN deposited in CNC, 1 female, 2 DN deposited in HNHM); stand 928-MX, plot 1, northeastern area, from understory vascular plants and leaf-litter on forest floor, 9.09.2006, leg. Díaz-Aguilar, I. (2 females deposited in HNHM, 2 males deposited in CNC); stand 928-MX, plots 1, 2 and 4, northeastern area, from understory vascular plants and leaf-litter on forest floor, 9.09.2006, leg. Díaz-Aguilar, I. (30 females, 5 males, 2 DN); stand 930-CD, plot 4, northeastern area, from mosses and needle leaf-litter on forest floor, 9.09.2006, leg. Díaz-Aguilar, I. (4 females); 940-DD, plot 6, northern area, from understory vascular plants and broadleaf-litter on forest floor, 8.09.2006., leg. Diaz-Aguilar, I. (23 females, 8 DN).

Diagnosis. Adult female. Central and submarginal setae of podonotum smooth, except j1, z2 and s6. J-, Z- and S-setae of opisthonotum pilose to varying degrees, R1 slightly pilose, other marginal R-setae smooth, thorn-like. Central members of J and Z setal-row inserted on enlarged setal bases. Setae J5 situated between dorsal cavities; Z3 reaching bases of Z4; S1 situated close to Z1, in posterolateral position. Pores Po2 situated inside the line connecting Z1 and Z2. Podonotum covered by circular, squamous pattern, the area between J setal-rows ornamented with relatively large, subtriangular protuberances. Dorsal cavities weakly sclerotised, with undulate anterior margin. Posterior end of peritrematal shield rounded, reaching beyond level of R3. Post-genital sclerites absent.

Description. Female. Length of idiosoma 342–360μm (mean 355); width 244–252μm (mean 250) (n = 7).

Dorsum (Figures 2.7, 2.22). Podonotum, 22 pairs of setae: j-row with six pairs, z-row with two pairs, s-row with six pairs, r-row with six pairs, p-row with two pairs. Setae j1 plumose, z2 and s6 often barbed, s3 elongate, plumose. Other j-, z- and s-setae short, smooth and needle-like. Marginal setae r3 and r6 elongate, plumose, other r setae shorter and delicately pilose (r1 may be smooth). Peritrematal seta p1 short and smooth, p2 elongate and pilose; both visible in dorsal view. Pores po1 situated on a line connecting the insertions of j2 and s1, po2 lying on a line connecting j4 and s4, near s4, po3 inside the line connecting s5 and s6. Whole podonotum covered by small, circular, irregular squamous ornamentation, mostly arranged in curved lines in the center of the shield (Figure 2.34). Circular ornamentation between setae z1 well-developed, strongly sclerotised. Opisthonotum (Figures 2.26, 2.30) with 23 pairs of setae: J-row with six pairs, Z-row with five pairs, S-row with four pairs and R-row with eight pairs. Setae J1-J5 elongate, pilose and pointed, J1 situated close together, distance between their bases 16 μm, J2-J5 diverging further away from each other. Setae J5 situated between dorsal cavities, J6 elongate, brush-like and plumose. Z-Z3 similar in shape and length to anterior J-setae, Z3 reaching bases of Z4. Setae Z4 long, broadening distally, brush-like and plumose, Z5 short, delicately pilose. Setae S1 similar in shape and length to Z1, situated close to Z1, distance between their insertions 11 μm. Setae S2-S4 elongate, densely plumose, extending beyond lateral margin of opisthonotal shield. Setae S2 situated anterolateral to Z2. Eight marginal R-setae short, smooth and thorn-like; in some specimens R1 delicately barbed. Setae J1-J5, Z1-Z4 and S1 inserted on broad setal bases. Pores Po2-Po4

enlarged, with undulate margins, Po1 situated anterior to Z1, Po2 axial to a line connecting the insertions of Z1 and Z2, Po3 enlarged, on a line connecting J4 and Z4, Po4 on a line connecting Z5 and S4. Lateral parts of opisthonotum sparsely covered by large, bulging spots, central area around J setae with large, distinct, subtriangular protuberances forming a central star-like pattern. Dorsal cavities weakly sclerotised, uniform, with undulate anterior margin, axes parallel to that of the body. The length of opisthonotal setae and the distances between their insertions as in Table 2.2.

Venter (Figure 2.8). Posterolateral ends of peritrematal shield arcuate, expanded posteriorly, reaching beyond level of R3 setae. Peritremes straight, with bent anterior tips. Post-genital sclerites absent. Anterior margin of ventri-anal shield with two pairs of setae. Pre-anal setae short simple, post-anal seta elongate, distally pilose. Ventri-anal pores situated lateral to adanal setae. Sternal shield with reticulate ornamentation, ventri-anal shield covered by squamous pattern.

Male. Length of idiosoma 263–267μm (mean 265); width 180μm (n = 2). Chaetotaxy, poroidotaxy and sculpturing pattern of dorsal shields (Figure 2.9) similar to female, but setae r5 may be slightly pilose. On the ventral side (Figure 2.10), sternogenital shield with straight posterior margin and five pairs of setae. Peritrematal shield and ventri-anal shield fused laterally, on the level of R3 setae, not separated from the body margin. Post-genital sclerites absent. Ventri-anal shield with one pair of setae on the anterior margin and 17 ventri-anal setae (Figure 2.10). The length of opisthonotal setae and the distances between their insertions as in Table 2.2.

Deutonymph (Figure 2.11). Length of idiosoma: 275–283μm (mean 280); width 178–188μm (mean 185) (n = 3). Setae j1 barbed, s3, r3 and r6 long, brush-like, plumose, other podonotal setae smooth, simple. Chatetotaxy and poroidotaxy of opisthonotum as in adult stages. Podonotal circular, irregular-squamous pattern and circular sclerotised markings weakly developed, central and lateral parts of opisthonotum covered by circular protuberances. The length of J, Z and S setae and the distances between their insertions as in Table 2.2.

Protonymph and larva. Unknown.

Etymology. The species is dedicated to Mr. Jason Edwards, EMEND field coordinator.

Remarks. There is a difference in the number of setae on the anterior margin of the ventri-anal shield between male and female specimens. All females observed bear two pairs of setae on the anterior margin of ventri-anal shield, in contrast to male specimens, which generally had one pair of setae but sometimes two. *Mixozercon jasoniana* is closely related to *M. albertaensis* sp. nov., and *M. borealis* sp. nov. by the shape of the dorsal cavities and the presence of enlarged setal bases, and also resembles *M. stellifer* on the basis of the similar sculpturing pattern and the pilosity of J-, Z-, and S-setae. The four species can be distinguished from each other according to the particular characteristics given in Table 2.4.

2.3.6. *Mixozercon borealis* sp. nov.

(Figures 2.12–15, 23, 27, 31, 35)

Material examined. Holotype: female collected in stand 902-MX, plot 6 (56° 45' 44.754" N, 118° 24' 53.369" W) at EMEND research study site, southwestern area, from understory vascular plants and leaf-litter on forest floor, 10.09.2006, leg. Díaz-Aguilar, I. (deposited in CNC). Paratypes: stand, plot, sampler and sampled season same that of the holotype (2 females, 1 male deposited in CNC, 1 female deposited in HNHM); stand 902-MX, plot 1, southwestern area, from understory vascular plants and leaf-litter on forest floor, 10.09.2006, leg. Díaz-Aguilar, I. (1 female deposited in CNC, 1 female, 1 male deposited in HNHM); stand 918-CD, plot 6, northern area, from mosses and needle leaf-litter on forest floor, 7.09.2006., Diaz-Aguilar, I. (1 female deposited in HNHM, 1 male deposited in CNC); stand 918-CD, plot 3 and 6, northern area, from mosses and needle leaf-litter on forest floor, 07.09.2006., Diaz-Aguilar, I. (15 females); stand 902-MX, plots 1, 3 and 6, southwestern area, from understory vascular plants and leaf-litter on forest floor 10.09.2006, Díaz-Aguilar, I. (24 females, 5 males).

Diagnosis. Adult female. Central and submarginal setae of podonotum smooth, except j1. Setae J1, Z1, Z5 and marginal R2-R8 smooth, R1 slightly barbed, other opisthonotal J-, Z- and S-setae pilose to varying degrees. Central members of J and Z setal-row inserted in extraordinarily enlarged setal bases, J5 situated between dorsal cavities, Z3 reaching the bases of Z4. Setae S1 situated close to Z1, in posterolateral position. Pores Po2 situated on a line connecting Z1 and Z2. Podonotum covered by circular, irregular-squamous pattern, area between J setal-rows densely ornamented by triangular protuberances. Dorsal cavities

weakly sclerotised, with undulate anterior margin. Posterior end of peritrematal shield truncate, reaching the level of R2. Post-genital sclerites absent.

Description. Female. Length of idiosoma 342–368μm (mean 360); width 260–275μm (mean 270) (n = 7).

Dorsum (Figures 2.12, 2.23). Podonotum with 22 pairs of setae: j-row with six pairs, z-row with two pairs, s-row with six pairs, r-row with six pairs, p-row with two pairs. Setae j1 barbed, s3 elongate, pilose, other j-, z- and s-setae short, smooth and needle-like. Marginal setae r3 and r6 elongate, plumose, other r setae shorter and delicately pilose. Peritrematal seta p1 short and smooth, and p2 elongate and pilose; both visible in dorsal view. Pores po1 situated medial to s1, po2 lying on a line connecting j4 and s4, po3 on a line connecting s5 and s6. Whole podonotum covered by small, circular, irregular-squamous pattern (Figure 2.35). Circular markings between setae z2 well-developed. Opisthonotum (Figures 2.27, 2.31) with 23 pairs of setae: J-row with six pairs, Z-row with five pairs, S-row with four pairs, R-row with eight pairs. Anterior J setae situated close to each other, J and Z setal-rows widely separated. Setae J1 shorter than other J-setae, smooth, situated close to each other, distance between their bases 21 μm. Setae J2-J5 similar in shape and length, pilose and pointed, tips not reaching the bases of the following seta. Setae J5 situated between dorsal cavities, extending beyond posterior margin of idiosoma. Setae J6 elongate, plumose. Setae Z1 similar in shape and length to J1, Z2-Z3 pilose, Z3 reaching base of the following seta. Z4 elongate, brush-like, distally expanded, Z5 short and smooth. Setae S1 slightly barbed, adjacent and posterolateral to Z1; distance between their

insertions 15 μm. Setae S2-S4 elongate, densely plumose, extending beyond the margin of idiosoma. Setae S2 situated anterolateral to Z2. Marginal R1-R8 setae short, smooth and thorn-like, R1 may be delicately pilose. Setae J1-J5, Z1-Z4 and S1 inserted on enlarged protuberant setal bases. Pores Po1 situated anterior to Z1, Po2 on a line connecting insertions of Z1 and Z2, Po3 small, lying on a line connecting J4 and Z4, near Z4, Po4 on a line connecting Z5 and S4. Lateral parts of opisthonotum densely covered by large, distinct, bulging spots, central area around J setae with distinct, subtriangular protuberances arranged in circles, forming a stellar pattern. Dorsal cavities weakly sclerotised, uniform, with undulate anterior margin and with axes parallel to that of the body. The length of opisthonotal setae and the distances between their insertions as in Table 2.3.

Venter (Figure 2.13). Slit between the peritrematal shield and the body margin relatively narrow. Posterior ends of peritrematal shield truncated, straight, reaching beyond the level of R1. Peritremes straight or slightly curved. Post-genital sclerites absent. Anterior margin of ventri-anal shield with two pairs of setae. Pre-anal setae short simple, post-anal seta elongate, distally pilose. Ventri-anal pores situated lateral to adanal setae. Sternal shield with reticulate ornamentation, ventri-anal shield covered by squamous pattern.

Male. Length of idiosoma 277–290μm (mean 285); width 195–202μm (mean 200) (n = 3).

Chaetotaxy, poroidotaxy and sculpturing pattern of dorsal (Figure 2.14) and ventral (Figure 2.15) shields similar to those on the female, J and Z setae less pilose. Sternogenital shield with straight posterior ending, bearing five pairs of

setae. Peritrematal shield and ventri-anal shield fused laterally at the level of setae R2, not separated from body margin. Post-genital sclerites absent. Anterior margin of ventri-anal shield with two pairs of setae (Figure 2.15). The length of J, Z and S setae and the distances between their insertions as in Table 2.3.

Immature stages. Unknown.

Etymology. The name of the species refers to the fact that it was found in the mixedwood boreal forests.

Remarks. *Mixozercon borealis* is closely related to *M. albertaensis* and *M. jasoniana* by the shape of the dorsal cavities and the presence of enlarged setal bases, and also resembles *M. stellifer* on the basis of the similar sculpturing pattern and the pilosity of the J-, Z-, and S-setae. This species can be distinguished from the other species of the genus according to the features given in Table 2.4.

2.4. Key to the females of the genus *Mixozercon*

1. Opisthonotal J-, Z- and S-setae situated on small setal bases 2

– Opisthonotal J-, Z- and S-setae situated on enlarged setal bases (Figures 2.25, 2.26, 2.27) 4

2. Setae J1-J2 and Z1 smooth; dorsal cavities saddle-like, with smooth anterior margin 3

– Setae J1-J2 and Z1 pilose; dorsal cavities with undulate anterior margin .... *Mixozercon stellifer* (Aoki, 1964)

3. Setae J3-J4 pilose, similar in shape and length to J5.....

..... *Mixozercon sellnicki* (Schweizer, 1948)

– Setae J3-J4 smooth, distinctly shorter than J5.....

..... *Mixozercon heterosetosus* (Balan, 1995)

4. Setae J1 and Z1 smooth; posterior ends of peritrematal shield truncated between the level of R1 and R2, straight 5

– Setae J1 and Z1 pilose; posterior ends of peritrematal shield expanded beyond the level of R3, rounded (Figures 2.7, 2.8) .....

..... *Mixozercon jasoniana* **sp. nov.**

5. Post-genital sclerites present; setae J5 inserted anterior to dorsal cavities, their tips not reaching posterior margin of idiosoma; J setae region ornamented with irregular pits or depressions (Figures 2.1, 2.25) .....

.... *Mixozercon albertaensis* **sp. nov.**

– Post-genital sclerites absent; setae J5 inserted between outer dorsal cavities, their tips reaching slightly beyond posterior margin of idiosoma; J setae region with subtriangular ornamentation arranged in circles (Figures 2.12, 2.27) .....

..... *Mixozercon borealis* **sp. nov.**

2.5. Genus *Boreozercon* gen. nov.

Diagnosis. Adults. Peritrematal shield bearing two setae, p1 short and smooth, p2 elongate and pilose, extending beyond lateral margin of idiosoma, situated in the middle of the shield, both visible in dorsal view. Peritrematal shield separated from the podonotal shield by a narrow slit of interscutal membranous cuticle; in the female its posterolateral ends are pointed and expanded posteriorly,

reaching setae R5, in the male its posterolateral ends fused to the ventri-anal shield. Peritremes short, straight or slightly bent. Adgenital gland openings gv2 not developed in female; in males a pair of adgenital pores present posterolateral to the sternogenital shield, with a very fine sclerotisation, as a small microplatelet. A pair of narrow post-genital sclerites may be present in female. Anterior margin of ventri-anal shield with one pair of setae, total number of ventri-anal setae 15, setae Vl1 absent. The antero-dorsal shield slopes abruptly anterior to the vertical setae. Lateral margin of opisthonotum with eight pairs of plumose R-setae. Dorsal cavities small, conspicuous. Epistome with a bifurcate medial process.

Notes on the genus. The new genus belongs to the group having short and smooth p1, longer p2, posteriorly expanded peritrematal shield and eight pairs of plumose R-setae on the margin of opisthonotum, similar to *Eurozercon* Halašková, 1979, *Paleozercon* Błaszak, Cokendolpher and Polyak, 1995, and *Xenozercon* Błaszak, 1976b. *Boreozercon* is unique among Zerconidae by having only 15 ventri-anal setae (Vm1, Vm2, Vm3, Vi2, Vi3, Vl2, Ad and Pa present, Vi1 and Vl1 absent). The new genus also differs from both Asian genera *Eurozercon* and *Xenozercon* by the presence of conspicuous dorsal cavities, the absence of adgenital pores in females, and the shape, and the position of the J and Z setae. Besides the ventri-anal chaetotaxy, *Boreozercon* can be distinguished from *Paleozercon* by the pilosity of setae p2, the arcuate posteromedial margin of peritrematal shield and the absence of gv2 in female.

Although the female of the genus *Amerozercon* Halašková, 1969b is unknown, the male bears several similar characters to that of the newly

established genus, for example plumose dorsal and marginal setae, medium-sized pilose p2 and the lateral fusion of peritrematal and ventri-anal shields. The two genera can be distinguished by the shape of the slit between the peritrematal and ventri-anal shields (peritrematal shield presumably truncated and not expanding posteriorly in *Amerozercon*) and the number of ventri-anal setae (Vi1 absent, Vl1 and two additional pairs of setae are also present).

Type species. *Boreozercon emendi* **sp. nov.**

Etymology. The name of the new genus refers to the boreal climate zone, where the type species has been collected. Gender masculine.

2.5.1. *Boreozercon emendi* sp. nov.

(Figures 2.16–20, 24, 28, 32, 36)

Material examined. Holotype: female collected in stand 930-CD, plot 5 (56° 48' 13.135" N, 118° 19' 31.446" W) at EMEND research study site, northeastern area, from mosses and needle leaf-litter, 9.09.2006, leg. Díaz-Aguilar, I. (deposited in CNC). Paratypes: stand, plot, collector and date as for holotype (2 males, 1 DN deposited in CNC, 1 female deposited in HNHM); stand 918-CD, plot 6, northern area, from mosses and needle leaf-litter on forest floor, 7.09.2006., Diaz-Aguilar, I. (2 females, 1 DN deposited in HNHM, 1 female deposited in CNC); stand 930-CD plots 3, 4 and 5, northern area, from mosses and needle leaf-litter on forest floor, 9.09.2006., Diaz-Aguilar, I. (30 females, 3 males, 5 DN); stand 918-CD, plot 6, northern area, from mosses and needle leaf-litter on forest floor, 7.09.2006, leg. Díaz-Aguilar, I. (3 females).

Diagnosis. Adult female. Podonotal setae j3-j5, z1 and s1-s2 smooth, others pilose. All opisthonotal setae pilose. J and Z setal rows inserted in small setal bases. Setae J5 situated anterior to the dorsal cavities. Setae S1 situated posterolateral to Z1. Pores Po2 situated inside a line connecting Z1 and Z2. Podonotum covered by circular, squamous pattern, the area between J setal-rows densely ornamented by small, subtriangular or irregular depressions. Dorsal cavities weakly sclerotised, with undulate anterior margins. Peritrematal shield expanded posteriorly, its posterolateral ends reaching beyond the level of R5. Post-genital sclerites present. Anterior margin of ventri-anal shield with one pair of setae.

Description. Female. Length of idiosoma 332–352μm (mean 345); width 245–260μm (mean 255) (n = 5).

Dorsum (Figures 2.16, 2.24). Podonotum with 22 pairs of setae: j-row with six pairs, z-row with two pairs, s-row with six pairs, r-row with six pairs, p-row with two pairs. Setae j1 and j2 barbed, j6, z2 and s3-s6 pilose to varying degrees, other j-, z- and s-setae short, smooth and needle-like. Marginal setae r1 short and smooth, others elongate, densely pilose. Pores po1 situated posterior to s1, po2 lying on a line connecting j4 and s4, po3 on a line connecting s5 and s6. Podonotum covered by irregular, disk-like, squamous pattern (Figure 2.36), the pair of circular markings between setae z1 well-developed. Opisthonotum (Figures 2.28, 2.32) with 23 pairs of setae: J-row with six pairs, Z-row with five pairs, S-row with four pairs and R-row with eight pairs. Setae J1-J5, Z1-Z4 and S1 uniform, slightly increasing in length posteriorly, densely pilose, pointed; J

and Z setae forming an arrangement of lines. Setae J5 situated above the line of the dorsal fossae. Setae J1-J4 and Z2 reaching the bases of the following seta, Z3 not reaching the insertion of Z4. Setae Z5 short, pilose. Setae S1 situated posterolateral to Z1, S2 lateral to Z2. Setae J6 and S2-S4 uniform, elongate, plumose, brush-like, extending beyond lateral margin of idiosoma. Opisthonotal J-, Z- and S-setae situated on small setal bases. Eight marginal R-setae short, curved and distinctly barbed. Pores Po1 situated anteromedial to Z1, Po2 inside a line connecting the insertions of Z1 and Z2, Po3 small, lying on a line connecting J4 and Z4, Po4 lying medial to insertions of S4. Lateral area of opisthonotum smooth, medial part covered by distinct, subtriangular or irregular pits (Figure 2.28). Dorsal cavities weakly sclerotised, uniform, with undulate anterior margin and axes parallel to that of the body. The length of opisthonotal setae and the distances between their insertions as in Table 2.5.

Venter (Figure 2.17). Peritrematal shield not separated from body margin, posterolateral ends pointed, expanded posteriorly, reaching beyond level of setae R5. Peritremes straight. One pair of post-genital sclerites present, adgenital gland openings absent. Anterior margin of ventri-anal shield with one pair of setae and 15 ventri-anal setae, Vl1 absent. Pre-anal setae short simple, post-anal seta elongate, distally pilose. Ventri-anal pores situated posterolateral to adanal setae. Sternal shield with reticulate ornamentation, ventri-anal shield covered by squamous pattern.

Male. Length of idiosoma 265 μm; width 185 μm (n = 1). Chaetotaxy, poroidotaxy and sculpturing pattern of dorsal shields similar to female (Figure

2.18), except setae s4 and s5 smooth and setae J4 not reaching the bases of J5. Sternogenital shield bearing five pairs of setae (Figure 2.19). Peritrematal shield and ventri-anal shield fused laterally, between the level of setae R3 and R4, not separated from the body margin. Two openings of glands gv2 situated on small adgenital sclerites. As for female, anterior margin of ventri-anal shield with one pair of setae, setae Vl1 absent. The length of J, Z and S setae and the distances between their insertions as in Table 2.5.

Deutonymph (Figure 2.20). Length of idiosoma: 283–287μm (mean 285); width 180μm (n = 2). Setae z2, s4-s6 and r5 barbed, s3, r3 and r6 elongate, densely pilose. Other podonotal setae smooth, needle-like. Chaetotaxy of opisthonotum as in adult stages, except that in deutonymphs the pilosity of marginal setae decreases posteriorly, and J5 is situated at the level of the dorsal cavities. Poroidotaxy of dorsal shields also similar to that of mature stages. The pattern of podonotum weakly developed, surface of opisthonotum finely punctate in the area of J setal-row. Length of opisthonotal setae and the distances between their insertions as in Table 2.5.

Protonymph and larva. Unknown.

Etymology. The name of the new species refers to the EMEND research study site, where it was collected.

2.6. Discussion

From an ecological point of view, the Zerconidae in the boreal mixedwood forest at EMEND were by far the most abundant Mesostigmata, representing

53.3% of the total frequency of occurrence from other mesostigmatan species. Five genera were identified and three of them were represented by only one species. *Skeironozercon tricavus* Błaszak, 1982 was the most dominant species with an occurrence of 60.9%, the second most abundant was *Parazercon radiatus* at 14.7% and *Boreozercon emendi* was the least abundant at 2.4%. *Zercon* and *Mixozercon* represented occurrences of 7% and 15% respectively, with each genus having several distinct species.

Different species of *Mixozercon* showed different patterns of occurrence and distribution in the different forest types (Figure 2.37). *Mixozercon albertaensis* had the widest distribution in the boreal mixedwood forest being found in the forest floor of coniferous, deciduous and mixed forests. *Mixozercon jasoniana* was mainly distributed in the forest floor of deciduous and mixed forests, and was not abundant in coniferous forests. *Mixozercon borealis* was found in the forest floor of coniferous and mixed forests, while in contrast, *Boreozercon emendi* occurred in the forest floor of coniferous forests.

The genus *Mixozercon* is distributed in North America, Europe and Asia together with *Parazercon* and *Zercon*. In contrast to the genus *Zercon*, *Parazercon* and *Mixozercon* are both characterised by relatively low species diversity (Balan, 1991; Ma, 2002). In the boreal or alpine forests, the distribution of *Mixozercon* species is quite similar to that observed in *Parazercon* species. The species with a wide North European distribution are *Parazercon radiatus* and *Mixozercon sellnicki*. Those species occuring with presumably narrow distribution are *Parazercon sergienkoae* Balan, 1991 and *Mixozercon*

heterosetosus in the East Carpathians, *Parazercon floralis* Ma, 2002 and *Mixozercon stellifer* in Eastern-Northeastern Asia, and *Mixozercon stellifer*, *Mixozercon albertaensis*, *Mixozercon jasoniana*, *Mixozercon borealis* and *Parazercon radiatus* in the boreal regions of North America. In addition, *Mixozercon* species distribution is not uniform across boreal mixedwood forest due to their preferences for different forest habitats, and *Boreozercon emendi* is added as a distinctive part of Zerconidae fauna of North America.

Based on morphological characters, two groups can be distinguished among the species of *Mixozercon*. The American and Asian species have well developed, often star-like ornamentation and weakly developed dorsal fossae with an undulate anterior margin. On the contrary, European species have less conspicuous dorsal ornamentation, smooth opisthonotal surface, saddle-like dorsal cavities with a smooth anterior margin, and small setal bases for the J and Z series setae. The similarity of the Japanese and West Canadian species suggests a trans-Beringian connection. Serious zoogeographical conclusions cannot be drawn since the fauna of the eastern coast of North America and most of the Asian territories are still unknown.

Nevertheless, based on the information presented here about the species in the genus *Mixozercon*, it seems that the distribution area of European species reaches only the borders of Western Asia, and the few East Asian species are confined to the eastern coast of Asia. Also, Northwestern American species may not occur in Southwestern areas. This distribution pattern is related to the fact that Zerconidae species are most likely associated with forested habitats, and their

dispersal through wide grassland habitats is probably restricted. Therefore, the wide grassland belts of North America (the prairie) and Asia (the steppe zone) may have served as an ecological barrier for the dispersal of these species, limiting their distribution to the present pattern. This phenomenon is also observed in other groups of the soil fauna, like earthworms (Csuzdi and Zicsi, 2003) and enchytraeids (Dózsa-Farkas and Christensen, 2002).

With regard to morphology of the genus *Mixozercon*, Halašková (1963) made the first correct diagnostic observations; however, some of these characters are unsuitable for generic ranking according to our present knowledge. Males of *Mixozercon* are described for the first time, with an important character, the fusion of peritrematal and ventri-anal shields, and in some species the males often bear only one pair of setae on the anterior margin of ventri-anal shield. Since males of European and Japanese species are undescribed so far, it will be necessary to determine whether these are common phenomena in the genus. Based on our results, the most important generic characters of *Mixozercon* should be the shape of peritrematal shield, considering the width of the slit separating it from the podonotum and its fusion with other shields in both males and females, the number and shape of peritrematal setae, the presence/absence of adgenital gland openings and the sclerotisation of the area around them, the number and distribution of ventri-anal setae, and the number of marginal setae on the opisthonotum, which often varies in a narrow range. According to the characters above mentioned, we have established a new key to the females of the Nearctic

Zerconidae genera (except *Amerozercon*, a monotypic genus described by a single male) including the new Canadian genus, *Boreozercon*.

2.7. Key to the females of the Nearctic genera of Zerconidae

1. Peritrematal shield with a single pair of setae ..... *Monozercon* Błaszak, 1984

– Peritrematal shield with more than one pair of setae 2

2. Peritrematal shield with two pairs of setae 3

– Peritrematal shield with three pairs of setae 18

3. Peritrematal shield posteriorly truncated 4

– Posterolateral ends of peritrematal shield expanded posteriorly 8

4. Peritrematal setae p1 short and smooth, p2 elongate and pilose 5

– Both peritrematal setae short and smooth 6

5. Peritrematal shield narrowly separated from dorsal shield; adgenital sclerites absent ..... *Mixozercon* Halašková, 1963

– Peritrematal shield widely separated from dorsal shield; adgenital sclerites present ..... *Zercon* C. L. Koch, 1836

6. Ventri-anal shield divided into three lobes by a pair of deep lateral incisions .... *Macrozercon* Błaszak, 1976

– Ventri-anal shield without lateral incisions 7

7. Peritrematal shield narrowly separated from dorsal shield; ventri-anal shield expanded anterolaterally; margin of opisthonotum with seven pairs of setae; dorsal cavities absent ..... *Lindquistas* Błaszak, 1981

– Peritrematal shield widely separated from dorsal shield; ventri-anal shield not expanded anterolaterally; margin of opisthonotum with eight pairs of setae; dorsal cavities present and conspicuous ..... *Bledas* Halašková, 1977

8. Peritrematal setae approximately uniform, both short and smooth 9

– Peritrematal setae diverse in form 11

9. Posterolateral ends of peritrematal shield free ..... *Bakeras* Błaszak, 1984

– Posterolateral ends of peritrematal shield fused to ventri-anal shield 10

10. Adgenital sclerites present, with two pores .....

..... *Blaszakiella* Sikora and Skoracki, 2008

– Adgenital sclerites absent, only a single opening of gv2 present .....

..... *Microzercon* Błaszak, 1976

11. Peritrematal setae p1 pilose, p2 short and smooth 12

– Peritrematal setae p1 short and smooth, p2 longer 15

12. Posterolateral ends of peritrematal shield connected to ventri-anal shield.....

..... *Cosmozercon* Błaszak, 1981

– Posterior ending of peritrematal shield free 13

13. Peritremes extremely long, reaching beyond the insertion of p2 .....

..... *Echinozeron* Błaszak, 1976

– Peritremes medium-sized, not reaching the level of p2 14

14. Posterolateral ends of peritrematal shield separated by a narrow slit, as a pair of free ventro-lateral shields; margin of opisthonotum with nine pairs of setae

..... *Krantzas* Błaszak, 1981

– Free ventro-lateral shields absent; margin of opisthonotum with eight pairs of setae ..... *Allozercon* Błaszak, 1984

15. Margin of opisthonotum usually with 16 pairs of setae .... *Caurozercon* Halašková, 1977

– Margin of opisthonotum with eight pairs of setae 16

16. Adgenital sclerites present ..... *Hypozercon* Błaszak, 1981

– Adgenital sclerites absent 17

17. Peritrematal setae p2 smooth; one pair of adgenital gland openings present; ventri-anal shield with 17 setae (Vl1 present) .... *Paleozercon* Błaszak, Cokendolpher and Polyak, 1995

– Peritrematal setae p2 pilose; adgenital gland openings absent; ventri-anal shield with 15 setae (Vl1 absent) ..... *Boreozercon* **gen. nov**.

18. Peritrematal shield posteriorly truncated .... *Skeironozercon* Halašková, 1977

– Posterolateral ends of peritrematal shield expanded posteriorly 19

19. Setae p1 and p2 pilose; adgenital sclerites and gland openings absent .... *Aspar* Halašková, 1977

– Setae p1 and p2 smooth; 2-3 pairs of adgenital gland openings on conspicuous adgenital sclerites present 20

20. Posterior margin of opisthonotum with six pairs of setae .... *Parhozercon* Błaszak, 1981

– Posterior margin of opisthonotum with seven pairs of setae .... *Parazercon* Trägårdh, 1931

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Table 2.1. Length of opisthonotal setae and longitudinal distances between their bases in *Mixozercon albertaensis* **sp. nov.** (measurements in µm).

	Female	Male	PN		Female	Male	PN		Female	Male	PN
I1	13	11	7	Z1	14	9	7	S1	15	10	21
I1-I2	35	21	20	Z1-Z2	29	22	21	S1-S2	34	31	22
I2	24	18	9	Z2	20	13	8	S2	33	25	23
I2-I3	30	23	19	Z2-Z3	27	20	15	S2-S3	45	30	20
I3	25	17	9	Z3	21	16	13	S3	33	25	24
I3-I4	33	19	18	Z3-Z4	34	26	17	S3-S4	49	35	23
I4	23	18	10	Z4	40	30	26	S4	35	28	27
I4-I5	28	23	23	Z4-Z5	51	44	25				
I5	26	19	8	Z5	13	10	7				
I5-I6	32	33	11								
I6	34	28	27								

Table 2.2. Length of opisthonotal setae and longitudinal distances between their bases in *Mixozercon jasoniana* **sp. nov.** (measurements in µm).

	Female	Male	DN		Female	Male	DN		Female	Male	DN
I1	23	16	13	Z1	22	14	11	S1	24	16	17
I1-I2	40	30	32	Z1-Z2	34	23	29	S1-S2	28	22	24
I2	24	16	16	Z2	28	17	16	S2	36	25	32
I2-I3	29	19	21	Z2-Z3	25	21	23	S2-S3	45	32	37
I3	24	19	16	Z3	28	18	19	S3	36	26	30
I3-I4	26	17	23	Z3-Z4	27	23	23	S3-S4	55	34	40
I4	29	17	18	Z4	39	23	34	S4	37	27	33
I4-I5	31	28	25	Z4-Z5	57	38	38				
I5	28	18	15	Z5	16	11	10				
I5-I6	29	20	18								
I6	35	26	33								

Table 2.3. Length of opisthonotal setae and longitudinal distances between their bases in *Mixozercon borealis* **sp. nov.** (measurements in µm).

	Female	Male		Female	Male		Female	Male
I1	18	13	Z1	18	13	S1	19	12
I1-I2	36	26	Z1-Z2	32	25	S1-S2	34	23
I2	23	16	Z2	21	14	S2	33	25
I2-I3	30	22	Z2-Z3	27	22	S2-S3	46	34
I3	22	15	Z3	22	19	S3	36	25
I3-I4	29	22	Z3-Z4	26	20	S3-S4	45	40
I4	23	17	Z4	42	28	S4	38	27
I4-I5	43	33	Z4-Z5	55	37			
I5	22	17	Z5	10	10			
I5-I6	19	12						
I6	37	28						

Table 2.4. Distinguishing characters between females of *Mixozercon stellifer*, *Mixozercon albertaensis* **sp. nov.**, *Mixozercon jasoniana* **sp. nov.**, *Mixozercon borealis* **sp. nov.**

M. stellifer	***M. albertaensis***	***M. jasoniana***	***M. borealis***
setae j2 pilose	setae j2 barely pilose	setae j2 smooth	setae j2 smooth
setae z2 and s6 pilose, j6 and s5 smooth	setae j6, z2, s5-s6 short, smooth	setae z2 and s6 often barbed, j6 and s5 smooth	setae j6, z2, s5-s6 short, smooth
pores po1 absent?	po1 above line joining bases of j2 and s1	po1 on line joining bases of j2 and s1	po1 situated medially to s1
setae J1 short (14 μm), pilose, distance between bases 38 μm	setae J1 short (13 μm), smooth, distance between bases 41 μm	setae J1 elongate (23 μm), pilose, distance between bases 16 μm	setae J1 intermediate (18 μm), smooth, distance between bases 21 μm
5 between dorsal cavities	J5 over the line of dorsal cavities	J5 between dorsal cavities	J5 between dorsal cavities, reaching past margin of idiosoma
Z3 not reaching the bases of Z4	Z3 not reaching the bases of Z4	Z3 reaching the bases of Z4	Z3 reaching the bases of Z4
Z4 elongate (32 μm), pilose, narrowing distally	Z4 elongate (40 μm), broadening distally, brush-like	Z4 elongate (39 μm), broadening distally, brush-like	Z4 elongate (42 μm), broadening distally, brush-like
Z5 smooth	Z5 pilose	Z5 barbed	Z5 smooth
S1 situated 20 μm posterolateral to Z1, both short (16–17 μm), pilose	S1 situated 23 μm lateral to Z1, both short (14–15 μm), smooth	S1 situated 11 μm posterolateral to Z1, both long (22–24 μm), pilose	S1 situated 15 μm posterolateral to Z1 both intermediate (18–19 μm), scarcely pilose
setae S2 situated anterolateral to Z2	setae S2 situated posterolateral to Z2	setae S2 situated anterolateral to Z2	setae S2 situated anterolateral to Z2
J, Z and S-setae without enlarged setal bases	J, Z and S-setae with enlarged setal bases	J, Z and S-setae with enlarged setal bases	J, Z and S-setae with enlarged setal bases
R1 much longer than other R-setae, pilose	setae R1 smooth	setae R1 finely barbed or smooth	setae R1 finely barbed or smooth

Continuation Table 2.4

M. stellifer	*M. albertaensis*	*M. jasoniana*	*M. borealis*
Po2 situated on a line connecting Z1-Z2	Po2 situated on a line connecting Z1-Z2	Po2 situated axially to line connecting Z1-Z2	Po2 situated on a line connecting Z1-Z2
Po3 small	Po3 medium-sized	Po3 large	Po3 medium-sized
medial podonotum covered by circular squamous ornamentation	medial part of podonotum covered by tile-like ornamentation	medial podonotum covered by circular irregular-squamous ornamentation	medial podonotum covered by circular irregular-squamous ornamentation
medial opisthonotum densely covered by large, subtriangular protuberances	medial opisthonotum covered by large, irregular pits	medial opisthonotum rarely covered by large, subtriangular protuberances	medial opisthonotum densely covered by large, subtriangular protuberances
posterior end of peritremal shield straight, reaching beyond the level of R2	posterior end of peritremal shield straight, reaching level of R1	posterior end of peritremal shield curved, reaching beyond level of R3	posterior end of peritremal shield straight, reaching beyond level of R2
post-genital sclerites absent?	post-genital sclerites present	post-genital sclerites absent	post-genital sclerites absent

Table 2.5. Length of opisthonotal setae and longitudinal distances between their bases in *Boreozercon emendi* **sp. nov.** (measurements in µm).

	female	male	PN		female	male	PN		female	male	PN
I1	21	18	15	Z1	20	14	15	S1	23	16	16
I1-I2	33	21	27	Z1-Z2	36	30	28	S1-S2	34	26	28
I2	27	18	16	Z2	25	16	16	S2	38	29	30
I2-I3	29	19	23	Z2-Z3	23	17	16	S2-S3	42	27	29
I3	26	17	19	Z3	25	18	20	S3	36	28	29
I3-I4	26	19	20	Z3-Z4	30	21	23	S3-S4	48	31	31
I4	27	20	19	Z4	26	19	17	S4	40	28	31
I4-I5	30	29	30	Z4-Z5	55	44	39				
I5	29	19	17	Z5	15	8	9				
I5-I6	44	30	22								
I6	38	27	30								

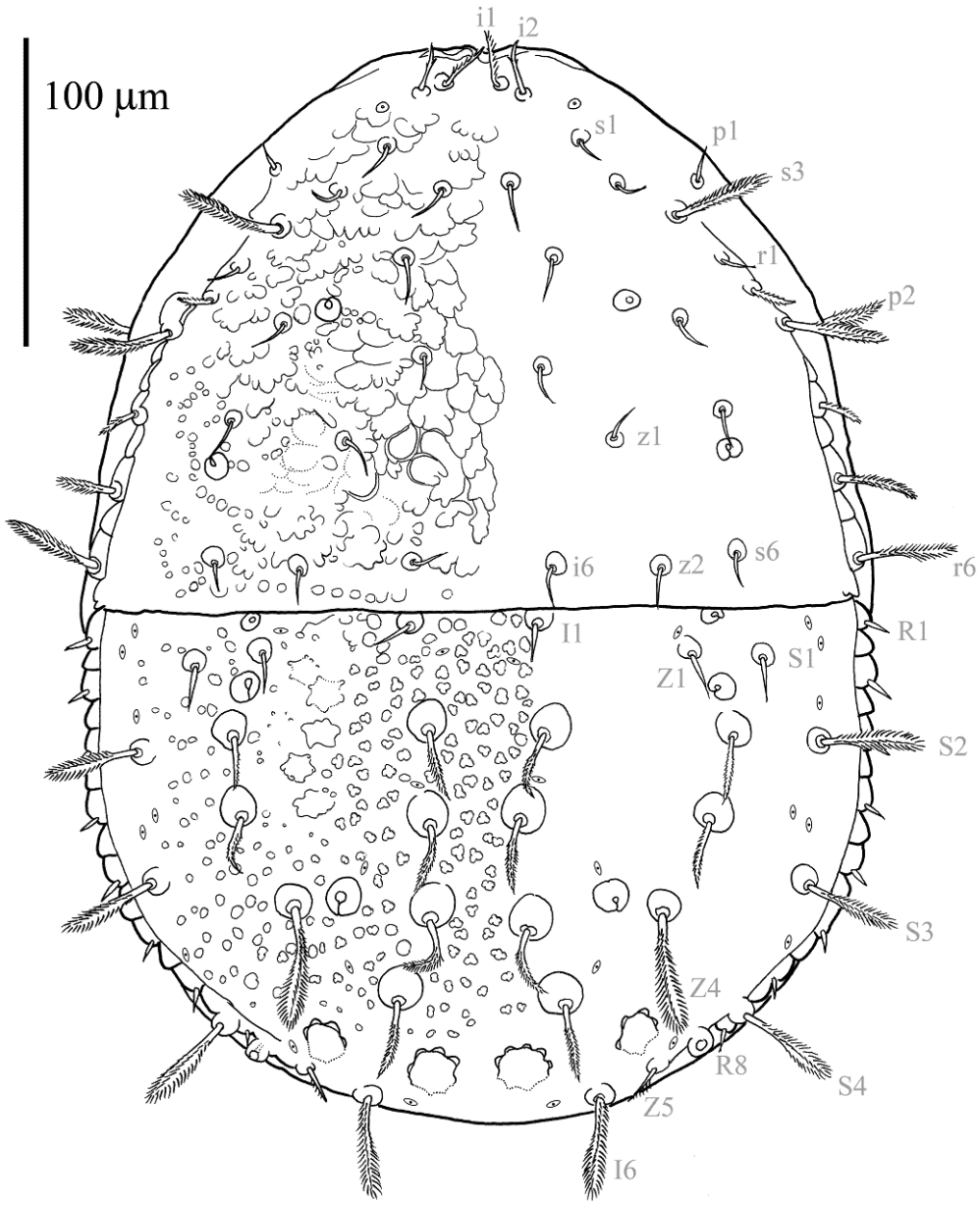
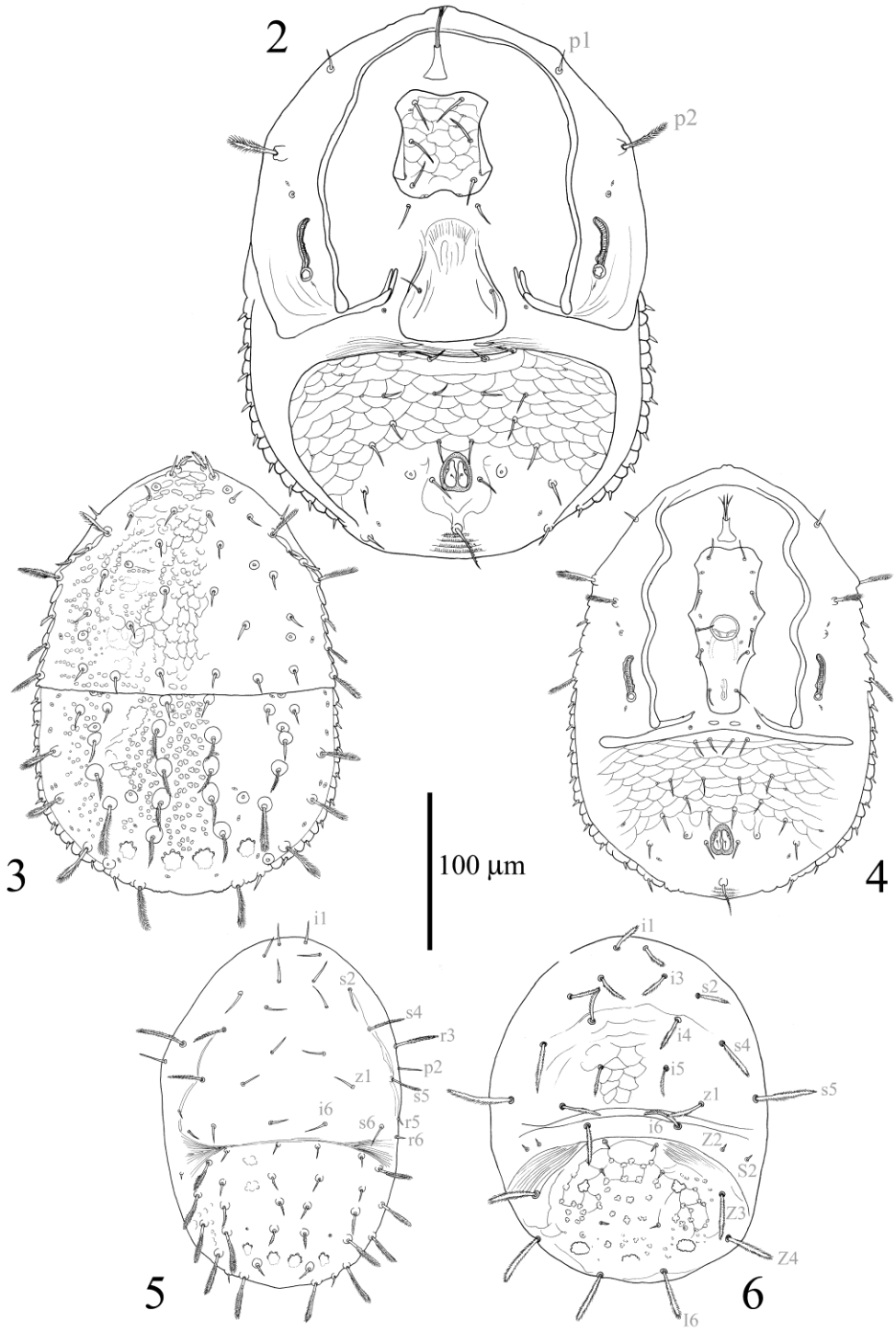


Figure 2.1. *Mixozercon albertaensis* **sp. nov.**, dorsal view of female.



Figures 2.2–2.6. *Mixozercon albertaensis* **sp. nov.** 2.2 Ventral view of female; 2.3. Dorsal view of male; 2.4. Ventral view of male; 2.5. Dorsal view of protonymph; 2.6. Dorsal view of larva.

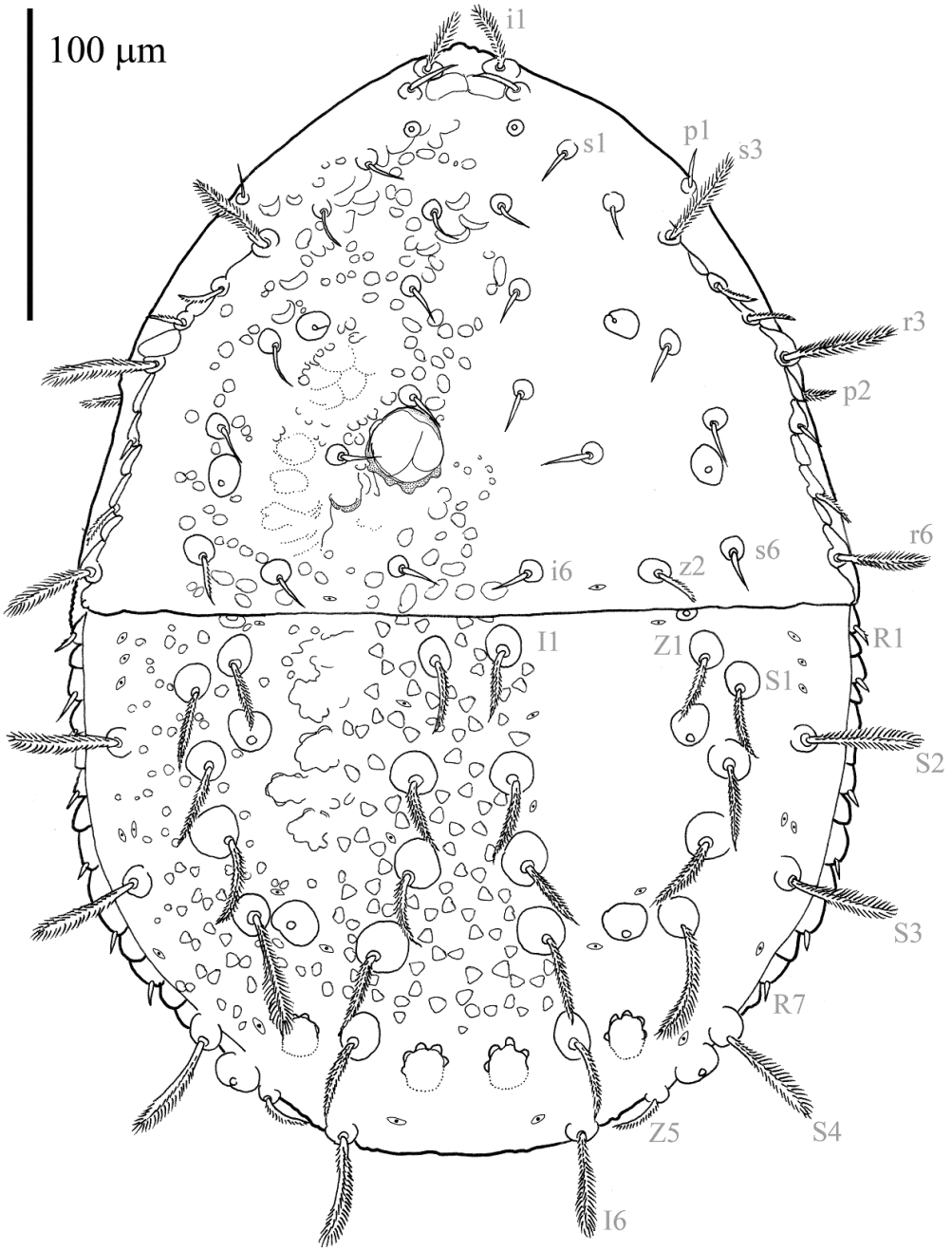
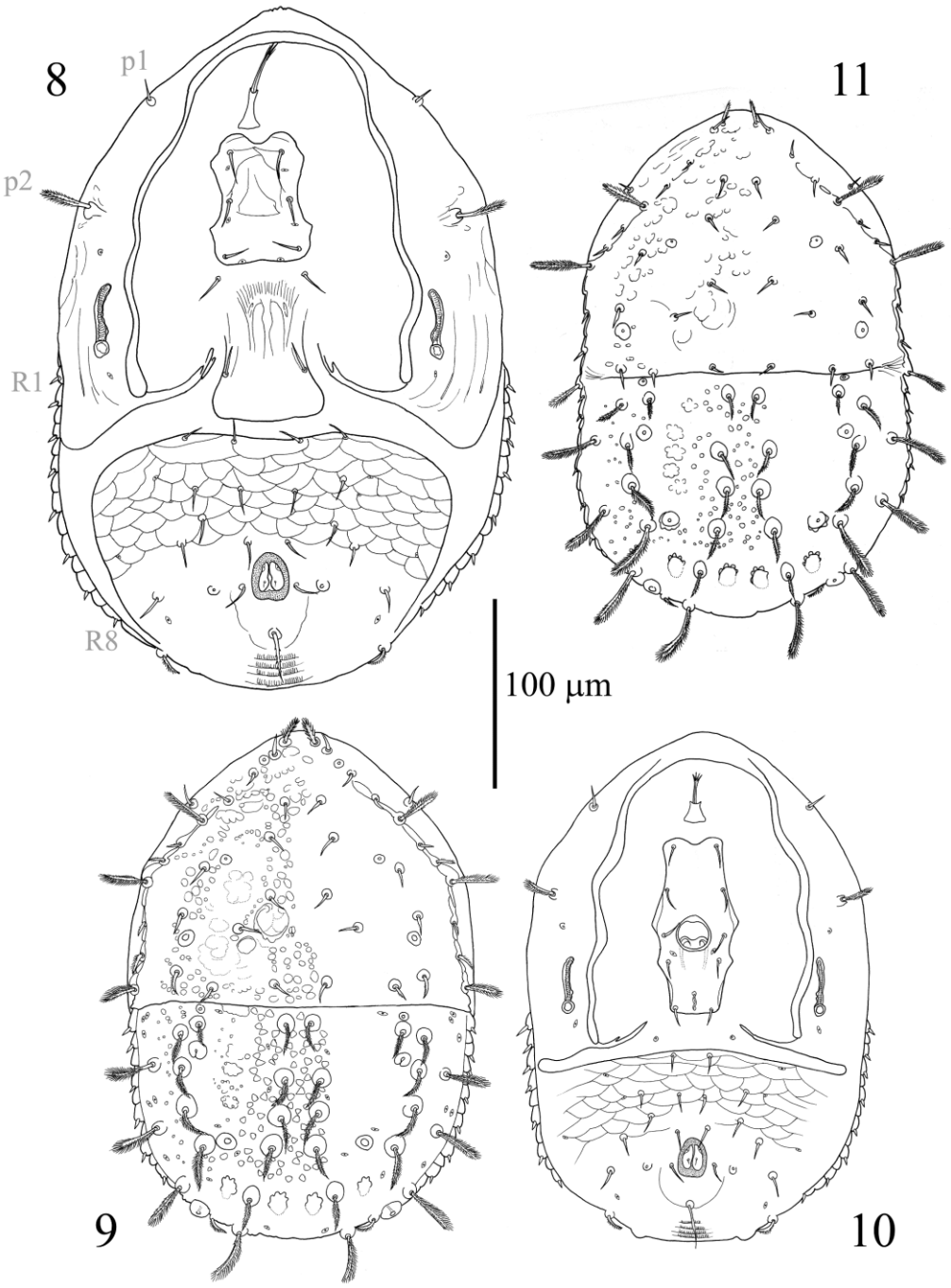


Figure 2.7. *Mixozercon jasoniana* **sp. nov.**, dorsal view of female.



Figures 2.8–2.11. *Mixozercon jasoniana* **sp. nov.** 2.8. Ventral view of female; 2.9. Dorsal view of male; 2.10. Ventral view of male; 2.11. Dorsal view of deutonymph.

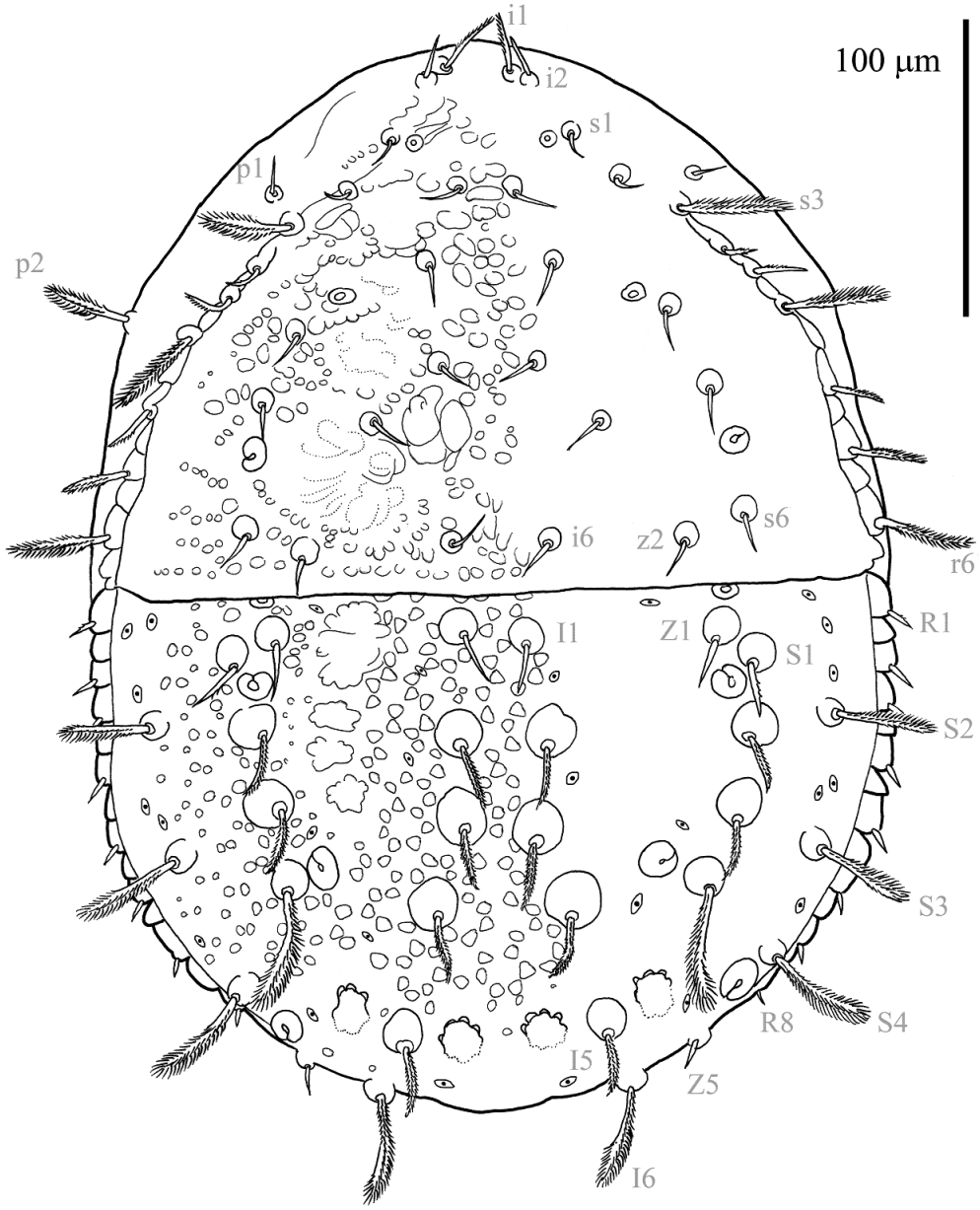
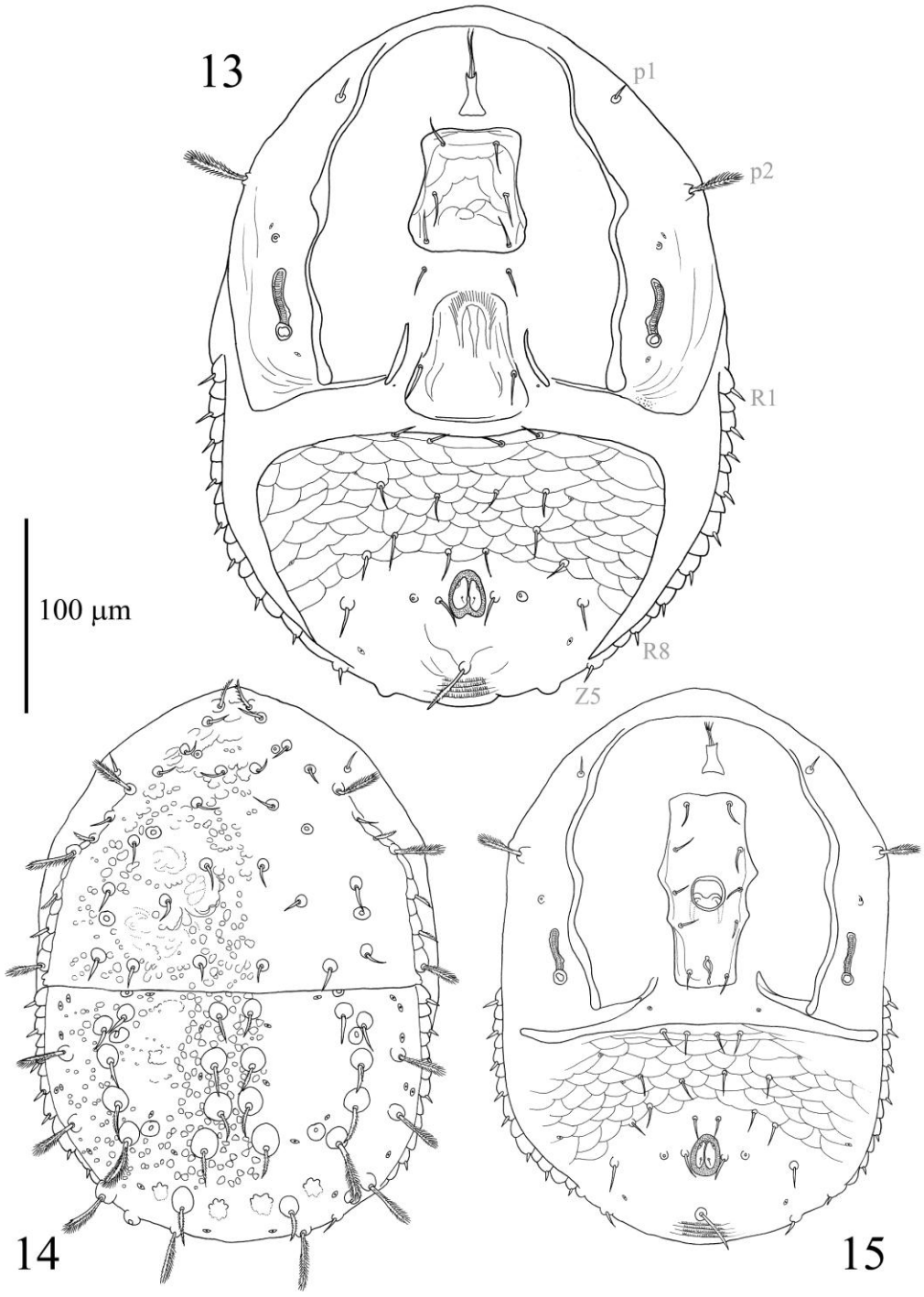


Figure 2.12. *Mixozercon borealis* **sp. nov.**, dorsal view of female.



Figures 2.13–2.15. *Mixozercon borealis* **sp. nov.** 2.13. Ventral view of female; 2.14. Dorsal view of male; 2.15. Ventral view of male.

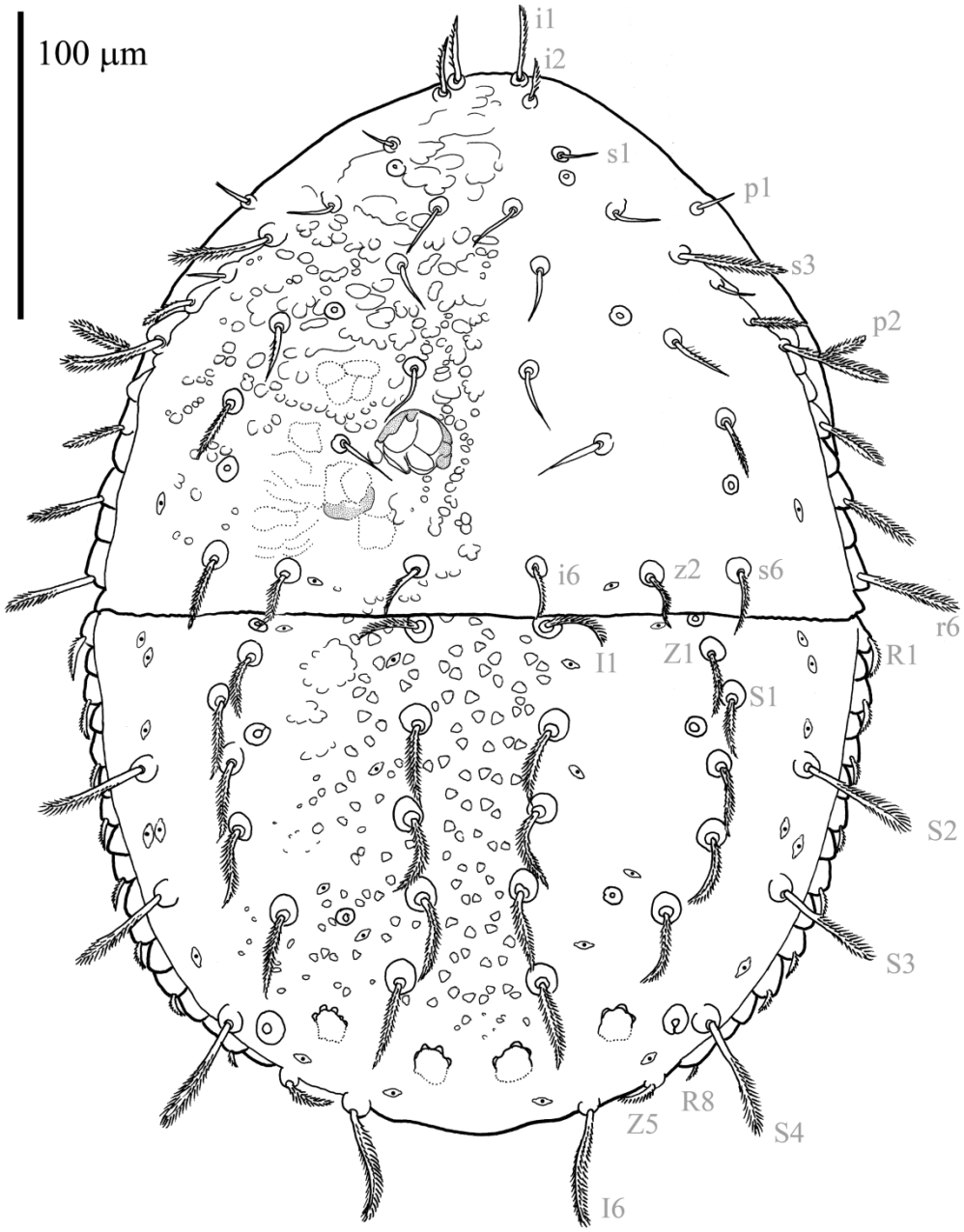
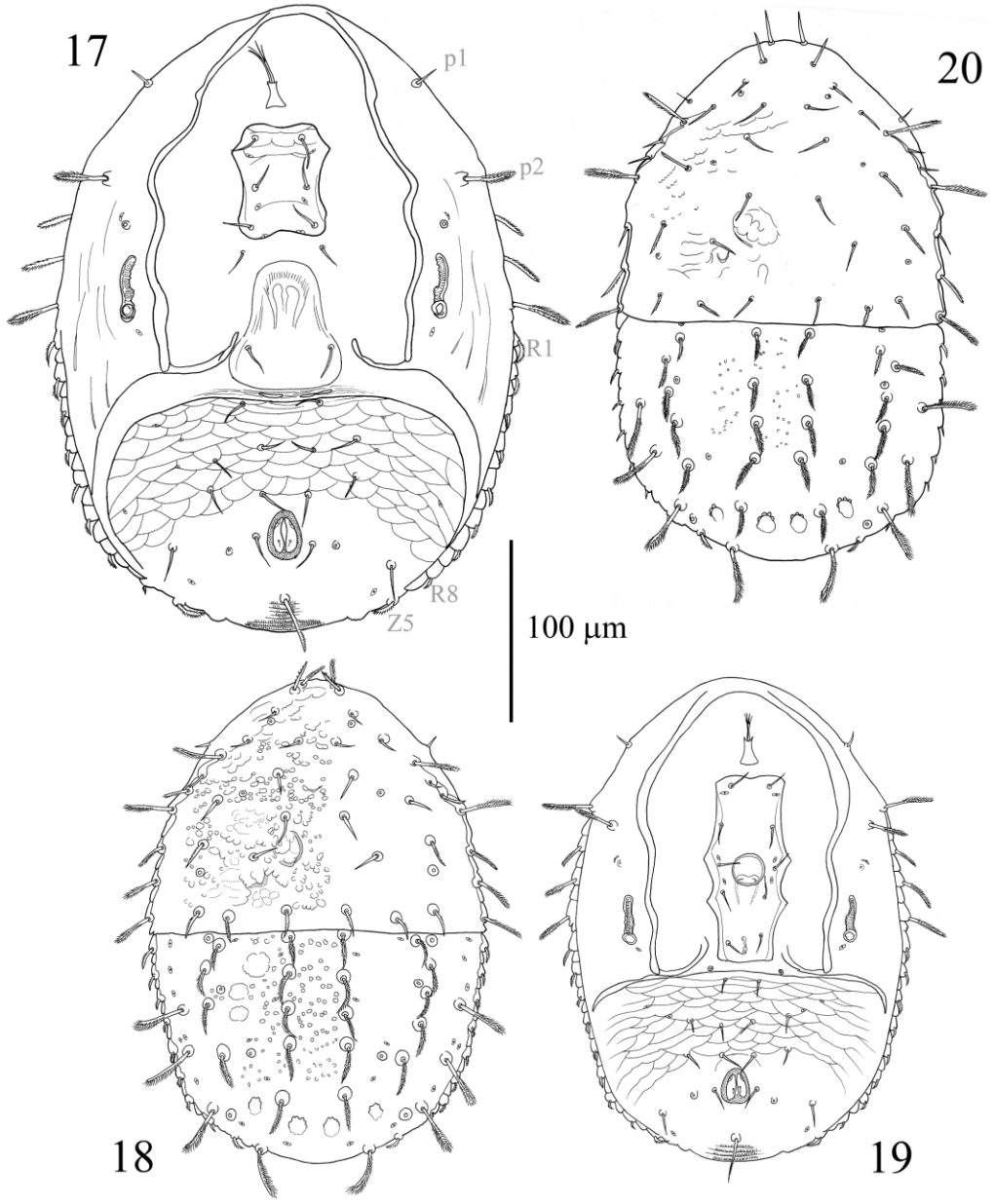
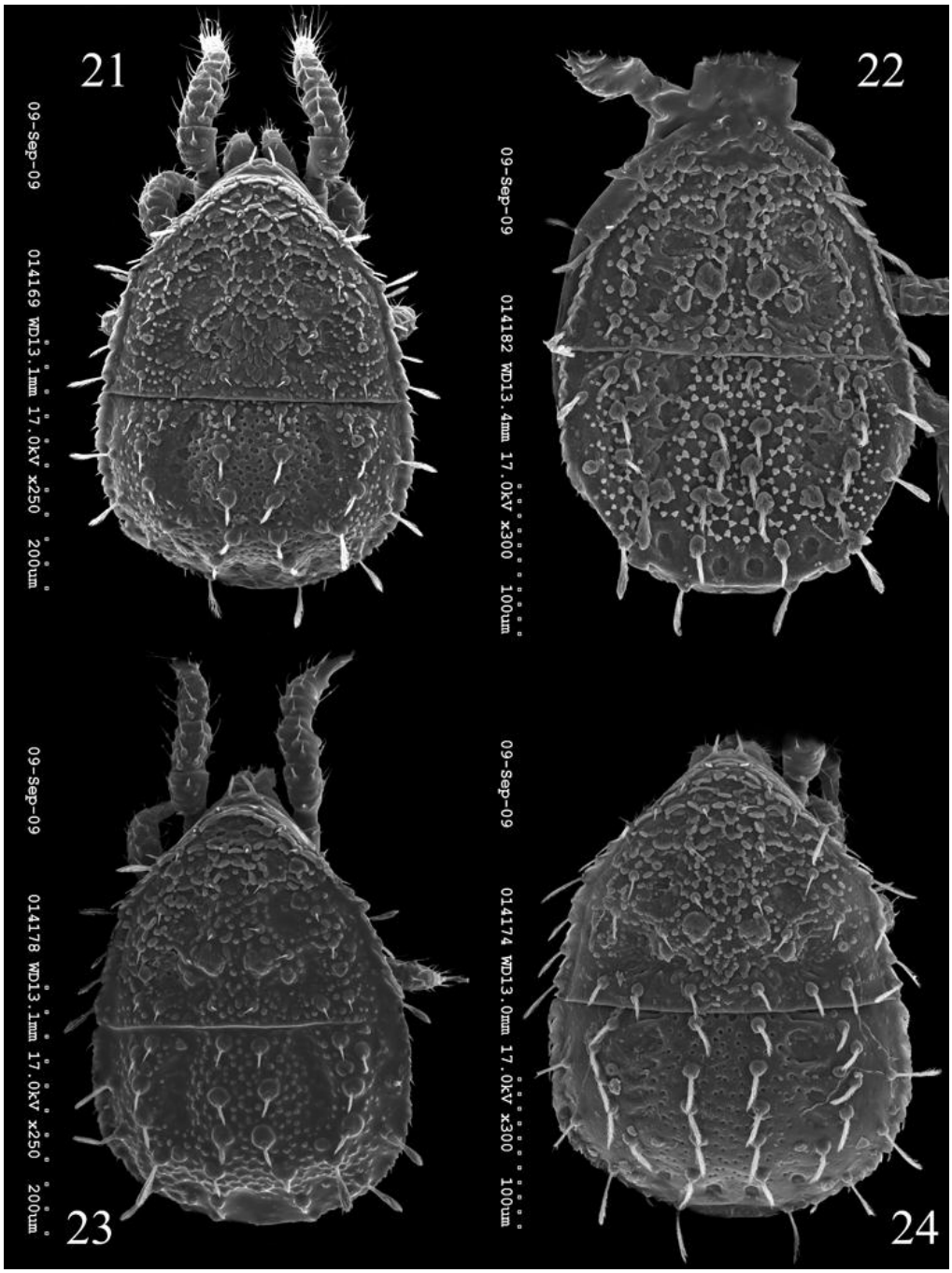


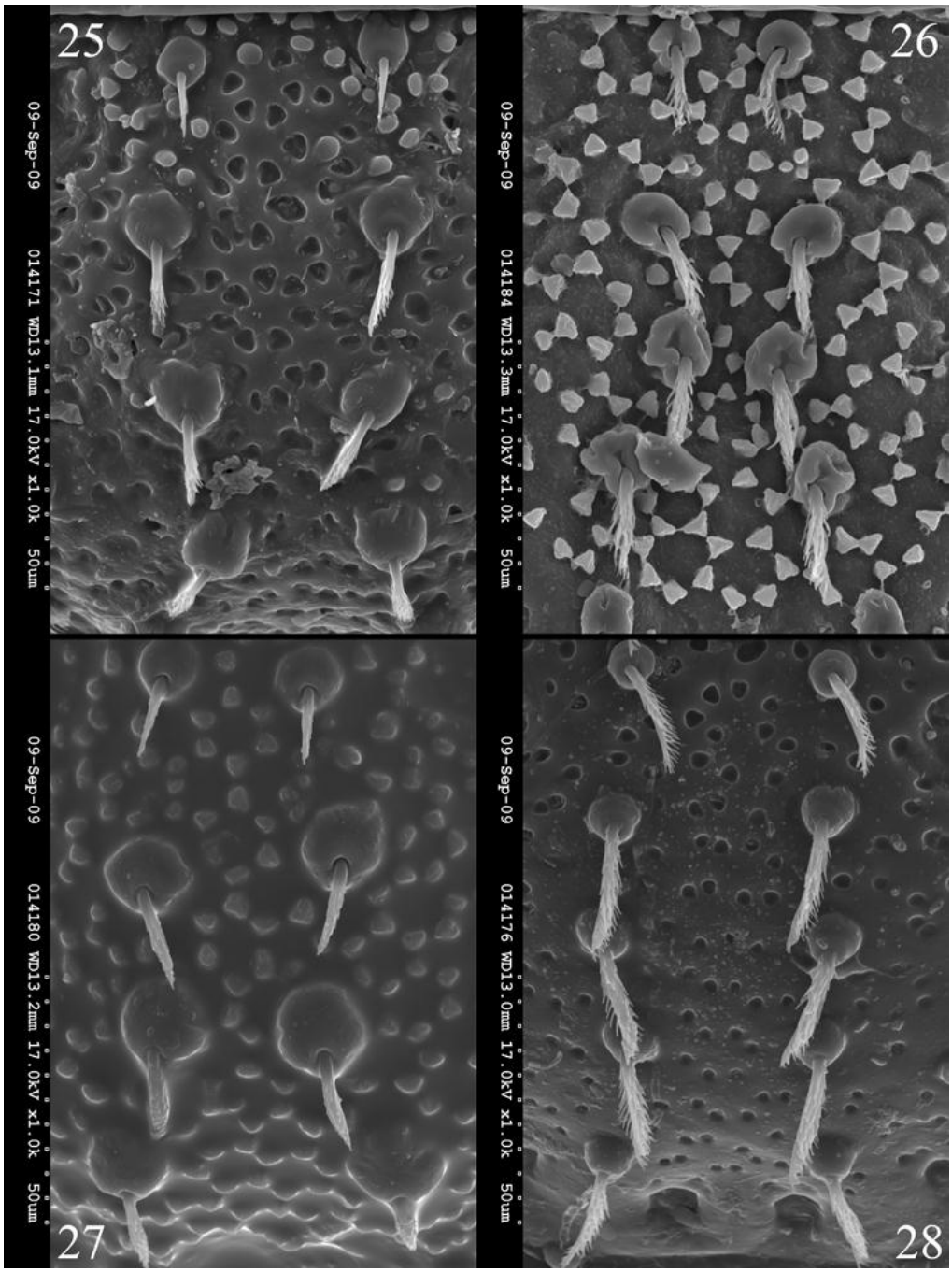
Figure 2.16. *Boreozercon emendi* **sp. nov.**, dorsal view of female.



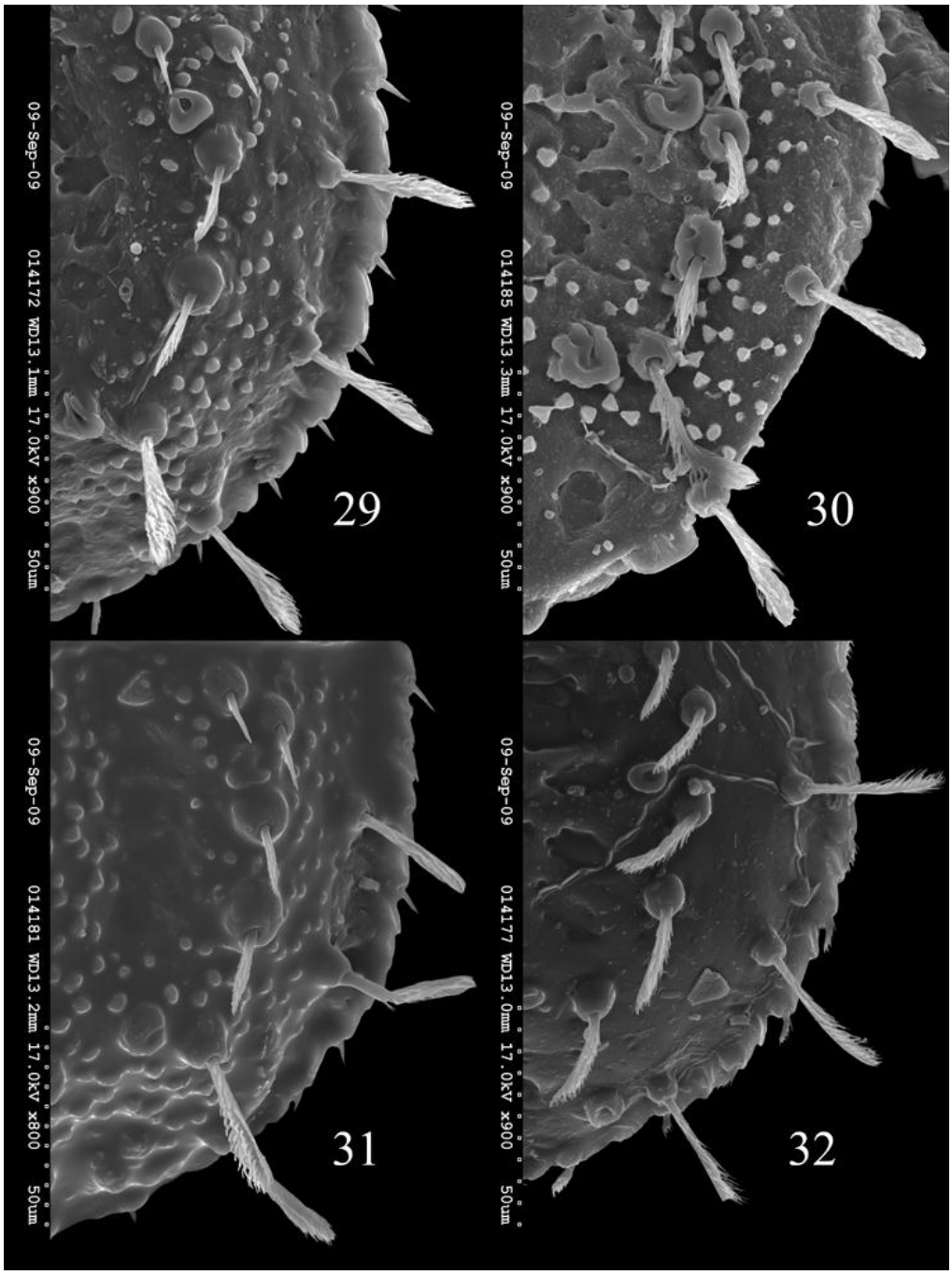
Figures 2.17–2.20. *Boreozercon emendi* **sp. nov.** 2.17. Ventral view of female; 2.18. Dorsal view of male; 2.19. Ventral view of male; 2.20. Dorsal view of deutonymph.



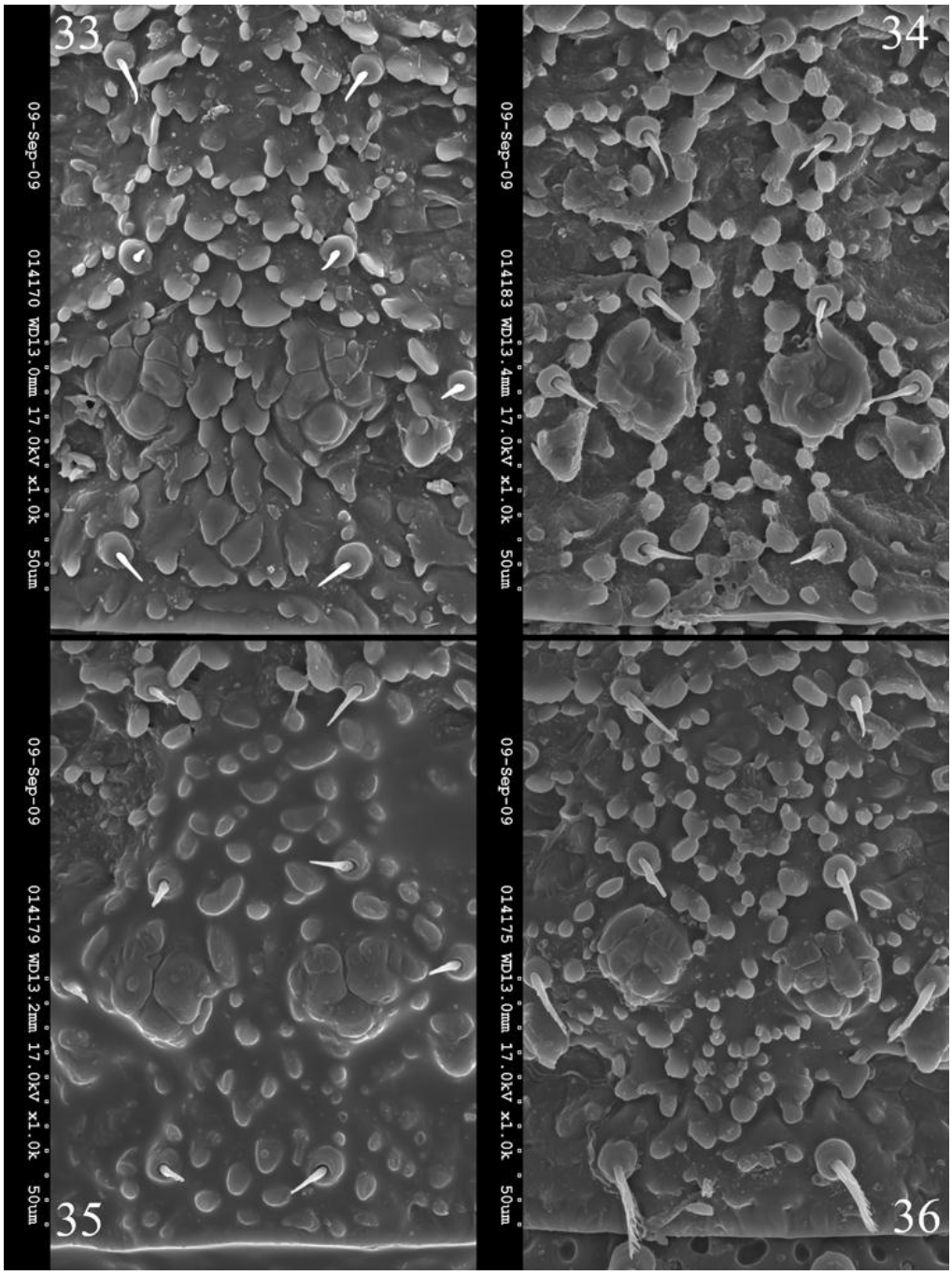
Figures 2.21–2.24. Females of the new species, dorsal view, SEM photos (scale bar 100 μm). 2.21. *Mixozercon albertaensis* **sp. nov.**; 2.22. *Mixozercon jasoniana* **sp. nov.**; 2.23. *Mixozercon borealis* **sp. nov.**; 2.24. *Boreozercon emendi* **sp. nov.**



Figures 2.25–2.28. Central surface of opisthonotum of the new species, SEM photos (scale bar 25μm). 2.25. *Mixozercon albertaensis* **sp. nov.**; 2.26. *Mixozercon jasoniana* **sp. nov.**; 2.27. *Mixozercon borealis* **sp. nov.**; 2.28. *Boreozercon emendi* **sp. nov.**



Figures 2.29–2.32. Lateral surface of opisthonotum of the new species, SEM photos (scale bar 25μm). 2.29. *Mixozercon albertaensis* **sp. nov.**; 2.30. *Mixozercon jasoniana* **sp. nov.**; 2.31. *Mixozercon borealis* **sp. nov.**; 2.32. *Boreozercon emendi* **sp. nov.**



Figures 2.33–2.36. Central surface of podonotum of the new species, SEM photos (scale bar 25μm). 2.33. *Mixozercon albertaensis* **sp. nov.**; 2.34. *Mixozercon jasoniana* **sp. nov.**; 2.35. *Mixozercon borealis* **sp. nov.**; 2.36. *Boreozercon emendi* **sp. nov.**

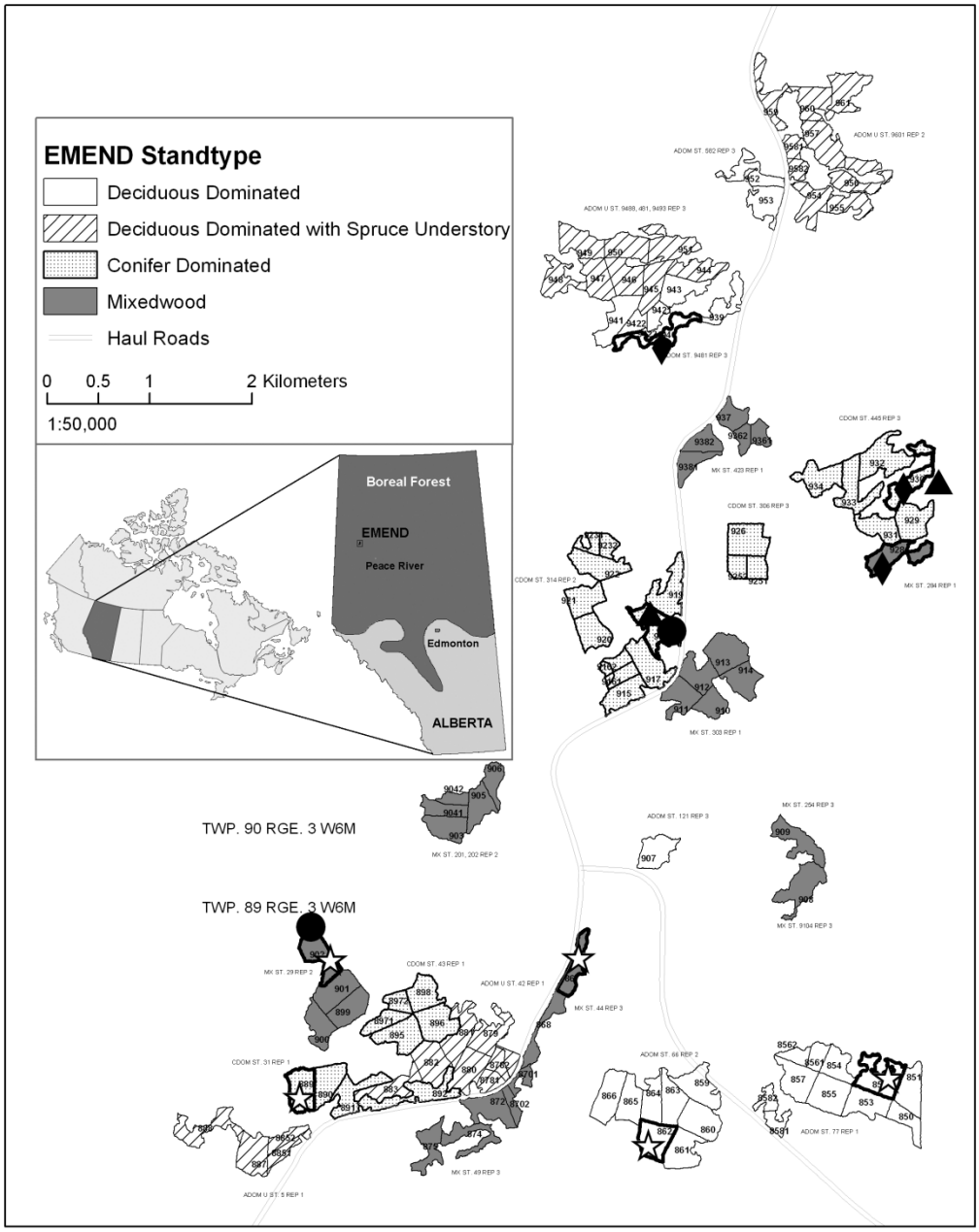


Figure 2.37. EMEND geographic location and sampled forest types indicating occurences and distribution of *Mixozercon* and *Boreozercon* species: *M. albertaensis* (☆), *M. jasoniana* (♦), *M. borealis* (●) and *B. emendi* (▲). Credited: EMEND project.

CHAPTER 3

Influence of stand composition on predatory mite (Mesostigmata) assemblages from the forest floor in western Canadian boreal mixedwood forests[2]

3.1. Introduction

The forest floor is a key component of boreal mixedwood forests, as it is where the biological activity that drives soil processes is focused (Coleman et al., 1983). The L (litter), F (fermentation), and H (humified) horizons that overlay the mineral soil are formed from the accumulation of dead leaves, twigs and woody materials in different states of decomposition (Green et al., 1993). These organic horizons create a wide range of microhabitats for microorganisms and microarthropods, and provide a basis for resource partitioning among species (Anderson, 1975, 1978). Natural disturbances by fire in the boreal mixedwood forests often create stands of different ages (Johnson et al., 1998) and canopy composition with varying proportions of deciduous trees, mainly *Populus* spp., and conifers, mainly *Picea glauca* (Moench) Voss (Rowe, 1972). Development of stand structures from the early seral stages to mature old-growth stands create the distinct chemical and biological characteristics associated with leaf litter and

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humus layers in these forest floors (Green et al., 1993; Laganière et al., 2010; Ponge, 2003).

Several studies have reported differences in the chemical properties of mixedwood forest floors from northwestern Alberta. For instance, the forest floors of aspen and spruce stands showed differences in organic carbon composition (Hannam et al., 2004), and nitrogen pools and fluxes, where mixed stands showed the highest rates of net mineralization (Jerabkova et al., 2006). Forest floor pH values were more acidic in coniferous and mixed stands than in deciduous stands (Jerabkova et al., 2006). The thickest forest floors have been measured under conifers, the shallowest in deciduous stands, and intermediate values have been recorded in the mixed stands (Hannam et al., 2004, 2006). Biological properties of mixedwood forest floors also vary among forest stands. For example, microbial community composition of forest floors in deciduous stands differed from that in mixed and coniferous stands (Hannam et al., 2006). Oribatid mites dominated the mesofaunal assemblages in forest floors of both deciduous and coniferous stands, but were more abundant in coniferous stands (Lindo and Visser, 2004). In contrast, the same authors report that mesostigmatan mites have low and similar abundances in deciduous and coniferous stands. Collembolans, which were more abundant than mesostigmatans, presented very similar abundances in both stands (Lindo and Visser, 2004). Lastly, different forest stand types supported unique ecological communities for several biotic groups, such as epigaeic arthropods (Work et al., 2004).

Among mesofauna, mesostigmatan mites that inhabit the soil are generally referred to as Gamasina or Uropodina, the two cohorts that contain the most species among the seven cohorts of the order Mesostigmata (Lindquist et al., 2009). They are often reported to be the least abundant mites, making up < 5 - 20% of the total Acari found in litter and soil (Petersen and Luxton, 1982). Most of them are spider-like, free-living microscopic predators inhabiting litter, moss and soil (Evans, 1992; Karg, 1993). Their main distinguishing character is their respiratory system in which the stigmata (air breathing pores) are open laterally in the middle of their bodies (Evans, 1992). In addition, they have mouthparts adapted for piercing, cutting, sucking and tearing (Wallwork, 1967; Lee, 1974; Evans, 1992; Walter and Proctor, 1999) and a conspicuous salivary stylet for external digestion (Lee, 1974; Evans, 1992). In terms of their hunting strategies, they are considered to be principally pursuit and ambush predators (Walter et al., 1988; Karg, 1993). For instance, gamasids are very efficient predators adapted to the narrowed leaf litter microhabitats (Martin, 1969). Thus, mesostigmatan mites play an important role in regulating population sizes of other soil organisms (Anderson, 1975; Emmerling et al., 2002; Karg, 1993; Krantz, 2009). Additionally, mesostigmatan mites may have an effect on nitrogen mineralization fluxes (Berg et al., 2001) due to nitrogen released as a result of their feeding behavior, mainly the body fluids of their prey (Evans, 1992; Karg, 1993). Calculations based on the food web model of Berg et al. (2001) estimated that predatory mites on average contribute to 25% of the total mineralization fluxes in temperate forest floors.

Despite the reported ecological importance of mesostigmatan mites, they are rarely considered in studies of Canadian boreal forests. Their abundances at the order level in deciduous versus coniferous stands have only been compared for one site in northwestern Alberta (Lindo and Visser, 2004). In addition, influences of chemical, physical and microclimatic characteristics of the forest floors on the taxonomic composition of mesostigmatan assemblages have not been investigated, and patterns of concomitant variation across different forest stand types are generally unknown in Canada. Most of the knowledge about community ecology of Mesostigmata in forest floor communities arises from studies in temperate and boreal European forests (Usher, 1971; Huhta and Niemi, 2003; Čoja and Bruckner, 2003; Błoszyk et al., 2004; Salmane and Brumelis, 2008, Makarova, 2011). In Canada, we are currently aware of only one study from temperate forests in southwestern Quebec, which has attempted to examine the influence of stand type on structuring oribatid mite communities (Sylvain and Buddle, 2010). More studies from European forests have compared oribatid assemblages (Siira-Pietikäinen et al., 2008) or the soil fauna communities (Scheu et al., 2003) from different forest types finding strong differences in community structure. Therefore, it is possible that mesostigmatan assemblages are also influenced by patterns of stand structure from different boreal forest types.

The main objective of this study was to examine how stand composition influenced the structure of mesostigmatan mite assemblages. The three forest types examined reflect successional shifts from deciduous to mixed to coniferous stands that are the typical successional pattern in the boreal mixedwoods of

northwestern Alberta. We also investigated whether variation in mesostigmatan assemblages is associated with forest floor properties. Knowledge of the relationships among stand composition, forest floor properties, and biological communities provides a template for anticipating and planning for effects of disturbance such as forest management. As such, this work contributes directly to the objectives of the Ecosystem Management Emulating Natural Disturbance (EMEND) project, an ecosystem-based research project providing a framework for boreal forest management and conservation of biodiversity in managed landscapes.

3.2. Materials and methods

3.2.1. Study area

This study was carried out at the EMEND research study site located approximately 90 km northwest of Peace River, Alberta, Canada (56° 46' 13" N - 118° 22' 28" W). The EMEND 1000-ha experimental site is situated in the Lower Boreal Highlands Natural Subregion, part of the Boreal Forest Natural Region (Natural Regions Committee, 2006). Climate in this region is characterized by cold winters and moderately warm summers. Mean temperatures range from –15.4 °C for January and 16.4 °C for July, the frost-free period is less than 90 days, and the mean annual precipitation is 378 mm occurring mostly in June and July (Environment Canada, 2011). The area under study ranges in elevation between 689 and 838 masl and has a gently rolling topography. Soils have predominantly formed on fine-textured glacio-lacustrine parent materials, with the

exception of the southwestern part of the experimental site where soils developed on glacial till (Lindsay et al., 1958). Orthic and Dark Gray Luvisols occupy most of the area, while Brunisols, Gleysolic and Solonetzic soils are found in smaller proportions (Kishchuk, 2004). These soils vary from well to imperfectly drained depending on texture and slope position.

This study focused on naturally disturbed forests of the EMEND experiment (i.e., the control plots) consisting of three successional stand types that originated from wildfires between ~80-140 years ago. There are no records of major disturbances by either fire or insect outbreaks nor any form of anthropogenic disturbances in the last 80 years. Forest stand types were classified as follows: (*i*) deciduous stands dominated by > 70% trembling aspen (*Populus tremuloides* Michx.), (*ii*) coniferous stands dominated by > 70% white spruce (*Picea glauca* (Moench) Voss), and (*iii*) mixed stands composed of approximately 35% *P. glauca* and 65% *P. tremuloides* (for more details see Spence et al., 1999; Volney et al., 1999). The understory of these stands contains diverse shrubs such as green alder (*Alnus crispa* (Ait.) Pursh), low bush-cranberry (*Viburnum edule* (Michx.) Raf.), prickly rose (*Rosa acicularis* Lindl.), and Canadian buffaloberry (*Shepherdia canadensis* (L.) Nutt.) (Macdonald and Fenniak, 2007). Among the native forbs on the floor also recorded by Macdonald and Fenniak (2007) are bunchberry (*Cornus canadensis* L.), fireweed (*Chamerion angustifolium* (L.) Holub), tall bluebell (*Mertensia paniculata* (Ait.) G. Don.), twinflower (*Linnaea borealis* L.), dewberry (*Rubus pubescens* Raf.), and perennial graminoids, particularly bluejoint grass (*Calamagrostis canadensis* (Michx.) P. Beauv.). The

ground layer in coniferous stands is composed mainly of mosses including stair-step moss (*Hylocomium splendens* (Hedw.) Schimp. in B.S.G.), knight's plume (*Ptilium crista-castrensis* (Hedw.) De Not.) and feather moss (*Pleurozium schreberi* (Brid.) Mitt.), given in order of their decreasing abundance (Caners, 2010).

3.2.2. Field sampling

Three replicate stands of each forest type covering ~10 ha in area each and randomly distributed across the EMEND landscape were chosen for this study (N=9 stands in total). The forest floor of each replicate was sampled for mesostigmatan mites in September 2006. The forest floors of coniferous stands, derived from decomposing spruce needles and covered for the most part by a thick moss layer, were classified as Humimors (Green et al., 1993), while the forest floors of the deciduous and mixed stands, derived from broadleaf litter, small twigs and dead wood, most closely resembled Mormoders (Green et al., 1993). Three subsamples were collected from each replicate stand from three of six permanent plots (2 m x 40 m) that are randomly distributed throughout each experimental stand (for details, see Volney et al., 1999), for a total of 9 subsamples per stand type (N=27 subsamples in total). In order to avoid interference with other projects and to minimize the influence of human disturbance, three random sampling points were established 10 m away to the left of the plot start, along the 40 m vertical side of each permanent plot. At the time

of sampling, we found that some plots were flooded mainly in one of the replicates in the coniferous stands.

In a previous study at EMEND, very low abundances of Mesostigmata were reported, consisting of ~ 8% of the total mite abundance (Acari) in the forest floor (Lindo and Visser, 2004). On average two mesostigmatid mites and 26 oribatid mites were obtained per g of forest floor dry mass. In this study, we increased the core size to ensure collecting a larger number of mesostigmatans at each sampling location. A large metal cylinder of 25 cm in diameter was used to sample the forest floor; thickness varied depending of the forest floor depth in each forest type. Samples were collected at each location and measurements of forest floor thickness were taken to estimate the volume of each subsample (Table 1). Along with thickness, three random temperature measurements were taken around the core cavity where the core was sampled at the interface of the F-H layers (Table 1) using a digital temperature probe (Thermor 9850).

Forest floor core samples were placed in plastic bags and stored in a portable cooler for transport to the Soil Biogeochemistry laboratory (University of Alberta). An average temperature of 10°C was maintained using cryopacks during transportation, and once in the laboratory, cores were stored at 5°C until mite extraction. Additional bulk forest floor samples were taken adjacent to each core sampling location for further environmental characterization. In the laboratory, each sample was further subdivided into two subsamples; one was oven dried (70°C) and reweighed to determine gravimetric moisture content and calculate bulk density, and the other one was air-dried, ground and used to estimate pH

(Table 1). The pH (0.01M $CaCl_2$ solution) was determined from a 1:10 slurry using 10g of ground LFH layer (Davey and Conyers, 1988).

3.2.3. Mite extraction and identification

Mesostigmatan mites were extracted from the forest floor samples using Tullgren type funnels (24.8 cm diameter). Tullgren extraction is recommended for species inventory in highly organic soils, such as those in coniferous and deciduous forest floors in this study (Crossley Jr. and Blair, 1991; Edwards, 1991); in most cases extraction efficiency is over 80% (van Straalen and Rijninks, 1982). Samples were kept in the funnels for ~ 5 days and all forest floor microarthropods were collected into 70% ethanol. Mesostigmatan mites were separated and sorted under a stereo microscope at 15-40x magnification, cleared in 85% lactic acid from one to several hours depending on the degree of transparency required for each specimen, slide-mounted individually in PVA medium (polyvinyl alcohol from BioQuip Products Inc.) and then dried at 45°C for 4-5 days using a slide warmer.

A total of 4045 slides were made. Mounted specimens were separated into immature and adult stadia and classified into morphospecies using a compound microscope, and subsequently identified to genus or species, when possible. Identification of Gamasina and Uropodina mites as well as mites of suborder Sejida required the use of information from different sources including electronic keys to broad taxonomic levels (Walter, 2006; Walter and Proctor, 2001). We used relevant taxonomic publications of soil Mesostigmata for identifications at

genus and species level (Błaszak, 1982; Chant and Hansell, 1971; de Leon, 1964; Emberson, 1967; Evans and Till, 1979; Halašková, 1977; Halliday, 1997; Hurlbutt, 1963; Karg, 1989, 1993; Lindquist and Evans, 1965; Makarova and Petrova, 1992; Moraza and Lindquist, 1998).

We also consulted specialists in the Zerconidae and Uropodina (Zolt Ujvári and Jenő Kontschán, respectively, from The Systematic Zoology Research Group of Hungarian Academy of Sciences, Eotvos Lorand University and Hungarian Natural History Museum) and Phytoseiidae (Gilberto J. de Moraes from The Department of Entomology and Acarology of ESALQ-University of São Paulo, Brazil). One direct outcome of this collaboration was the description of new zerconid species (Díaz-Aguilar and Ujvári, 2010). Tentatively identified specimens were compared with specimens held at the Canadian National Collection of Insects, Arachnids and Nematodes (CNC), at Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada, to verify their identity. Voucher specimens of each taxon were deposited in the CNC for future reference.

3.2.4. Statistical analyses

Abundances of mesostigmatan mites including adults and immature stages (deutonymphs and protonymphs), but excluding the larval stages because they are often difficult to identify to the genus or species level, were used in statistical analyses. Abundance counts were used to calculate density (number of individuals per square meter) to estimate mite densities among stand types. We divided the mites into Gamasina and Uropodina groups, excluding sejid mites due to low

number of individuals, for making comparisons of densities among stand types. Gamasina and Uropodina densities were compared among stand types using one way analysis of variance. Multiple comparisons were tested using Tukey's *post hoc* test (α=0.05). Data were log-transformed ($x' = \log(x+1)$) when necessary and analyzed using SAS/STAT software, version 9.2 (SAS Institute Inc., Cary, NC, USA).

Species richness of mesostigmatan mites was compared between stand types using individual-based rarefaction curves. Because richness is sensitive to sample size, rarefaction generates comparable species richness adjusted for the same number of individuals collected from different assemblages; this is also referred to as sampling effort or comparable levels of abundance (Buddle et al., 2005; Colwell et al., 2004). The pooled species richness for each stand type was used to compute the rarefaction estimates using the 'vegan' package (Oksanen et al., 2010) in R statistical software version 2.12.2 (R Development Core Team, 2011). Additionally, we determined whether sampling was sufficient to characterize the mesostigmatan assemblages being indicated when the rarefaction curves start to level off (Buddle et al., 2005).

Differences in mesostigmatan assemblage structure among stand types were tested by permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) based on one-way design. This analysis was performed using the computer program PERMANOVA (Anderson, 2005) on the Hellinger distance measure and the test of significance ($\alpha = 0.05$) estimated after 9999 permutations. *Post hoc* pair-wise comparison tests were further performed to detect which

mesostigmatan assemblages differed between stand types, and significance was assessed after Bonferroni correction of *p*-values.

The abundance matrix for species was transformed using Hellinger transformation which is the square root of the proportion obtained from the abundance of each species divided by the total abundance in the site (Legendre and Gallagher, 2001). This transformation reduces the importance of abundant species but keeps the variations in relative species composition among sites (Borcard et al., 2011). Afterwards, a forward selection of explanatory variables as indicated by Blanchet et al. (2008) was carried out to select among the following forest-floor environmental variables: temperature, thickness of the organic layer, bulk density and pH (Table 1), those that explain the largest portion of the variance of the response data (Borcard et al., 2011). Only the significant exploratory variables ($p \leq 0.05$) and the largest adjusted coefficient of multiple determination (R^2_{adj}) were used as constraints in the final canonical ordination.

We used a redundancy analysis (RDA, Rao, 1964) based on the Hellinger-transformed species matrix and the significant explanatory variables to visualize how forest-floor environmental variables correlated with the mesostigmatan assemblages. RDA is a constrained ordination, a direct extension of principal component analysis (PCA), used to model multivariate response data constrained by explanatory variables (Borcard et al., 2011). Although RDA is based on Euclidean distance, data transformation allows the use of other distances normally associated with community composition data (Borcard et al., 2011; Legendre and Gallagher, 2001), including non-linear responses along environmental gradients

and matrices containing many zeros (Legendre and Anderson, 1999). The significance of the overall final model, canonical axes and exploratory variables were tested using 999 permutations under the reduced model and the significance level of the tests was α=0.05. Forward selection was performed using the 'packfor' package (Dray et al., 2007), and Hellinger transformation and RDA were computed using the 'vegan' package (Oksanen et al., 2010) in R statistical software version 2.12.2 (R Development Core Team, 2011).

We used the species-dominance metric as defined by Pinzón and Spence (2010) for comparing changes in dominance structure of mesostigmatan mites associated with the successional change from deciduous to mixed to coniferous forests. Briefly, a dominance value (*DV*) is calculated as the product of the relative abundance and the relative frequency of each species. Species dominance values are then relativized in relation to the total sum of all *DV* values in the assemblage, resulting in a relative dominance value (*DV*') for each species. To observe the dominance structure and patterns within and between stand types, the relative dominance values (*DV*') were ranked in order of importance according to seral stages of development and depending on the relative degree of dominance, each species was identified as dominant, subdominant, common or uncommon.

Indicator species analysis (ISA, Dufrêne and Legendre, 1997) was used to identify mesostigmatan species characteristic of a specific stand type. Indicator species analysis generates an indicator value (*IndVal*=% of indication), which results from the frequency and abundance of a species in a given group (in our case, stand types). Significant indicator species ($p \leq 0.05$) were selected after a

permutation test of significance, and species with *IndVal* > 40 were identified as strong indicators. Indicator species analysis was performed in R statistical software version 2.13.1(R Development Core Team, 2011) using the 'labdsv' package (Roberts, 2010).

3.3. Results

3.3.1. Stand type densities

A total of 3937 individual mites (out of a total of 4045 specimens that were mounted), including 16 families, 25 genera and 46 species, were identified in the present study (Table A.1). Of these, 1229 individuals and 28 species were collected from the deciduous stands, 1650 individuals and 35 species from the mixed stands, and 1058 individuals and 33 species from the coniferous stands. Thirty-eight species belonged to Gamasina and only one species to Sejida; the remaining seven species were Uropodina. *Skeironozercon tricavus* (Błaszak), *Parazercon radiatus* (Berlese), *Dendrolaelaps* sp.1, *Gamasellus vibrissatus* (Emberson), *Asca garmani* (Hurlbutt), *Zercon alaskaensis* (Sellnick), *Arctoseius cetratus* (Sellnick), *Mixozercon albertaensis* (Diaz-Aguilar and Ujvári) and *Arctoseius semiscissus* (Berlese) accounted for 81% of Gamasina species and *Trachytes* sp. accounted for 82% of Uropodina species.

Although there was no statistical difference among cover types for both densities of Gamasina ($F_{[2,6]}$=1.87, p=0.234) and Uropodina ($F_{[2,6]}$=1.21, p=0.362), the mean density of Gamasina tended to be highest in the mixed stands (3606 individuals m^{-2}), intermediate in the deciduous stands (2687

individuals m^{-2}), and lowest in the coniferous stands (2098 individuals m^{-2}) (Fig. 1). In contrast, the mean density of Uropodina was highest in the coniferous stands (297 individuals m^{-2}) and lowest in the deciduous stands (88 individuals m^{-2}). Nonetheless, this lack of statistical difference was possibly due to high variations among sampled plots from each forest stand type. The largest within-stand variation was observed in the coniferous stands (Fig. 1), most likely as a result of one experimental unit being flooded at the time of sample collection.

3.3.2. Species richness

Rarefaction curves of the three stand types did not reach asymptotes (Fig. 2); however, they followed a curvilinear shape, which is a good indication that sampling had been sufficient for appropriate comparisons of mesostigmatan mite richness among stand types even though true estimates of total richness had not been reached. Individual-based rarefaction curves at a comparable sampling effort of 1060 individuals indicated that the estimated species richness was lowest in deciduous stands (27 spp.) compared to coniferous and mixed stands, both of which recorded the same number of species (33 spp. each); thus, no differences were detected between mixed and coniferous stands (Fig. 2). These richness estimates suggest a relationship between species richness and stand composition, with a notable conifer influence on richness.

3.3.3. Community composition

The PERMANOVA results showed significant differences in the

assemblages of mesostigmatan mites ($F_{[2,24]}$=2.25, p=0.0005). Pair-wise comparisons between stand types indicated that mesostigmatan assemblages in deciduous and mixed stands were not statistically different (t=1.13, p=0.6015), whereas significant differences were observed between coniferous and mixed stands (t=1.46, p=0.009), and between coniferous and deciduous stands (t=1.81, p=0.0009). Canonical redundancy analysis (RDA) produced a significant ordination of the forest-floor environmental variables and stand types, with p=0.001 following 999 permutations (Fig. 3). The first two axes explained 16.8% of the total variance in the species data. The first canonical axis explained 10.3% of the constrained variance and had the largest species-environment correlation (0.779); this axis mainly differentiated the mesostigmatan assemblages among stand types. The second axis explained 6.5% of the constrained variation and also had a large species-environment correlation (0.7497) (Table 2). Forward selection of the environmental variables indicated that only two, thickness and pH (R^2 adj=5.3%, p=0.004 and R^2 adj=9.9%, p=0.008, respectively), were significant descriptors of the mesostigmatan species data. Thickness of the forest floor was positively correlated and pH was negatively correlated with coniferous stands, which coincides with the characteristics of the humus form of humimors characterized by low pH and thick organic horizons. Besides, pH was positively correlated and thickness was negatively correlated with deciduous stands and their associated mormoder humus forms. Mixed stands were found to have intermediate thicknesses and low pH (Fig. 3a).

The relationships between species and the environmental variables displayed by RDA showed that species such as *Mixozercon albertaensis* (Malber) and *Dendrolaelaps* sp.3 (Dendro 3) were correlated with the higher pH found in deciduous stands. *Parazercon radiatus* (Para), *Boreozercon emendi* (Boreo), *Zercon alaskaensis* (Zalask) and *Trachytes* sp. (Trachy) were correlated with the lower pH associated with coniferous forest floors (Fig. 3b). Other species associated with the relatively acidic forest floors from mixed stands were *Arctoseius semiscissus* (Actosem), *Arctoseius cetratus* (Arctcet) and *Dendrolaelaps* sp.2 (Dendro 2). Thicker forest floors tended to be correlated with Uropodina species of genus *Dinychus* (Diny 2 and Diny 4) and *Arctoseius* sp.3 (Arcto 3). In contrast, the shallower forest floors typical of deciduous stands were correlated with the species *Gamasellus vibrissatus* (Gama) and *Dendrolaelaps* sp.1 (Dendro1) (Fig. 3b).

3.3.4. Dominance structure

Mesostigmatan mite assemblages were mainly composed of a few dominant species, a set of subdominant and common species, whose degree of dominance varied depending on stand composition, and a large number of uncommon species (Table 3). Overall, the assemblages were dominated by *Skeironozercon tricavus*, which had the highest relative dominance (*DV'*) values in all three stand types and the highest proportion in the coniferous stands. Few species were dominant for a given stand type and their dominance changed during succession (Table 3). For instance, *Gamasellus vibrissatus* was largely dominant in the deciduous stands (*DV'*=17.84), it became subdominant in mixed stands, and

it further decreased in the coniferous stands where it was ranked as an uncommon species (Table 3). While they were subdominant species in deciduous and mixed stands, *Parazercon radiatus* (*DV'*=16.34) and *Trachytes* sp (*DV'*=10.78) became dominant species in coniferous stands. *Dendrolaelaps* sp.1 was the only dominant species shared by both deciduous and mixed stands (*DV'*=14.55 and *DV'*=14.01, respectively). Other species, such as *Arctoseius semiscissus*, were common in deciduous stands but then became subdominant in both mixed and coniferous stands. Interestingly, *Boreozercon emendi* was the only subdominant species in the coniferous stands. Among the common or uncommon species, uropodines of genus *Dinychus* were present in coniferous stands, while *Uroobovella* sp. was uncommon species in deciduous stands (Table 3).

3.3.5. Indicator species

Five mesostigmatan species received significant indicator values. These results were consistent with the results of relative dominance values (*DV*') reported above associated to dominant or subdominant species within a forest stand type (Table 3). Only one species, *Gamasellus vibrissatus* (*IndVal*=65, *p*=0.001) was a strong indicator associated with deciduous stands. Two species, *Dendrolaelaps* sp. 2 (*IndVal*=49.9, *p*=0.013) and *Artoseius semiscissus* (*IndVal*=45.7, *p*=0.033) were significant indicators of the mixed stands, and two others, *Dinychus* sp.4 (*IndVal*=50.5, *p*=0.007) and *Boreozercon emendi* (*IndVal*=41.6, *p*=0.020) were strong indicators for the coniferous stands.

3.4. Discussion

3.4.1. Species richness

We found significant differences in estimated species richness between deciduous and coniferous stands but not between coniferous and mixed stands (Fig. 2), while the tendency of the mean density was highest in the mixed stands (Fig. 1). Taken together, these results suggest the importance of the conifer component in driving changes in species composition of mesostigmatan mites in mixedwood forests. Green moss-spruce forests support greater species richness of mesostigmatid mites when compared to different coniferous forests of the Pechoro Ilychskii Nature Reserve in Russia (Marakova, 2011). However, these results are difficult to compare with ours because mixed or deciduous stands were absent in that study.

It has been observed that abundance and richness of oribatid mites tended to be higher in spruce than in aspen stands (Lindo and Visser, 2004). In contrast, a similar richness of oribatid mites has been observed in coniferous and deciduous stands (Sylvain and Buddle, 2010). Litter quality, rate of decomposition and forest floor accumulation differs among stand types, all of which generate different classes of humus forms that can support different soil biota (Green et al., 1993), resulting in variations in species diversity (Ponge, 2003). Species richness of soil fauna is known to increase with ecosystem complexity and heterogeneity within the forest floor (Anderson, 1978). The stands under aspen have shallower forest floors (Table 1), which may lead to lower niche differentiation because the distribution of mesofauna may be restricted by the reduced vertical stratification

of the forest floor (Anderson, 1978). However, under other deciduous cover such as American beech (*Fagus grandifolia* Ehrenberg), whose decomposition rate is slow and similar to conifers (Preston et al., 2000), species richness has been reported to be similar to that of conifers (Sylvain and Buddle, 2010). Slow decomposition rate and litter accumulation may maintain diverse microhabitats over time within L, F and H horizons (Anderson, 1978) in spruce stands, compared to faster decomposition rates associated with aspen stands (Preston et al., 2000); thus, the former containing a higher species richness than the later with shallower forest floors.

In addition, the moss layer can directly contribute to species richness (Čoja and Brukner, 2003) and diversity of Gamasina mites (Salmane and Brumelis, 2008). While we did not estimate moss cover in our study, Salmane and Brumelis (2008) indicated that mosses, e.g. *Hylocomium splendens* (Hedw.) Schimp. in B.S.G., *Ptilium crista-castrensis* (Hedw.) De Not., and *Pleurozium schreberi* (Brid.) Mitt. (also present at our study site), play important roles in structuring Gamasina communities. The dominance of *Picea glauca* (Moench) Voss in coniferous forests as well as the proportion of *Picea* trees in mixed forests supported greater moss cover (Caners, 2010) than deciduous stands. This indicates that coniferous and mixed stands may be characterized with higher species richness and a unique composition of mesostigmatan mites due to species-specific microhabitats and foraging resources provided by the moss layer.

The overlap of mesostigmatan mite richness between coniferous and mixed forests highlights the importance of the conifer component for supporting

higher species richness (Fig. 2), as it has been observed on several studies at EMEND; for example, in coniferous stand with oribatid mites (Lindo and Visser, 2004), non-vascular plants (Caners, 2010) and spiders (Pinzon et al., 2011), and in mixed stands with vascular plants (Macdonald and Fenniak, 2007). The distinct tree species create greater diversity of microhabitats (e.g., microclimate, forest floor properties, and light intensity) that support assemblages of soil fauna associated with each stand type (Cavard et al., 2011).

3.4.2. Community composition

Mesostigmatan assemblages were differentiated by stand type as indicated by PERMANOVA analysis. These differences were mainly driven by the increased proportion of conifer trees (RDA, Fig. 3a). Mixed stands are generally known to maintain higher species diversity and different community composition of aboveground organisms (Macdonald and Fenniak, 2007), but there is still little evidence to support this understanding for soil microarthropods (Cavard et al., 2011). In Germany, Scheu et al. (2003) found that in mixed stands, soil faunal communities were more similar to those of Norway spruce (*Picea abies* (L.) H. Karst.) stands than those of beech (*Fagus sylvatica* L.) stands. In contrast, maple and mixed stands supported similar oribatid assemblages while pure beech or conifers stands had oribatid assemblages that were completely distinct (Sylvain and Buddle, 2010). The latter results more closely resemble the results of our research with mesotigmatid mites. It is evident that further information is required about the relationships between mite assemblages and forest stand types because

it appears that tree species can strongly affect those relationships. Stand types need to be considered in managed forests because tree composition changes during management which may impact mesosigmatan assemblages, especially in large areas of managed spruce forests.

Our results showed that stand type influenced the assemblage structure of mesostigmatan mites and that coniferous forests were characterized by a different mesostigmatan assemblage; as indicated by the presence of Zerconidae species from the genera *Zercon* and *Boreozercon* and Uropodina species from the genera *Dinychus* and *Iphidinychus* (Table A.1). Therefore, forests from late successional stages should be recognized for leading to differences in community composition. Several similarities and many differences can be found if we compare the mesostigmatan assemblages in our study with European boreal forests and Russian taiga. Overall, gamasina mites showed a different community composition in the EMEND spruce forests when compared to spruce forests from the Paleartic Region (Makarova, 2011; Salmane and Brumelis, 2008). For example, common characteristics include the dominance of *Parazercon radiatus* (Hågvar, 1984; Huhta and Niemi, 2003; Makarova, 2011; Salmane and Brumelis, 2008; Usher, 1971). The differences would point to the diversity of zerconid mites, especially with regards to their richness and the presence of some unique *Mixozercon* species (Diaz-Aguilar and Ujvári, 2010). In European boreal forests and Russian taiga only *Mixozercon sellnicki* is generally reported (Huhta and Niemi, 2003; Makarova, 2011) while, as far as we are aware, *Skeironozercon* is the only genus reported in North America (Błaszak, 1982). Uropodine mites

presented similar composition to that in European boreal and temperate forests and Russian taiga; for example, a great diversity of *Dinychus* species, and the occurrence of *Iphidinychus* and *Trachytes* species. However, those forests are characterized by a greater species richness of *Trachytes* mites (Błoszyk et al., 2004; Makarova, 2011).

In our study, species of the families Ascidae, Digamasellidae and Melicharidae dominated the mesostigmatan assemblages. The absence of species of the families Veigaiidae, Parasitidae and Macrochelidae was notable, especially since these are frequently reported in European temperate (Čoja and Bruckner, 2003) and boreal forests (Huhta and Niemi, 2003; Salmane and Brumelis, 2008), as well as in the Russian taiga (Makarova, 2011). Overall, gamasina mites showed a different community composition in the coniferous forests when compared to spruce forests from the Paleartic Region (Makarova, 2011; Salmane and Brumelis, 2008).

An objective in describing species richness and community composition in the EMEND study is to identify thresholds for disturbance as a basis for forest management decisions, for example, at what levels of disturbance biological communities may be affected. Our work on species identification and taxonomy provides new knowledge of the species present, and their natural range of variability under the environmental conditions associated with the stand composition in these mixedwood forests. This knowledge will allow us to better understand the response of mesostigmatan communities to forest management through potential changes in forest floor conditions.

3.4.3. Relationships between mesostigmatan assemblages and forest floor characteristics

Several abiotic factors have been shown to correlate with distinct mite species. Among them, pH (Huhta and Niemi, 2003), temperature and moisture (Huhta and Hänninen, 2001), and thickness of the organic layer and microbial biomass (Laganière et al., 2009) have often been featured as the most important in structuring mesofauna communities. In our study, the patterns of association between species composition and forest floor characteristics indicated that pH and thickness most significantly influenced mesostigmatan species distributions. The influence of forest floor thickness on the distribution of Mesostigmata may be related to spatial habitat and body anatomy. For instance, *Gamasellus vibrissatus* was correlated with deciduous stands, having shallower litter layers and, likely large open habitats formed by wider aspen leaves. It is a large and long legged predatory mite, is also fast moving and thus may require an open habitat for chasing preys (Lee, 1974; Karg, 1993); thus, shallower forest floors may be more propitious for its hunting activities than those of the thicker and moss-covered forest floors.

In addition, *Gamasellus montanus* has been reported in high abundances in a 120-year old Norway spruce from temperate forests in Austria (Čoja and Bruckner, 2003) and also *G. vibrissatus* in eastern conifer forests of *Abies* spp. and black spruce from Quebec and Ontario (Emberson, 1967). An explanation for these results can, perhaps, be found in the understory vegetation in those coniferous forests due to harvesting disturbances. The wavy hairgrass, *Avenella flexuosa* (L.) Drejer growing in Austria coniferous stands (Čoja and Bruckner,

2003), can prevent moss growth (Vávrová et al., 2009) and harvesting also reduces the moss layer and overall forest floor thicknesses (Emberson, 1967). The warmer forest floors as those of deciduous stands can also promote higher activity in predator mites; in this study, however, temperature was not a variable affecting predator assemblages even though aspen stands tended to have warmer forest floors (Table 1).

Deep layers of humimors and moss layers in coniferous stands may be favorable for large, heavily sclerotized and slow-moving mites such as Uropodina of the genus *Dinychus* (Athias-Binche et al., 1989) (Fig. 3b). Under coniferous trees, the interface between the living moss layer and the forest floor forms numerous biologically active habitats unlike those of deciduous forest floors, making these specialized microhabitats more favorable to slow moving mites. It should be noted that *Dinychus* species, occur in well-defined types of habitats (Błoszyk et al., 2004), such as moss in coniferous forest floors (Athias-Binche et al., 1989) and in spruce forests (Makarova, 2011). Our results support the fact that *Dinychus* species are associated with the thicker forest floors from coniferous stands since the thickness vector on the RDA ordination clearly pointed to *Dinychus* sp.2 and *Dinychus* sp.4 (Fig. 3b). The relationship between thickness and *G. vibrissatus* (negative) and *Dinychus* sp.4 (positive) is not surprising because they were species indicators for deciduous and coniferous forests, respectively (Table 3). Thus, *G. vibrissatus* is an indicator of early successional stages and *Dinychus* sp.4 of old growth forests. Thickness was significantly correlated with contrasting mesostigmatan mites (Gamasina vs. Uropodina). This

pattern support the argument than characteristic LFH-thickness supports different mesostigmatan assemblages.

Mites have a broad range of pH preferences that vary from 2.9 to 7.6 (van Straalen and Verhoef, 1997), a range much wider than what is present in the forest floors from our study. In the literature there are not many comparable data on the influence of pH on the distribution of mesostigmatan mites. In our ordination, more mesostigmatan species were constrained by forest floor pH (Fig. 3b), which is an important variable that explains differences in mite community structure in natural and disturbed forests (Huhta and Niemi, 2003). The pH in the forest floors of this study ranged from 4.5 in coniferous, 4.8 in mixed and 5.3 in deciduous (Table 1). Although the pH values were all within a relatively narrow range, there was a statistical relationship between pH and community composition of mesostigmatan mites. In our study, *P. radiatus* was associated with lower pH values, being a dominant species in coniferous stands; however, it is also a subdominant species in deciduous and mixed stands (Table 3). Hågvar and Amundsen (1981) observed a reduction in abundance of *P. radiatus* at pH lower than 4.

We observed increasing dominances of *Parazercon radiatus*, *Arctoseius semiscissus*, *Dendrolaelaps* sp.2, *Trachytes* sp. and *Arctoseius* sp.2, along the successional sequence mixed to coniferous (Table 3), which may suggest a better competitive ability for these species in acidic forest floors (Hågvar, 1990) of coniferous and mixed stands Similarly, the correlation of *Mixozecon albertaensis* and *Dendrolaelaps* sp3 with the higher pH of deciduous forest floors appears to

reflect the better competitive ability of these species at less acidic pH (Hågvar, 1990). Mor and moder humus are filled by higher abundance of mites and collembolans, being associated with flourishing fungal colonies (Wallwork, 1970). Thus, the abundance of food resources (presence of prey) may result in favorable habitat and increasing predator competitiveness due to their efficient predator skills (Martin, 1969). As we had indicated, mesostigmatan mites showed a gradual change in dominance of species from deciduous-mixed-coniferous stands that may be influenced by decreases in pH.

Species dominance changes as the forest matures, in addition to the appearance of new species being driven by forest floor properties such as thickness and pH associated with a particular seral stage. Forest floor properties may also change under disturbance. Where forest management practices are applied to a complex ecosystem such as the boreal mixedwood forest, is it necessary to understand ecosystem properties to better anticipate response to disturbance, and to develop strategies for conservation of landscape elements. This work further contributes to the larger body of work being obtained from the EMEND study on the ecological capital of the boreal mixedwood forest, its distribution under the varying conditions in this forest, changes in ecosystem properties and communities under disturbance, and conditions important for biological conservation.

3.5. Conclusions

Forest floors are the primary habitat for predatory mites. Our results

indicated that there is a natural pattern of mesostigmatan mites according to stand type which holds considerable importance as indicators of site and soil dynamics. Specific differences among forest floors in deciduous, mixed and coniferous stands were associated with mesostigmatan mite assemblages. The presence of coniferous trees significantly influenced species richness, community structure and dominance; which further indicated the importance of the conifer component in maintaining mesostigmatan assemblages. This study highlights the importance of stand structure differences in explaining most of the observed variation in mesostigmatan assemblages.

Furthermore, knowledge about the underlying mechanisms driving mesotigmatan assemblages in undisturbed stands will inform forest management decisions aimed at the preservation of diversity of predatory mites in boreal mixedwood forests of Alberta. Future research must address the role of forest management on mesostigmatid mites, and our results can contribute to identifying the possible effects of management within each stand type. Overall, our results imply that later successional stages are essential for maintaining forest floor diversity of mesostigmatan mites.

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Table 3.1. Forest floor explanatory variables used in redundancy analysis (RDA) and other environmental variables in deciduous, mixed and coniferous forest stands.

Properties	Deciduous	Mixed	Coniferous
Explanatory variables:			
Temperature (°C)	10.6 (0.5)	11.2 (0.9)	9.6 (0.2)
Forest floor thickness (cm)	6.1 (0.9)	8.2 (2.0)	11.1 (2.2)
Moisture content (%) †	71.1 (2.8)	74.3 (4.3)	122.1 (47.6)
Bulk density LFH layer (kg m^{-3})	55.0 (6.9)	45.0 (3.0)	40.7 (3.5)
pH (0.01M $CaCl_2$)	5.3 (0.1)	4.8 (0.2)	4.5 (0.3)
Other environmental variables:			
Forest floor volume (cm^3)	3000 (454)	4036 (968)	5427 (1087)
Abundance of mesostigmatan mites	136 (2.0)	183 (17.4)	118 (41.0)

Note: Values are means (n = 3) and standard errors are given in parentheses.
†Moisture content not included in forward selection analysis because it put more importance on the flooded plots.

Table 3.2. Results of redundancy analysis (RDA) related to canonical axes including inter-set correlations of exploratory variables (chosen by forward selection) and permutation tests of significance.

RDA summary	Axis 1	Axis 2
Eigenvalues	0.1027	0.0654
Species-environment correlations	0.7794	0.7497
Cumulative percent variance explained		
of species data	0.1027	0.1681
of species-environment relationship	0.6109	1.0000
Inter-set correlations		
pH	0.6296	0.4420
Thickness of LFH	-0.4165	0.6337
Permutation test by axes	***F***	***p-value***
Fist canonical axis	2.9634	0.0010***
Second canonical axis	1.8872	0.0376*
Permutation test by explanatory variables	***F***	***p-value***
pH	2.5893	0.0020**
Thickness	2.2613	0.0070**

Table 3.3. Relative abundance values (*DV'*) of mesostigmatan mites from the forest floor of three stand types: deciduous, mixed and coniferous, ranked according to (*DV'*) of deciduous stands.

Species	Deciduous	Mixed	Coniferous
Skeironozercon tricavus	33.89 D	41.62 D	47.49 D
Gamasellus vibrissatus	17.84 D †	5.24 S	0.03 U
Dendrolaelaps sp.1	14.55 D	14.01D	
Parazercon radiatus	10.70 S	5.70 S	16.34 D
Asca garmani	6.31 S	5.96 S	2.80 S
Mixozercon albertaensis	4.61 S	2.55 S	0.21 C
Zercon alaskaensis	3.60 S	2.65 S	3.91 S
Trachytes sp.	2.35 S	2.77 S	10.78 D
Arctoseius sp.2	1.23 S	0.72 C	2.22 S
Arctoseius cetratus	1.01 C	4.72 S	0.86 C
Mixozercon jasoniana	0.94 C	1.55 S	0.06 U
Arctoseius semiscissus	0.76 C	3.16 S †	2.84 S
nr. *Coprozercon* sp.	0.51 C	1.55 S	3.38 S
Arctoseius sp.1	0.48 C	0.78 C	1.33 S
Mixozercon borealis	0.29 C	1.44 S	0.53 C
Dendrolaelaps sp.3	0.25 C	1.04 C	0.02 U
Arctoseius sp.3	0.14 U	0.42 C	1.24 C
Zerconopsis sp.1	0.14 C	0.11 C	
Uroobovella sp.	0.12 U		
Sejus sp.	0.11 U	0.19 C	
Dendrolaelaps sp.2	0.02 U	2.40 S †	0.74 C
Dinychus sp.4		0.04 U	0.81 C †
Zercon columbianus			0.36 C
Dinychus sp.2			0.22 C
Dinychus sp.3			0.07 U
Dinychus sp.1	0.01 U		0.03 U
Boreozercon emendi		0.01 U	3.02 S †

Note: D=dominant; S=sub-dominant; C=common; U=uncommon species.
† Indicator species: *Gamasellus vibrissatus* (*IndVal*=65, *p*=0.001), *Artoseius semiscissus* (*IndVal*=45.7, *p*=0.033), *Dendrolaelaps* sp.2 (*IndVal*=49.9, *p*=0.013), *Dinychus* sp.4 (*IndVal*=50.5, *p*=0.007), *Boreozercon emendi* (*IndVal*=41.6, *p*=0.020).

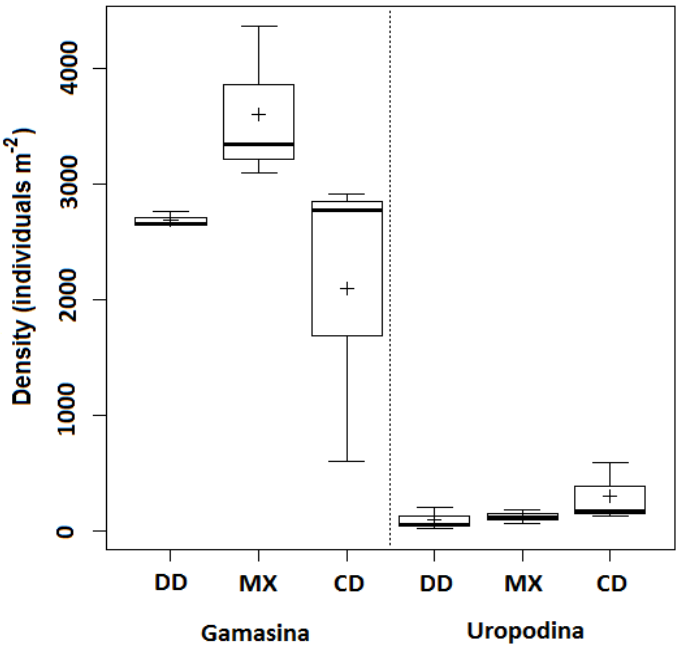

Figure 3.1. Density (individuals m^{-2}) of Gamasina and Uropodina mites from forest floor in deciduous-dominated by aspen (DD), mixed (MX) and coniferous-dominated by spruce (CD) stands.
Note: The plus (+) sign indicates the average density (*n*=3).

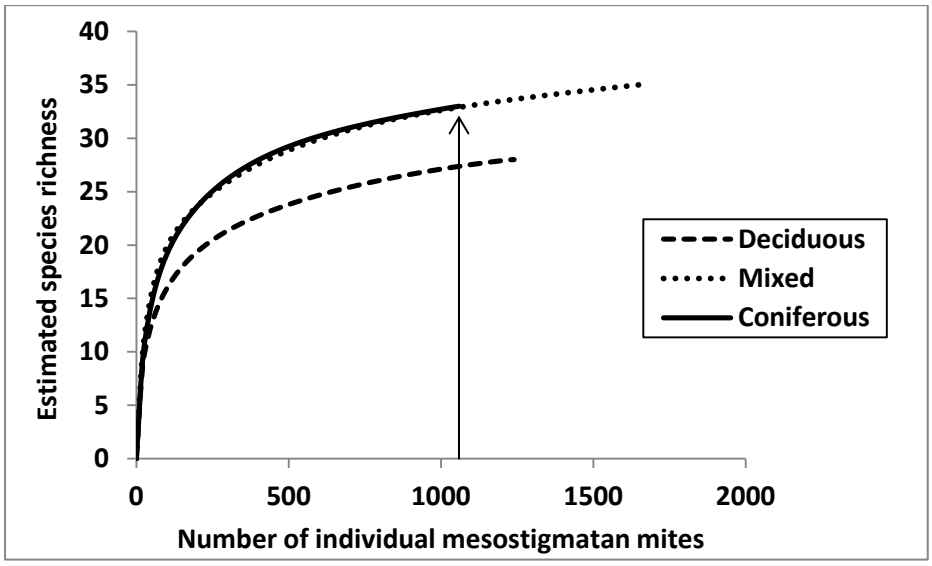

Figure 3.2. Individual-based rarefaction curves of estimated species richness of mesostigmatan mite assemblages, standardized by minimum sample size of 1060 individuals indicated by the arrow, from the forest floor of deciduous, mixed and coniferous stands.

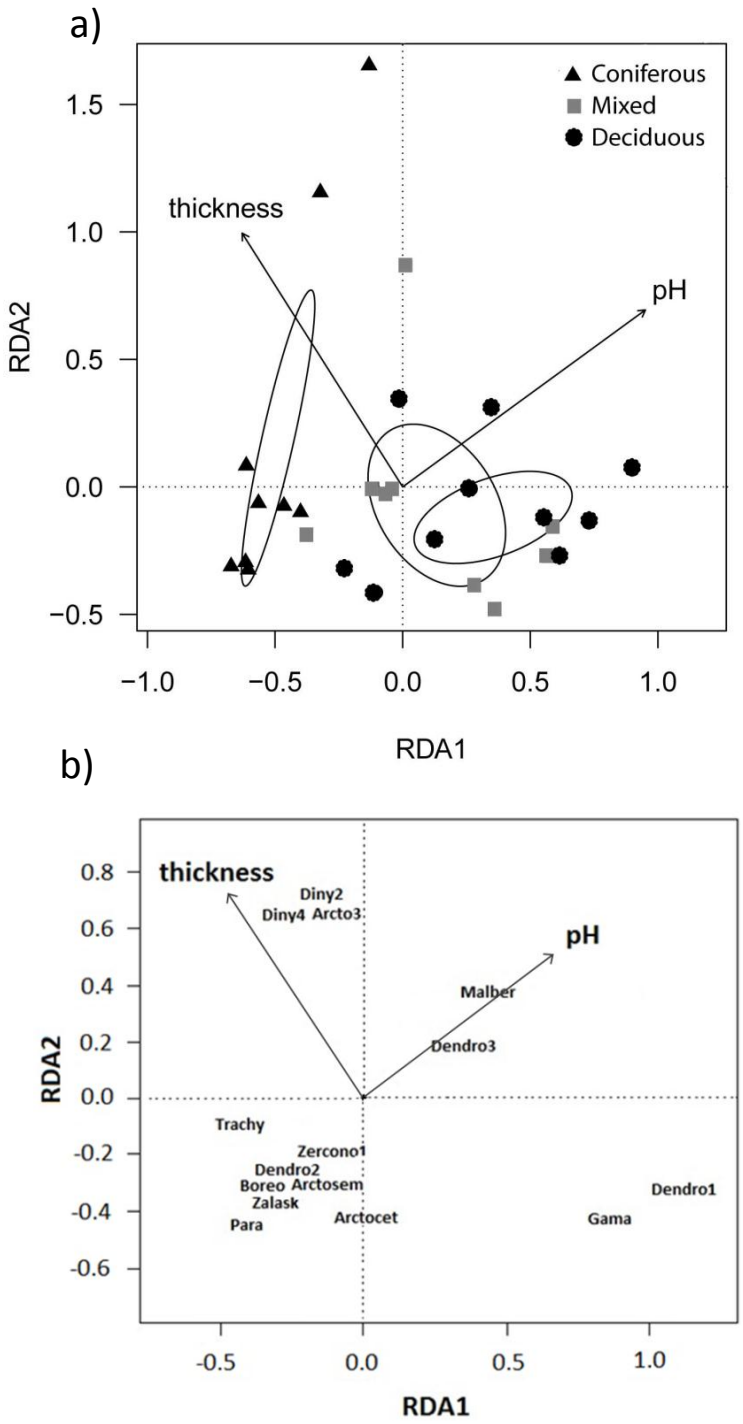

Figure 3.3. Redundancy analysis (RDA) ordinations of mesostigmatan mite assemblages constrained by significant forest floor variables chosen by forward selection: pH and thickness: a) sites and b) species showing those with the greatest explained variance (for species codes see Table A1). Ellipses with 95% confidence limits correspond to categorical variable stand type: deciduous, mixed and coniferous stands. Explained variance by axes: RDA1=0.1027 and RDA2=0.0654.

CHAPTER 4

Trophic ecology of mesostigmatan mites in harvested and control mixedwood boreal forests using ^{15}N stable isotope analysis[3]

4.1. Introduction

Stable isotopes are a powerful tool for reconstructing trophic relationships in soil food webs, as they reflect resource utilization and energy flows driven by soil fauna (Scheu and Falca, 2000; Schneider et al., 2004; Chahartaghi et al., 2005; Illig et al., 2005; Pollierer et al., 2009). The two naturally occurring, stable isotopes of nitrogen, ^{15}N and ^{14}N, present systematic patterns of variations during the various biochemical transformations that comprise the soil nitrogen cycle (Peterson and Fry, 1987; Nadelhoffer and Fry, 1994). In particular, linked to biological discrimination against the heavier isotope ^{15}N, nitrogen isotopic composition differs significantly among different components of the soil food web (Minagawa and Wada, 1984). This provides insight into the many nitrogen transformations mediated by soil organisms (Nadelhoffer and Fry, 1994; Evans, 2007).

Because of the biological fractionation of nitrogen isotopes the value of $\delta^{15}N$ increases with trophic level (Peterson and Fry, 1987). Mean isotopic

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fractionation is estimated at 3.4‰ per trophic level (Minagawa and Wada, 1984; Post, 2002) and this value has been widely used to assess trophic levels in marine food webs (Hobson and Welch, 1992; Fisk et al., 2001; Hobson et al., 2002; Møller, 2006), although it has been far less frequently employed for soil food webs (Illig et al., 2005). Recently, it has been reconfirmed that fractionation varies among trophic positions, with the lower positions being relatively less enriched than the higher trophic levels (Pollierer et al., 2009; Oelbermann and Scheu, 2010). Although 3.4‰ should not be used to rigidly calculate a given trophic position, it may still be a useful guide for explaining the spread of $\delta^{15}N$ values within the food web.

As proposed by Walter et al. (1988) and Scheu (2002), the concept of trophic guild more accurately characterizes the groups of interacting organisms using similar food resources than the trophic level does. While the trophic level concept encloses organisms in a static category, the trophic guild encompasses the dynamics of an assemblage of interacting species focusing on their feeding relationships. This permits better insight into the complex food relationships among species such as omnivory (Post, 2002). The trophic guild can be further divided into functionally similar groups (i.e.; subguilds) to help explain specific prey-predator interactions (Walter et al., 1988).

In boreal forest ecosystems where soil nitrogen is limited (Sah and Ilvesniemi, 2007), tree harvesting typically leads to ^{15}N enrichment in the forest floor (Pardo et al., 2002), as nitrogen losses preferentially remove ^{14}N through nitrification followed by nitrate leaching, ammonia volatilization, and

denitrification (Nadelhoffer and Fry, 1994; Pardo et al., 2002; Sah and Ilvesniemi, 2007). However, some studies have reported no increase in nitrate production following clear-cutting (Jerabkova and Prescott, 2007). These different responses to harvesting illustrate the complexity of soil nitrogen transformations and the sometimes difficult interpretation of soil $\delta^{15}N$ values (Evans, 2007).

Stable isotopic analysis has made it possible to estimate the trophic structure of macro-and mesofaunal communities (Scheu and Falca, 2000), including that of oribatid mites from temperate forests (Schneider et al., 2004), arthropods from boreal forests (Bennett and Hobson, 2009), and has helped with the reconstruction of soil food webs in tropical montane rain forests (Illig et al., 2005) and a mature temperate forest (Pollierer et al., 2009). However, none of these studies has investigated the effect of harvesting. As harvesting has been shown to cause changes in the abundance and community composition of soil microarthropods (Blair and Crossley, 1988; Lindo and Visser, 2004), there is a need to evaluate if variation in $\delta^{15}N$ values in microarthropod assemblages also occurs following harvesting

The number of studies on soil food webs has increased in the last decade, but, for the most part, studies of mesofauna have focused on oribatid mites and springtails. Predatory mites such as those from the order Mesostigmata are comparatively understudied. Recently, the first trophic structure of mesostigmatan mites has been published for Central European beech forests (Klarner et al., 2013). Most mesostigmatans are free-living predators inhabiting litter and soil (Walter and Proctor, 1999; Krantz, 2009). Although they are the least abundant

group of mites in soil (Petersen and Luxton, 1982), Mesostigmata play a key role as they regulate the population sizes of other soil fauna (Krantz, 2009). Martin (1969) demonstrated that gamasids are efficient predators under the confined leaf litter microhabitats. They also indirectly affect nitrogen fluxes (Berg et al., 2001) as a result of their feeding habits, especially for feeding on their prey's body fluids (Walter and Proctor, 1999), and also because they consume relatively nitrogen-rich prey (Pearson et al., 2003) that detritivorous oribatid mites.

Although their biological importance has been demonstrated (Petersen and Luxton, 1982; Walter and Proctor, 1999; Krantz, 2009), and their feeding behavior relatively well documented (e.g.; Walter, 1988; Walter et al., 1988; Martikainen and Huhta, 1990; Walter and Proctor, 1998; Beaulieu and Walter, 2007), the trophic ecology of Mesostigmata is poorly understood. Trophic structure generalizations are not possible because of differences in mesostigmatan species found in different continents and forests, such as those in Central European beech forests (Klarner et al., 2013) and in Canadian boreal forests.

Hence, our main objective was to investigate the trophic guilds of mesostigmatan mites in the forest floors of coniferous and deciduous stands of western Canadian boreal mixedwood forest. In addition to mature (control) stands, we also studied the potential effect of clearcutting on these trophic guilds. We used the $\delta^{15}N$ values of the mesostigmatan mite bodies to position them along a trophic gradient. In addition, we compared these values to published information from feeding experiments to help define likely predator-prey interactions in these mite communities.

4.2. Materials and methods

4.2.1. Study area

This study was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) research site (56°46'13" N, 118°22'28" W), located approximately 90 km northwest of Peace River, Alberta, Canada. Climate in this region is continental, with mean monthly temperatures ranging from –15.4 °C in January to 16.4 °C in July; the mean annual precipitation is 378 mm (Environment Canada, 2011). For the most part, soils are fine-textured Orthic and Dark Gray Luvisols that have formed from glacio-lacustrine parent materials (Kishchuk, 2004). The EMEND experiment consists of ~10 ha compartments of well-defined stand types characteristic of the boreal mixedwood forest where various degrees of variable retention harvesting (2%, 10%, 20%, 50%, 75% and 100%) were achieved in the winter of 1998-1999 (for details see Volney et al., 1999; Work et al., 2010). All stands were left to naturally revegetate following harvesting.

Our study focused on the control (100% canopy retention) and clearcut (2% retention) treatments from the coniferous and deciduous-dominated stands; in addition, only one 20% retention treatment was included for the coniferous-dominated stands because the same treatment in deciduous stands did not have enough specimens. The deciduous-dominated stands encompass > 70% trembling aspen (*Populus tremuloides* Michx.), with lower proportions of balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.). The

coniferous-dominated stands are > 70% white spruce (*Picea glauca* (Moench) Voss), with less abundant species including black spruce (*Picea mariana* (Mill.) B.S.P.), lodgepole pine (*Pinus contorta* var. *latifolia*), and balsam fir (*Abies balsamea* (L.) Mill.) (Spence et al., 1999; Volney et al., 1999). The vegetation in the deciduous and coniferous clearcuts was similar in that they both showed a dense suckering by *Populus* (Frey et al., 2003). Each combination of forest type and harvesting treatment was replicated three times across the EMEND experimental site, thus, a total of 15 experimental units were sampled for our study.

4.2.2. Field sampling

In the summer of 2007, from July 11th to August 4th, we sampled the forest floors in the control, clearcut and 20% retention treatments using a metal cylinder of 25 cm in diameter. Nine subsamples were taken 10 m away from three of the six permanent transects (2 m x 40 m) that had been established throughout each experimental compartment (Volney et al., 1999). Hence a total of 27 samples were taken from each treatment and stand type (9 subsamples for each of three replicated compartments), corresponding to a total of 135 samples for the study.

Forest floor samples were placed in plastic bags, stored in a portable cooler and transported to the Soil Biogeochemistry laboratory (University of Alberta). An average temperature of 10°C was maintained using cryopacks during transportation, and once in the laboratory, cores were stored at 5°C until mites were extracted. Additional bulk forest floor samples were taken adjacent to each

core sampling location to obtain the isotopic values of the baseline. the baseline isotopic values. Various plant materials characteristic of the forest stands were also collected, including step moss (*Hylocomium splendens* (Hedw.) Schimp. in B.S.G.), aspen leaves (*Populus tremuloides* Michx.), grass (*Calamagrostis canadensis* (Michx.) P. Beauv.), and fireweed (*Chamerion angustifolium* (L.) Holub). Bulk forest floor and plant samples were air dried to reduce moisture and stored in paper bags.

4.2.3. Mite extraction and identification

Mesostigmatid mites were extracted from the forest floor samples using Tullgren type funnels and collected in vials with 70% ethanol. The vials were maintained at -5°C until mite identification and preparation for isotopic analysis. Ethanol preservation was chosen, as this does not significantly change the $\delta^{15}N$ signature in tissue samples from several organisms (Hobson et al., 1997; Edwards et al., 2002; Sarakinos et al., 2002; Barrow et al., 2008). Similarly, no effect on $\delta^{15}N$ was reported in studies of boreal forest arthropods (Bennett and Hobson, 2009) and epigeic soil fauna (Oelbermann and Scheu, 2010) that used ethanol-based preservation. On the other hand, this mode of conservation precluded the analysis of $\delta^{13}C$ values of the preserved mites (Sticht et al., 2006; Krab et al., 2012).

Mites were separated and sorted under a stereo microscope and identified to genus or species level, when possible (Table 4.1). Because we found a small number of individuals per species in samples, we pooled all mites of a given

species within each treatment and repetition, which led to a total of 80 samples. For the large mite species, two to four individuals were sufficient for isotopic analyses; on the other hand, for small species, up to 110 individuals *were* combined to reach the required sample size. For each treatment, two or more replicates of the same species (see Figures 4.2 and 4.3) were analyzed when possible.

Some samples of oribatid mites were also included in the study mainly to enable differentiation within the hypothetically lower trophic levels. Mites were placed into 4 x 6 mm tin capsules (Elemental Microanalysis Ltd), oven-dried at 60°C for 48 h, and then weighed on a micro-analytical balance; capsules were closed and sent for isotopic analysis. Bulk forest floor samples were analyzed to set the isotopic baseline for the soil food web (Schneider et al., 2004; Illig et al., 2005; Oelbermann and Scheu, 2010). These samples as well as the plant samples were oven-dried at 70°C until each sample maintained a constant weight, and then finely ground using a Brinkmann ball grinder (Retsch, MM200). After drying and grinding, samples were weighed into tin capsules (5 x 3.5mm) prior to isotope ratio analysis.

4.2.4. Stable isotope analysis

The isotopic ratios of nitrogen ($^{15}N/^{14}N$) of all mite samples were determined with an elemental analyser (Vario EL III manufactured by Elementar, Germany) coupled to an isotope ratio mass spectrometer (Delta XP Plus Advantage manufactured by Thermo, Germany) via a ConFlo II at the G.G. Hatch

Isotope Laboratories (University of Ottawa, Ontario, Canada). Atmospheric nitrogen (N_2, air) served as the primary standard and was normalized to internal standards calibrated against several International Standard Reference Materials (IAEA-N1, IAEA-N2, USGS-40 and USGS-41). Forest floor and plant samples were analyzed using a Costech ECS 4010 Elemental Combustion System (Costech Analytical Technologies Inc. Valencia, CA USA) interfaced to a continuous flow Finnigan Delta Plus Advantage IRMS (ThermoFinnigan, Bremen, Germany) at the Elemental Analysis and Stable Isotope Ratio Mass Spectrometry laboratory in the Renewable Resources Department (University of Alberta).

The nitrogen stable isotope ratios ($^{15}N/^{14}N$) are reported in delta (δ) notation, in parts per thousand (‰, or per mil) units, and the δ-value is calculated as: $\delta^{15}N(‰) = (R_{sample} - R_{standard}/ R_{standard}) \times 1000$, where R is the ratio of the abundance of the heavy to the light isotope. Delta values are reported relative to atmospheric N_2 (air). In a sample, a more positive $\delta^{15}N$ value indicates enrichment, meaning that it contains proportionally more of the heavy stable isotope, while a negative value of $\delta^{15}N$ indicates depletion of the ^{15}N isotope (Peterson and Fry, 1987).

4.2.5. Statistical analysis

We tested if the baseline values (i.e., the forest floor samples) differed among treatments by comparing the control plots (100% retention) and clearcuts (2% retention) from the coniferous and deciduous stands. We used a two-way

analysis of variance (ANOVA) and least square means (Lsmeans) for multiple comparisons of means linked to stand type (conifers vs deciduous stands) and harvesting treatments. The level for declaring statistical significance was set at $P < 0.05$. The statistical analysis was carried out using SAS software, version 9.2 (SAS Institute Inc., Cary, NC, USA). Mite specimens were placed in trophic guilds according to the diet of species analyzed from previously published feeding experiments (Table 4.1). Subsequently, mites within a guild were further divided into subguilds in order to explain predator-prey relationships as proposed by Walter et al. (1988). Due to the lack of replicate samples for some of the mites, the $\delta^{15}N$ values of mites were not statistically analyzed; instead, data are presented as mean ±SD values shown as descriptive graphics.

4.3. Results

4.3.1. Influence of harvesting on baseline $\delta^{15}N$ signatures

The $\delta^{15}N$ results for the coniferous forest floor samples (corresponding to the baseline values) averaged -0.76‰ (SE ± 0.17) for the undisturbed (control) stands and -0.30‰ (SE ± 0.29) for the clearcut treatments. The $\delta^{15}N$ value for the single coniferous plot that was sampled from the 20% retention treatment was intermediate at -0.56‰ but not included in the statistical analysis for lack of repetitions. The deciduous baseline values averaged -0.35‰ (SE ± 0.31) for the control and 0.53‰ (SE ± 0.39) for the clearcut plots. The baseline $\delta^{15}N$ signatures did not differ significantly between the control and clearcut treatments (p=0.053). Similarly, there was no significant interaction between forest type and treatment

(p=0.496), nor was there any significant differences between the coniferous and deciduous stands (p=0.066).

Although not significant at α=0.05, an enrichment in $\delta^{15}N$ was observed in the following increasing order: coniferous control < coniferous clearcut ≈ deciduous control < deciduous clearcut (Figure 4.1). Hence, the coniferous baselines tended to be more depleted than the deciduous baselines and the controls more depleted than their respective clearcuts. The $\delta^{15}N$ values of the litter material falling onto the forest floor from trees and understory vegetation were reflected in part in the $\delta^{15}N$ signatures of the baselines. Indeed, step moss, which was only present in the coniferous stands, had the most negative $\delta^{15}N$ value (-3.8‰) of all collected plant materials (Figure 4.2), while the $\delta^{15}N$ values for fireweed (-1.08‰) and aspen leaves (-0.91‰), both collected within the deciduous stands were slightly less negative (Figure 4.3).

4.3.2. $\delta^{15}N$ signatures of mesostigmatid and oribatid mites

Overall, the $\delta^{15}N$ values of forest floor mites from coniferous and deciduous stands spanned a gradient of 10.2 δ units, ranging from 0.27‰ (*Phthiracarus boresetosus*, Phthiracaridae, Oribatida, found in two of the three types of coniferous treatments) to 10.48‰ (*Dinychus* sp., Dinychidae, Uropodina). The spread of data somewhat varied between harvesting treatments because the oribatid mites with the lowest $\delta^{15}N$ sometimes showed higher $\delta^{15}N$ values than *P. boresetosus*. In particular, the lowest $\delta^{15}N$ value for the coniferous 20% retention treatment was 2.66‰, which corresponded to *Scheloribates pallidulus*, and

yielded an overall gradient of 7.5 units for this stand type (Figure 4.2b). Similarly, for the deciduous clearcuts, the lowest value was 1.25‰ (corresponding to *Propelops* nr. *alaskensis)*, which resulted in an overall gradient in $\delta^{15}N$ values of 8.8 δ units (Figure 4.3b). Finally, the $\delta^{15}N$ signatures of mesostigmatan mites spanned 6.11 δ units ranging from *Zercon alaskaensis* with 4.00‰ to *Dinychus* with 10.11‰ (Table 1).

Differences in $\delta^{15}N$ signatures located the mesostigmatid and oribatid mites along a hypothetical trophic gradient (Figures 4.2 and 4.3), which was compared to known feeding habits previously reported in the literature (Table 4.1). This approach allowed the separation of three main trophic guilds: detritivores, omnivores (overlapping with predators) and predators. The detritivores were enriched in ^{15}N compared to the baseline by on average 1.2‰; this group was solely composed of oribatid mites that showed the lowest $^{15}N/^{14}N$ ratios (< 1.6‰). The ^{15}N signatures among species located within this trophic guild did not vary strongly, but two different subguilds of specialized species can be differentiated based on known feeding preferences (Table 4.1): saprophagous /xylophagous, including *Phthiracarus boresetosus* (O1) with the lowest mean measured $\delta^{15}N$ values (0.32‰), and mycophagous, composed of *Propelops* nr. *alaskensis* (O2) and *Eremaeus* sp. (O5), with $\delta^{15}N$ values ranging between 0.96 and 1.54‰.

The omnivore (overlapping with predators) guild, ranging in $\delta^{15}N$ mean values from 2.66 to 6.61‰ (Table 4.1) was enriched in ^{15}N compared to the detritivores by an average 3.6‰. This guild included both oribatid and

mesostigmatid mites. The following oribatid species were present: *Scheloribates pallidulus* (O3), *Pilogalumna* sp. (O4) and *Ceratozetes* sp. (O7), and the mesostigmatid species encompassed *Zercon alaskaensis* (Z2), *Zerconopsis* sp. (Sp9) and *Sejus* sp. (S). Based on published feeding observations, they can be further divided into two main subguilds: fungivorous/nematode feeders and microarthropod feeders.

The predators ($\delta^{15}N$ values > 7‰) were enriched in ^{15}N compared to omnivorous mites by on average 5.2‰ and to detritivorous mites by on average 7.6‰. This guild included only one oribatid mite, *Epidamaeus* sp. (O6), but most mesostigmatan species fell into this category including *Parazercon radiatus* (Z2), *Gamasellus vibrissatus* (Sp4), *Trachytes* sp. (U1) and its deutonymph U1 (Dn), *Skeironozercon tricavus* (Z1) and *Dinychus* sp. (U7). Similarly to the omnivorous guild, two subguilds can be identified, likely separating the predators of nematodes from the predators of arthropods according to feeding habits reported by Walter (1988) and Walter et al. (1988). Interestingly, we found that the species *Veigaia kochi* (Sp25) presented $\delta^{15}N$ values that were intermediate between the values of omnivores and those of predators; thus, this species was located in the transition zone from one trophic guild to another (Figures 4.2 and 4.3).

The $\delta^{15}N$ signatures of mesostigmatan mites differed strongly between the large and small species, with the larger species being relatively less enriched in the heavier isotope. For example, one of the large species of the Zerconidae, *Zercon alaskaensis* (body size 442 μm), had a distinctly lower $\delta^{15}N$ value (4.0‰) than those of the smaller zerconid species such as *Parazercon radiatus* (345 μm)

and *Skeironozercon tricavus* (368 μm), which showed $\delta^{15}N$ values of 8.39‰ and 9.70‰, respectively (Table 4.1). Other large-sized and less ^{15}N-enriched species were *Sejus* sp. (5.52‰) and the previously mentioned *Veigaia kochi* (6.84‰). Finally, the $^{15}N/^{14}N$ ratios of the *Trachytes* species (Uropodina) did not vary between the mature (9.05‰) and the immature deutonymphs (8.84‰), indicating that both adult and deutonymph individuals likely have the same feeding preferences.

4.3.3. Harvesting effect on trophic structure of mesostigmatan mites

The $^{15}N/^{14}N$ ratios of mite species did not differ between harvesting treatments (Figures 4.2 and 4.3). This was also illustrated by the relatively low standard deviations reported in Table 4.1. Our results further indicated that neither clearcutting nor stand type affected the trophic structure of the mesostigmatid and oribatid mites observed at EMEND. Similarly, the same pattern was observed in the 20% retention treatment (Figure 4.2b). Although some intraspecific variations in $\delta^{15}N$ values could be seen for some mite species, all mites maintained their position within their respective trophic guilds regardless of the stand type or harvesting treatment (Figures 4.2 and 4.3).

4.4. Discussion

4.4.1. Baselines of harvested and unharvested treatments

Estimations of trophic positions are based on baseline signatures (Post, 2002). Differences in baseline $\delta^{15}N$ signatures have been observed among forest

types (Casey and Post, 2011) and we had hypothesized that isotopic baselines would be modified by harvesting. However, in our study, no significant differences in $\delta^{15}N$ were observed between the control and the clearcut plots, or between the coniferous and deciduous stands. The ^{15}N-enrichment following a (non-significant) trend with the deciduous stands following clearcutting having higher $\delta^{15}N$ values than the coniferous stands (Figure 4.1).

In published literature, observed ^{15}N-enrichment has been attributed to an increased level of nitrification and high nitrate losses of ^{14}N in harvested sites (Nadelhoffer and Fry, 1994; Pardo et al., 2002; Sah and Ilvesniemi, 2007). However, previous studies at EMEND did not report higher nitrate concentrations or higher net nitrification rates in the clearcuts compared to the unharvested plots (Jerabkova and Prescott, 2007). Two and a half years after harvesting, only a minor change in available NO_3-N in deciduous clearcuts was reported, and differences were not statistically different (Lindo and Visser, 2003). Accordingly, 8 years postharvest, we found no evidence that clearcuts had further ^{15}N-enrichment than did the control, undisturbed forested stands.

Aspen regeneration was evident in the coniferous clearcuts (Frey et al., 2003). Thus, it might be that the slightly increased $\delta^{15}N$ values in the baselines of the coniferous clearcuts were due to a shift in vegetation. Several studies have reported differences in ^{15}N natural abundance among co-existing plants in the same forest due to differences in the N sources that they exploit (Schulze et al., 1994), as well as because of their mycorrhizal associations (Evans, 2001). Discrimination against ^{15}N during nitrogen transfer by mycorrhizal associations

has been suggested as the key reason for differences in ^{15}N natural abundance in the host plants (Högberg et al., 1999; Hobbie and Ouimette, 2009).

Aspen leaves and grasses had higher $\delta^{15}N$ values than mosses (Figure 4.2), which may be associated with their source of nitrogen supply. For example, nitrogen uptake of *Calamagrostis canadensis* is mainly from the deeper soil horizons (Schulze et al., 1994; Sah and Ilvesniemi, 2007), which are more ^{15}N-enriched (Nadelhoffer and Fry, 1994). Furthermore, Martinelli et al. (1999), which reported $\delta^{15}N$ values in a range of sites from tropical and temperate forests, showed that deciduous species such as *Populus tremuloides* (-1.4‰) were generally more enriched in ^{15}N than coniferous species such as *Picea glauca* (-3.3‰).

We can observe the same trend at EMEND, with the deciduous stands showing slightly higher $\delta^{15}N$ values than the coniferous stands (Figure 4.1). In addition, the occurrence of more ^{15}N-enriched forest floors in the clearcuts may indicate a shift towards more ^{15}N-enriched litter (e.g. aspen leaves and grasses). Alternatively, decomposition and mineralization processes typically result in an increase in $\delta^{15}N$ values, which may explain why the clearcuts, with limited litter inputs but continued decomposition, showed greater ^{15}N enrichment than the control stands (Quideau et al., 2003).

4.4.2. Trophic structure of mesostigmatan mites

The $\delta^{15}N$ signatures of the mesostigmatid and oribatid mites spanned 10 δ units, which is a range similar to that reported for mites of temperate forests

(Scheu and Falca, 2000; Pollierer et al., 2009) and tropical montane rain forests (Illig et al., 2005). These results indicate that the food web length of soil microarthropods is consistent among different forest ecosystems. In general, the trophic structure of soil microarthropods contains three or four trophic positions depending on the identified clusters of species; for instance, trophic levels (Scheu and Falca, 2000), feeding guilds (Schneider et al., 2004), trophic groups (Illig et al., 2005), compartments (Pollierer et al., 2009) and trophic guilds (Oelbermann and Scheu, 2010). According to the $\delta^{15}N$ values in the oribatid and mesostigmatan mites that we isolated, we identified three main trophic guilds: detritivores, omnivores (overlapping with predators) and predators. Each guild could be divided into two subguilds, which are discussed below.

4.4.2.1. Detritivorous mites

Because of their presumed detritivorous diet, oribatid mites were included to build the lower trophic positions of the soil food web. The detritivore guild was composed of oribatid species that included primary and secondary decomposers that we split into two main subguilds. The saprophytic /xylophagy guild consisted of *Phthiracarus boresetosus*, which had a $\delta^{15}N$ value very close to that of baseline from coniferous forest floors (Table 4.1 and Figure 4.2). This is an endophagic mite whose immature forms (larvae and nymphs) hollow out partially decayed conifer needles (Jacot, 1939; Luxton, 1972) while as an adult, it is a litter feeder (Anderson, 1975); in our study, this mite was more abundant in the coniferous treatments (Figure 4.2).

The second subguild included the mycophagous mites which feed strictly on fungi and yeasts (Luxton, 1972) and contained the species *Propelops* nr. *alaskensis* and *Eremaeus* sp., both showing an average ^{15}N enrichement of 1.2‰. Species of the genus *Eremaeus* have been reported to be leaf-litter inhabitants (L-horizon) in aspen stands where they feed mainly on the mycelium of pigmented fungi (Mitchell and Parkinson, 1976). We found that our results corresponded to those reported by Schneider et al. (2004), who placed *P. boresetosus* as primary decomposer and one *Eremaeus* species as secondary decomposer.

Pollierer et al. (2009) pointed out that microarthropods at the base of the food web included organisms feeding on diets with low protein and high carbon content. Their low $\delta^{15}N$ values hence may result from low diet quality or protein-sparing effect; i.e., reserving protein for tissue maintenance rather than catabolizing it for energy (Castellini and Rea, 1992) or excreting it as nitrogenous wastes (Berg et al., 2001). For instance, the high content of melanin in pigmented fungi makes them hard to digest (Maraun et al., 2003), decreasing the food quality. Fungal feeders may also take advantage of the exo-enzymes produced by the fungi and, thus, digest organic compounds containing nitrogen that are released during organic matter decomposition (Scheu and Setälä, 2002; Maraun et al., 2003). Consequently, nitrogen retention in fungal feeding decomposers is an indication that detritivorous mites do not contribute in any substantial fashion to nitrogen mineralization processes in soils. Based on the calculations of the food web model from Berg et al. (2001), oribatids are responsible for less than 5 % of

total mineralization rates in forest floors. However, nitrogen utilization by mites from the lower trophic positions clearly deserves further detailed attention.

4.4.2.2. Omnivorous (overlapping with predator) mites

The importance of omnivory has been a prevalent feature in the structure of soil food webs (Scheu and Setälä, 2002; Schneider et al., 2004; Pollierer et al., 2009). Omnivory represents the largest compartment and includes fungal feeders/predators (Pollierer et al., 2009) as well as scavengers (Schneider et al., 2004; Heidemann et al., 2011). Among the species studied, *Scheloribates pallidulus* has been classified as fungal feeder (Wallwork, 1958; Hartenstein, 1962); however, the analysis of gut contents of individuals from the field contained few fungal hyphae (Wallwork, 1958). Later, it was found by Muraoka and Ishibashi (1976) that *S. pallidulus* fed avidly on the fluids of nematodes. That being said, we chose to locate this species in the omnivorous trophic guild as it showed a ^{15}N enrichment of 2.66‰ (Table 4.1 and Figure 4.2b).

Pilogalumna species (Galumnidae) have been reported feeding on fungal hyphae and moss spores (Walter et al., 2011), on living or dead nematodes and springtails, as well as on algae (Walter, 1988). Using the stable isotope approach, *Pilogalumna* mites were located in the carnivore-scavenger-omnivore feeding guild by Schneider et al. (2004). Likewise, *Pergalumna* and *Galumna* species, other members of the Galumnidae family, have been reported to eagerly devour whole living nematodes (Rockett and Woodring, 1966; Muraoka and Ishibashi, 1976; Rockett 1980; Walter, 1988).

Similarly, analysis of gut contents from *Ceratozetes* mites living in aspen forest floors showed that dark pigmented mycelia were their main food source (Mitchell and Parkinson, 1976). In a laboratory test, Muraoka and Ishibashi (1976) observed that *Ceratozetes* were nematode feeders feeding on body fluids. However, these species did not feed on nematodes to the same extent as species of the Galumnidae (Muraoka and Ishibashi, 1976; Walter, 1988), which may indicate that they prefer to feed on other types of food. Taken together, results confirm that saprophytic oribatid mites may also be important regulators of nematode populations, as was first suggested by Rockett and Woodring (1966).

In our study, we located some mesostigmatan species in the omnivore guild based on their ^{15}N enrichment, which averaged 4.0‰ compared to the detritivorous guild; in comparison, Post (2002) reported a mean trophic fractionation of 3.4‰ for one trophic level. In general, these mites were large-sized species with the exception of *Zerconopsis* sp. (which is of medium size). Species of the family Zerconidae have generally been considered to be oligophagous predators (Evans and Till, 1979), and to exclusively feed on nematodes (Walter, 1988). Unfortunately, there are no records of the feeding habits of *Zercon alaskaensis*, but it is likely to also be a nematode feeder. Similarly, unknown *Zerconopsis* species have been observed feeding on nematodes (Walter and Lindquist, 1995).). Contrary to our results, Klarner et al. (2013) reported that *Zerconopsis remiger* presented the highest $\delta^{15}N$ signature, which located it as a predator. This indicates that even between species of the

same genus, there may be an ample range of prey preferences (e.g., fungal feeder nematode or predatory nematode), separating them in different trophic niches.

Little is known about the food preferences of Sejidae. An unidentified Australian species of *Sejus* was observed eagerly feeding on nematodes, although the degree of feeding tended to be much lower than that in predatory Gamasina mites (Beaulieu and Walter 2007). It was also seen seizing springtails with its chelicerae but did not seem to feed on them. Other *Sejus* species were observed as aggressive predators of nematodes, collembolans and small arthropods, feeding only on the prey fluids of pre-digested material (Walter and Proctor, 1998). According to the $\delta^{15}N$ signatures obtained from *Sejus* mites, we may infer that they are opportunistic omnivores rather than strict predators; indeed they likely switch to other food resources when nematodes or microarthropods are not immediately available (Lekveishvili, 2012, personal communication). Since that they are fluid feeders (Walter and Proctor, 1998), *Sejus* mites may feed on fungi by piercing their mycelia and sucking their fluid content.

Similarly to *Ceratozetes* sp., *Veigaia kochi* possessed $\delta^{15}N$ values that located this mite in the omnivorous guild (Table 4.1). Feeding observations have shown that species of the genus *Veigaia* are fast pursuit predators (Hurlbutt, 1968; Walter et al., 1988) and fluid feeders (Lee, 1974). Walter et al. (1988) also reported that Veigaiidae species prey on springtails, small arthropods, and sometimes on nematodes. Most of the laboratory feeding experiments that we have cited has relevance for corroborating our trophic positions. However, there is no evidence for mycophagy *sensu stricto* because additional food sources that

mesostigmatids might consume under field conditions are not offered to them during laboratory experiments.

Trophic position and body size have been proven to be positively correlated in marine food webs (Jennings et al., 2008). For generalist predators, the trophic position decreases with body size, reflecting a shift in diet to prey of a lower trophic guild such as primary decomposers (Jennings et al., 2008). There is only one study referencing body size together with trophic position in soil food webs, but the authors did not find any relationship between those two parameters (Klarner et al., 2013). Predator mites have been placed in two predator levels, one mainly feeding on primary decomposers and the other one on secondary decomposers (Illig et al., 2005); however, the authors did not mention about the body size of the mites. Similarly, Klarner et al. (2013) situated different *Veigaia* species in two predator levels. In our study, mesostigmatans clearly showed different body sizes, with the bigger mites being lower in abundance. In general, Mesotigmata can feed on prey that are bigger than they are (Walter and Proctor, 1999). The ^{15}N signatures of *V. kochi* (large-sized mite) appeared to be more related with a diet of small prey (e.g., Collembola) that are primary decomposers as proposed by Illig et al. (2005). On the other hand, a diet primarily composed of bacterial feeding nematodes seems to increase $\delta^{15}N$ values and a diet on primary decomposers decreases $\delta^{15}N$ signatures (Klarner et al., 2013). In all cases, the relationship between body size and trophic position in soil food webs requires further attention.

According to what is stated above, we named the ominivorous guild as omnivorous (overlapping with predators) because we observed an overlap between omnivorous and predator mites, where the latter may feed mainly on primary decomposers. This guild contains two subguilds: fungivorous/nematode feeders, including mainly orbatid mites, *Z. alaskaensis* and *Zerconopsis* sp., and microarthropod feeders of primary decomposers, including the large-sized mesotigmatid mites *Sejus* and *V. kochi*. These data confirm that omnivores gain most of their energy from the lower trophic levels on which they feed (Hastings and Conrad, 1979), and that they appear to be generalist rather than specialist feeders.

4.4.2.3. Predators

The predators were enriched in ^{15}N compared to the detritivorous mites by on average 7.6‰, as ^{15}N signatures spanned more than two trophic levels. There was only one oribatid mite (*Epidamaeus* sp.) ascribed to the predatory guild, and similarly Illig et al. (2005) identified one species of this genus as a predator. In contrast to our results, species of *Epidamaeus* have been found with fungal hyphae, often pigmented, and remains of organic matter in their gut contents (Walter et al., 2011). These contrasting results may be a consequence of differences in food preferences among oribatid species of the same *Epidamaeus* genus (Schneider et al., 2004). Our measured $\delta^{15}N$ value for *Epidamaeus* sp. was 7.25‰ (Table 4.1), which clearly indicates that this is a predator mite, since an

average 3.4‰ enrichment of ^{15}N is reported for each trophic level (Minagawa and Wada, 1984; Post, 2002).

In an attempt to group soil predators, Walter et al. (1988) identified a number of representative guilds. Based on such analysis, we identified two subguilds, one including nematode-feeding mites such as the zerconid species *Parazercon radiatus, Skeironozercon tricavus* and the uropodine *Trachytes* sp., including its immature stage (deutonymphs), which has been previously identified as a specialized predator of nematodes (Walter, 1988; Martikainen and Huhta, 1990). Among the mites that have been found to be nematophages (i.e.; oligophagous predators), zerconid mites were seen to significantly decrease nematode populations, although *Trachytes* mites also had an intermediate impact on nematodes (Martikainen and Huhta, 1990). In general, *Trachytes* have been considered to be fungi/saprophytic feeders (Evans and Till, 1979; Athias-Binche, 1983), but our results support the laboratory experiments of Martikainen and Huhta (1990), who concluded that *Trachytes* mites were predators. Similarly, neither adults nor deutonymphs changed their stable isotope signatures showing that the prey spectrum does not change during ontogeny (Klarner et al., 2013). According to our results, it appears that small Zerconidae are more specialized and search for specific prey items (e.g., predatory nematodes), because their small size may be less restrictive to move in water- filled micropores, where nematodes live in, while the larger-sized zerconids may not move as easily. Furthermore, predators at the top of the food web present complex interactions such as

intraguild predations which may increase their $^{14}N/^{15}N$ ratios (Ponsard and Arditi, 2000).

The second identified subguild included the arthropod predators that prey on diverse taxa such as springtails, soft bodied mites, arthropod eggs and larvae (Lee, 1974; Walter et al., 1988); thus, these species may feed from more than a single trophic level. In this subguild was located *Gamasellus vibrissatus*, which is a pursuit mite of small prey as well as prey that may be larger than itself; this mite mainly feeds on the fluids of its prey (Walter et al., 1988). The same feeding behavior was noted by Lee (1974) in other species of genus *Gamasellus*. Lee (1974) also indicated that yeast and fungal spores can be part of their diet, as well as fungal spores (Evans and Till, 1979), but it is likely that this is only the case in a small amount.

In tropical ecosystems, Illig et al. (2005) reported several unspecified Uropodina as predators, and some of these showed the highest $\delta^{15}N$ values of the soil food web. Similarly, we found that uropodine species (e.g.; *Dinychus* sp.) had the highest $\delta^{15}N$ signatures that located them at the top of the predator guild. Unfortunately there are no records about feeding habits of *Dinychus* mites; however, they may be either generalist fluid feeders (feeding on slow moving prey, e.g., fly larvae, nematodes and soft mites) or microphagous/nematode feeders (feeding on e.g., unicellular algae, yeast, bacterial colonies and nematodes) as has been reported for other Uropodina (Athias-Binche, 1983; Athias-Binche, 1989; Martikainen and Huhta, 1990).

The $\delta^{15}N$ values in the predatory guild when compared to the detritivorous and omnivorous (overlapping with predators) guilds imply that ^{15}N enrichment increases as the concentration of nitrogen in the diet rises (Pearson et al., 2003). On high protein diet, excretion of nitrogen as waste is more possible due to the quality of the protein consumed (Pearson et al., 2003). Therefore, predator fluid feeders will directly influence nitrogen mineralization rates by excreting nitrogenous wastes. Calculations based on the food web model of Berg et al. (2001) estimated that predatory mites may contribute on average 25% of the total mineralization in forest floors. In general, animals retain ^{15}N and excrete ^{14}N (Minagawa and Wada, 1984). The ^{15}N enrichment may also be an indicator of intraguild predation and cannibalism, which could be widespread in the predatory guild; for instance, this has been reported for the top species in the food web of epigeic soil arthropods (Oelbermann and Scheu, 2010). In our study, the trophic positions of mesostigmatid and oribatid mites as defined from $\delta^{15}N$ analysis tended for the most part to corroborate the laboratory feeding experiments or observational feeding studies. Together, they provided insights into how detritious food webs are structured in boreal mixedwood forests.

4.4.3. Effect of harvesting on the trophic structure of mesostigmatan mites

Stable nitrogen isotope ratios provide a basis for evaluating changes in soil nitrogen processes following disturbance such as harvesting (Pardo et al., 2002). However, because spatial variation in forest floor $\delta^{15}N$ signatures is common, sometimes it is not possible to explain whether patterns are mostly derived from

the within-site variation or are due to harvesting. In addition, harvesting does not necessarily alter soil nitrogen processes (Jerabkova and Prescott, 2007). When there is measurable variation in harvested sites or in contrasting forest types in terms of their nitrogen isotopic values, we may expect to observe variation in the food webs of soil microarthropods. In our study, we observed very little variation in the $\delta^{15}N$ values of given species of oribatid or mesostigmatid mites across the two forest types and their managed stands (eight years after clearcut).

Food web studies that encompass several forest types have typically grouped all soil fauna in only one individual food web because species maintained their trophic position in spite of slight isotopic differences among the baselines from the distinct forest types (Schneider et al., 2004; Pollierer et al., 2009; Oelbermann and Scheu, 2010). Thus, isotopic nitrogen fractionation appears to be independent of habitat (Minagawa and Wada 1984). Particular mite taxa seem to feed on similar resources regardless of the forest habitat in which they live, and they may maintain their feeding habits by consuming alternative foods as demonstrated during feeding experiments. As a result, food resources are always coming from organisms with similar metabolic processes, hence similar $\delta^{15}N$ signature, resulting in the mites conserving their trophic position within the soil food web.

Harvesting disturbances in forested ecosystems may cause isotope changes that are shorter lived than in agro-ecosystems or other ecosystems where the shift in the native vegetation takes longer to recover (Darling and Bayne, 2010). Changes in $\delta^{15}N$ values along linear features such as pipelines compared to

undisturbed forests were not large enough to be useable as a reliable indicator of potential changes in the feeding habits of soil fauna (Darling and Bayne, 2010). However, it is necessary to better evaluate the trophic ecology of mesostigmatan mites in forest ecosystems where management is more intense. That information could help to test whether intense forest management can affect the structure of food webs. In this respect, clearcuting has been shown to modify the abundances of forest floor mites (Lindo and Visser, 2004) and prescribed burning after clearcuting changed their community composition and species richness (Déchêne and Buddle, 2009). It is therefore crucial to obtain a better understanding of the processes that occur in such instances, and especially to determine why such processes do not generate changes in isotope fractionation of the same order such as those observed in the mite community structure.

4.5. Conclusions

In this study, we used natural $\delta^{15}N$ values of mesostigmatan mites to assess their trophic status. In addition, feeding habits as reported in the literature were used to corroborate the mite trophic positions. Differences in $\delta^{15}N$ values separated the mesostigmatid and oribatid mites in three main trophic guilds: detritivores, omnivores (overlapping with predators) and predators. Each trophic guild was further subdivided into two subguilds based on feeding relationships. The saprophagous/xylophagous and mycophagous subguilds of the detritivorous mites were mostly composed of oribatid mites. Omnivorous (overlapping with predators) mites were differentiated into fungivorous/nematode feeders and

microarthropod feeders, while predators were separated based on whether they fed (hypothetically) on nematodes or arthropods.

Since no significant variation in ^{15}N values was observed among the different stands studied, it can be concluded that the trophic structure of the mesostigmatan mites present at EMEND was not strongly modified by either clear-cutting or forest type. Hence, our most important result was that the trophic position of these forest floor mites stayed constant regardless of their habitat. Indeed, we can conclude that the well-defined degree of isotopic fractionation within the mite food web may be only dependent on their feeding relationships because the degree of isotopic enrichment (or depletion) of predators reflects their diet.

4.6. References

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Table 4.1. Species of mesostigmatan and oribatid mites studied showing the mean (± SD) of their $\delta^{15}N$ values, including the mites of the same species for all treatments, and their feeding habits as reported in the literature.

Sp. code	Species	$\delta^{15}N$ (‰)	Feeding habits
O1	*Phthiracarus boresetosus*	$0.32(\pm0.43)_3$	Coniferous needles from the inside (Jacot, 1939)
O5	*Eremaeus* sp.	1.06	Mycelium of pigmented fungus (Mitchell and Parkinson, 1976)
O2	*Propelops* nr. *alaskensis*	$1.25(\pm0.29)_3$	Fungal hyphae and spores (Walter et al., 2011)
O3	*Scheloribates pallidulus*	2.66	Fungal hyphae, spores and nematodes (Muraoka and Ishibashi, 1976; Walter et al., 2011)
O4	*Pilogalumna* sp.	2.67	Fungal hyphae, moss spores and nematodes (Walter, 1988; Walter et al., 2011)
Z2	*Zercon alaskaensis*	$4.00(\pm0.59)_3$	Oligophagous predator (Evans and Till, 1979)
Sp9	*Zerconopsis* sp.	$4.93(\pm0.63)_3$	Predator of nematodes (Walter and Lindquist, 1995)
S	*Sejus* sp.	$5.52(\pm0.55)_3$	Predators of small invertebrates and worms (Walter and Proctor, 1998)
O7	*Ceratozetes* sp.	6.61	Fungivorous and predaceous (Mitchell and Parkinson, 1976; Muraoka and Ishibashi, 1976)
Sp25	*Veigaia kochi*	$6.84(\pm1.26)_8$	Predator of collembolans, proturans, pauropods and soft mites (Hurlbutt, 1968)
O6	*Epidamaeus* sp.	7.25	Fungal hyphae and remains of organic matter (Walter et al., 2011), and predaceous (Illig et al., 2005)
Z5	*Parazercon radiatus*	$8.39(\pm1.34)_9$	Oligophagous predator of nematodes (Martikainen and Huhta, 1990)
Sp4	*Gamasellus vibrissatus*	$8.53(\pm0.85)_{11}$	Predator of springtails, soft bodied mites, arthropod eggs and larvae (Lee, 1974)
U1	*Trachytes* sp. (Dn)†	$8.84(\pm1.21)_{13}$	
U1	*Trachytes* sp.	$9.05(\pm0.98)_5$	Fungivorous and saprophagous (Athias-Binche, 1983), and predators of soft-bodied invertebrates (Walter and Latonas, 2011)
Z1	*Skeironozercon tricavus*	$9.70(\pm0.88)_8$	Oligophagous predator of nematodes (Walter, 1988)
U7	*Dinychus* sp.	$10.11(\pm0.34)_5$	Detritivorous and certain Uropodina are predators (Athias-Binche, 1983)

† Immature stadia (Dn: deutonymph).
Small numbers after the (±SD) indicate the number of samples.
Number of analyzed samples=79.

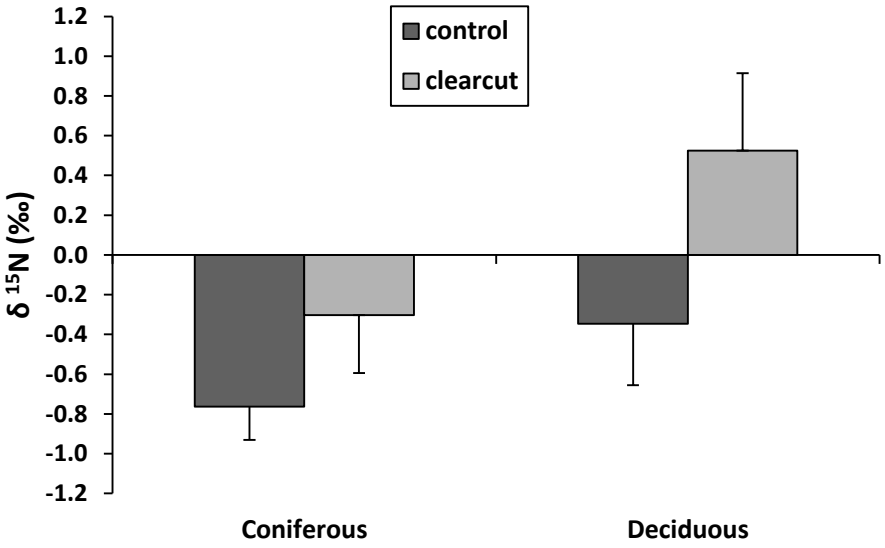

Figure 4.1. Mean $\delta^{15}N$ values (± SE) of baseline (forest floor) of control (100% retention), and clearcut (2% retention) from stands dominated by white spruce and stands dominated by aspen in the northwestern boreal mixedwood forests of Alberta.
Note: number of repetitions (n=3).

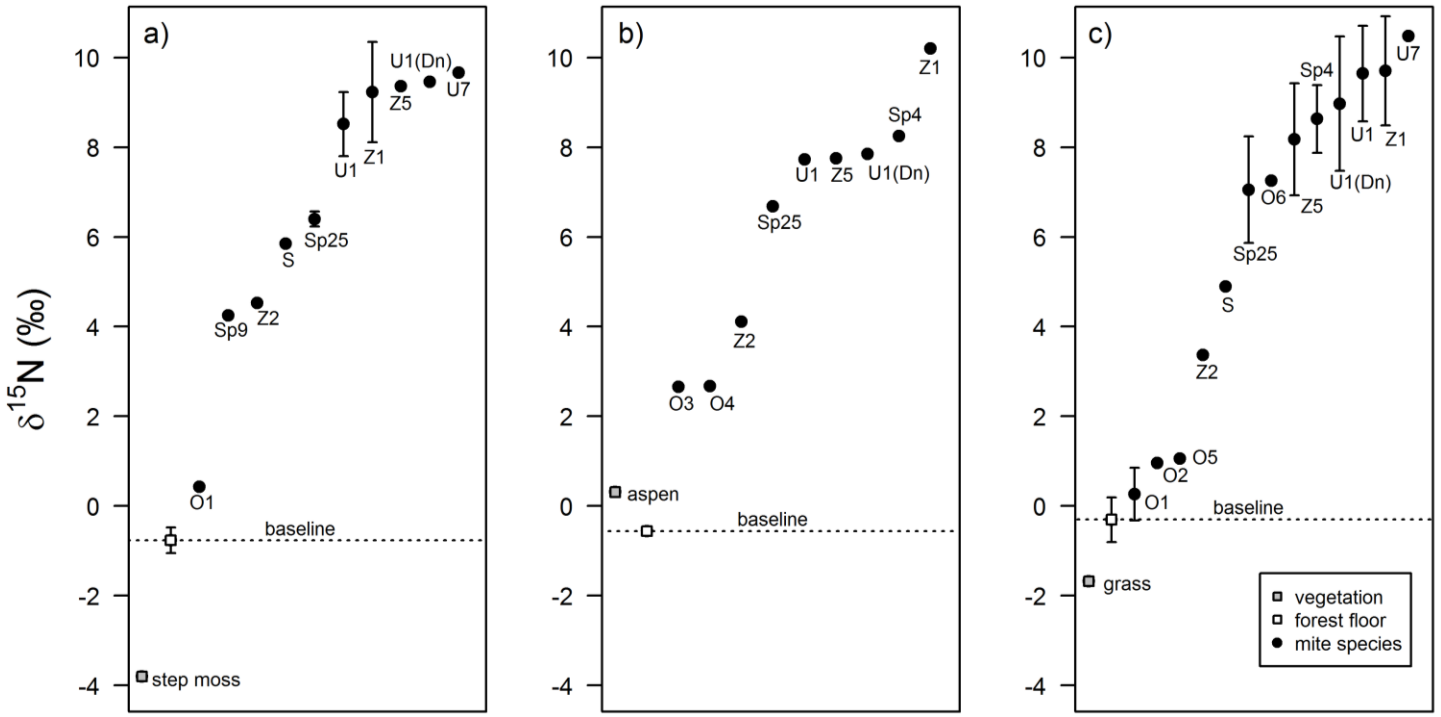

Figure 4.2. Mean $\delta^{15}N$ values (± SD) of baseline (forest floor), plant material, mesostigmatid and oribatid mites of the treatments: **a**) control (100% retention), **b**) 20% retention, and **c**) clearcut (2% retention) in coniferous-dominated stands.

Oribatid mites: $O1_{(1,0,2)}$ *Phthiracarus boresetosus*, O2 *Propelops* nr. *alaskensis*, O3 *Scheloribates pallidulus*, O4 *Pilogalumna* sp., O5 *Eremaeus* sp., O6 *Epidamaeus* sp.
Mesostigmatid mites: $Z1_{(2,1,2)}$ *Skeironozercon tricavus*, $Z2_{(1,1,1)}$ *Zercon alaskaensis*, $Z5_{(1,1,4)}$ *Parazercon radiatus*, $Sp4_{(0,1,4)}$ *Gamasellus vibrissatus*, $Sp9_{(0,0,1)}$ *Zerconopsis* sp., $Sp25_{(2,1,2)}$ *Veigaia* cf. *kochi*, $S_{(1,0,1)}$ *Sejus* sp., $U1_{(2,1,6)}$ *Trachytes* sp., $U1(Dn)_{(1,1,3)}$ *Trachytes* sp., $U7_{(1,0,1)}$ *Dinychus* sp.
Note: Single measurements are represented by dots with no standard deviation.
The number of repetitions per treatment is indicated in parenthesis.

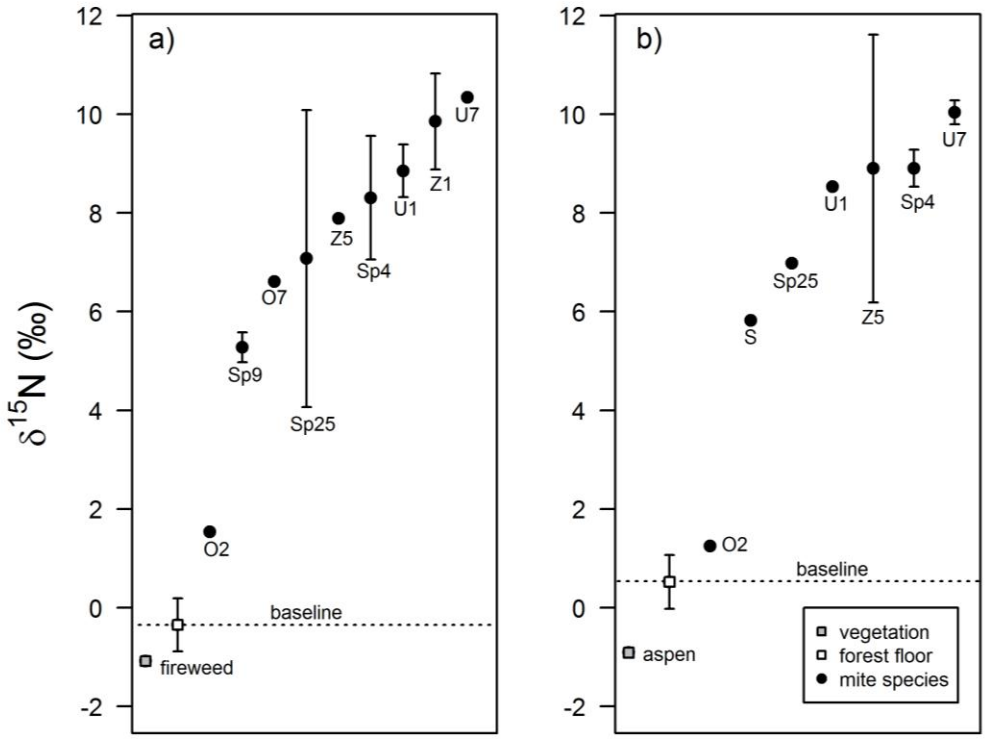

Figure 4.3. Mean $\delta^{15}N$ values (± SD) of baseline (forest floor), plant material, mesostigmatid and oribatid mites of the treatments: **a**) control (100% retention), and **b**) clearcut (2% retention) in deciduous-dominated stands.

Oribatid mites: $O2_{(1,1)}$ *Propelops* nr. *alaskensis*, O7 *Ceratozetes* sp.
Mesostigmatid mites: $Z1_{(3,0)}$ *Skeironozercon tricavus*, $Z5_{(1,2)}$ *Parazercon radiatus*, $Sp4_{(4,2)}$ *Gamasellus vibrissatus*, $Sp9_{(2,0)}$ *Zerconopsis* sp., $Sp25_{(2,1)}$ *Veigaia* cf. *kochi*, $S_{(0,1)}$ *Sejus* sp., $U1_{(3,1)}$ *Trachytes* sp., $U7_{(1,2)}$ *Dinychus* sp.
Note: Single measurements are represented by dots with no standard deviation.
The number of repetitions per treatment is indicated in parenthesis.

CHAPTER 5

General conclusions

5.1. Overview

This dissertation consists of chapters addressing the taxonomy and ecology of mesostigmatan mites that inhabit the forest floor of boreal mixedwood forests in northwestern Alberta. I provide information about mesostigmatan mites that creates a basis for understanding these predator mites in their native habitats. The information generated in this research contains points of ecological importance about forest floor mesofauna such as predator mites which should be taken into account in considering ecological impacts resulting from anthropogenic disturbances. This information is also valuable for meeting biodiversity conservation goals established for sustainable forest management.

5.2. Systematics of zerconid mites

Zerconid mites are important components of the soil fauna of northern forests (Halašková, 1977). I found a significant number of zerconid mites of the genus *Mixozercon* (Halašková, 1963) in my study area. However, their identification presented considerable difficulties due mainly to large variation in the morphospecies relevant to this genus, but eventually led to the discovery of new species. Prior to my research, only three species had been placed in this

genus worldwide: *Mixozercon sellnicki* Halašková, 1963, *Mixozercon stellifer* Aoki, 1964 and *Mixozercon heterosetosus* Balan, 1995. The three new species described in chapter two, then, double the number of *Mixozercon* species known and their discovery is significant for understanding biodiversity in Alberta. I named these species, respectively, as *Mixozercon albertaensis*, *Mixozercon jasoniana*, and *Mixozercon borealis*. The descriptions found in this chapter were based on the analysis of 267 individuals, including immature stages (deutonymphs, protonymphs and larvae). I included a map indicating the distribution of *Mixozercon* species in other counties and in Canada (Figure 5.1). Furthermore, in the EMEND study area, I determined that *M.* albertaensis was the most abundant species found mainly in deciduous stands and *M. borealis* was the least abundant species found in the mixed and coniferous stands. *M. jasoniana* presented intermediate abundances and preferred deciduous and mixed forests over coniferous stands.

Evidence from the literature suggests that *Mixozercon* mites can be abundant in northern forests. For example, one species of this genus (*Mixozercon sellnicki*) is widely distributed in the Palaearctic region in Central and North Europe [e.g., Sweden, Germany, Latvia, Poland, Slovakia, Romania, Switzerland, (Halašková, 1963; Athias-Henriot, 1980) and the Pinega reserve in Russia (Makarova, 2011)]. Additionally, this species is not limited to the European continent and has been found in Iceland (Athias-Henriot, 1980). Until now, the other two species of *Mixozercon* have only been reported locally, e.g. *M. stellifer* in Mt. Hirugatake in Tanzawa Mountains, Japan (Aoki, 1964), and *M.*

heterosetosus in the Steppe zone of Ukraine (Balan, 1995). The full distributions of *Mixozercon albertaensis*, *Mixozercon jasoniana* and *Mixozercon borealis* (Díaz-Aguilar and Ujvári, 2010) are presently unknown. However, in light of present knowledge northwestern boreal mixedwood forests of Alberta, Canada possess the highest *Mixozercon* diversity and so this matter deserves further study that I hope will be stimulated by my work.

The wide distribution of *Mixozercon sellnicki* suggests that it is a cosmopolitan species; however, it would be incorrect to say that the other species are endemic because it is possible that they are distributed in other areas of the Holarctic region at high latitudes. Currently, there is no published information on the distribution of *Mixozercon* species in the Nearctic region. I visited the Canadian National Collection of Insects, Arachnids and Nematodes (CNC), at the Department of Agriculture and Agri-Food Canada in Ottawa, Canada to examine their collection of Zerconidae. I found *Mixozercon* species distribution spread south to the Cypress Hills Provintial Park, Saskatchewan in spruce-poplar litter as well as to U.S. forests in mosses (i.e., Lake Wenatchee, Washington and Proxy Falls Deschutes County, Oregon) indicating that their distribution range is wider than previously thought. Also, I noted that *Mixozercon borealis* was the species that I most frequently observed among the species of the collection; indicating that *Mixozercon* may be more diverse in northwestern boreal mixedwood forest in Canada than elsewhere. These considerations require further studies based on the examination of zerconid mites in North America.

5.3. Influence of stand type on mesostigmatan assemblages

An important aspect of this dissertation was documenting the interaction between the stand dynamics occuring within boreal forests and the structural patterns in the natural communities of predatory mites (Mesostigmata). The forest mosaic present in the EMEND experimental area includes the main successional patterns of the boreal mixedwoods (Lieffers et al., 1996), making it an ideal setting to address the objectives of Chapter 3. There is a shift in dominant tree species during succession from deciduous to mixed to coniferous that affects forest floor characteristics and, thus, tree species may have an effect on forest floor-microarthropod comunities. The different stand types in this study were essential for testing hypotheses about tree species interactions with mesostigmatan assemblages.

Forest floor litter found in aspen-dominated forests is composed mostly of aspen leaves and this does not accumulate in large quantities due to rapid decomposition (Hannam et al., 2006; Jerabkova et al., 2006). In contrast, forests dominated by spruce have forest floors with thick organic layers below the moss-covered surface, while the intermediate stages of mixedwood stands are differentiated by forest floors with intermediate thicknesses (Hannam et al., 2006; Jerabkova et al., 2006). Hence, differences in litter production and decomposition directly influence the formation of microhabitats and environmental characteristics within the organic horizons of boreal forest soils. These habitats differ among seral stages (or stand types) and were reflected in the distinct

assemblages of mesostigmatan mites, similarly to that observed with oribatid mites in temperate forests from southwestern Quebec (Sylvain and Buddle, 2010).

The variation that I observed in the mesostigmatan assemblages from the EMEND successional sequence suggests that forest management practices should maintain natural ranges of variation across the landscape. I documented that coniferous stands contained greater species richness and harbored mite assemblages that differed in composition from deciduous stands. This led me to conclude that late successional stage forests host species that are not seen in early seral stages. Furthermore, the data presented in this chapter showed that mesostigmatan assemblages follow the same patterns seen in the communities of bryophytes (Caners, 2010), which is probably related to the close association between the moss layer and mesostigmatan diversity (Salmane and Brumelis, 2008). Similarly, epigaeic arthropods, such as carabid beetles, which are associated with mosses, forbs, and coarse woody materials present a distinct community composition within the coniferous stands compared to the deciduous stands (Work et al., 2004, 2010).

The identification of ecological generalizations begins with a search for repeated patterns in nature and focuses on defining the processes that produce these patterns. My results indicate that the forest floor structure in coniferous stands affects the patterns of diversity and assemblages of species found there. Thus, species typical of older stands in particular should be considered in forest management to ensure the conservation of their biodiversity. On the other hand, mesostigmatan assemblages in deciduous forest floors differed from and were less

diverse than those of mixed and coniferous stands. From this I can conclude that: 1) mesostigmatan assemblages have evolved together in a recognizable pattern with the boreal forest succession resulting from natural disturbances and 2) that the diversity of mesostigmatan mites in the mixedwood reaches its maximum in old coniferous forests.

5.4. Trophic ecology using nitrogen stable isotopes

In general, the food web structure of soil fauna is poorly understood. This is even truer for the mites of the order Mesostigmata. Stable isotope analysis using nitrogen isotopes ($^{15}N/^{14}N$) is an important tool for studying tropic positions, reconstructing diets, describing trophic relations and building food webs (Minagawa and Wada, 1984; Peterson and Fry, 1987; Post, 2002; Sulzman, 2007; Boecklen et al., 2011). Additionally, stable isotope analysis provides a standardized metric for comparing among the trophic positions in different habitats. Organisms display particularly strong isotopic signals because they accumulate the heavier stable nitrogen isotope, ^{15}N, in their bodies (Fry, 2006). The extra neutron present in ^{15}N results in stronger covalent bonds which may cause slower reaction rates compared to ^{14}N. These results in isotopic fractionation and this can be used to determine trophic relationships between predator and prey, as each level will have a distinct isotopic signature (Fry, 2006; Sulzman, 2007).

In Chapter 4 of my dissertation I describe the trophic relationships of the most abundant mesostigmatan species observed in the EMEND control (100%

retention) and clearcut (2% retention) deciduous and coniferous stands. I used the natural ^{15}N abundances in mesostigmatan mites with the aim of unraveling their trophic ecology. The isotope ratios were also used to confirm or reject results from studies that reconstructed diets through feeding experiments. My isotopic results spanned three functionally different trophic guilds, including detritivores (Oribatida only), omnivores overlapping with predators, and predators. Each guild was further divided into different subguilds based on similar feeding preferences of different species.

The trophic guilds highlighted by the stable isotope ratios support the results from other published research that examined diet and prey preferences of similar mesostigmatan species (Lee, 1974; Walter, 1988; Walter et al., 1988; Martikainen and Huhta, 1990; Beaulieu and Walter, 2007). The trophic position within a forest type did not change in response to clearcut or stand type. In most circumstances, clear-cutting is not an appropriate strategy for maintaining ecological parameters (Niemelä, et al., 1993; Hannam et al., 2005; Rosenvald and Lõhmus, 2008). However, feeding relationships studied at EMEND did not seem to be impacted by harvesting as has been observed in species diversity i.e., abundance patterns (Lindo and Visser, 2004) or species composition (Déchêne and Buddle, 2009). The stable isotope ratios of the oribatid and mesostigmatid mites were a useful tool in successfully placing the mites within their corresponding trophic guilds, and demonstrating that $\delta^{15}N$ values did not reflect any changes in the predatory-prey relationships. These results can be relevant for

the short -term responses to harvesting in this case 8 years after clear-cutting; however, long-term impacts may vary.

Stable isotope ratios of predator mites at the higher trophic positions may also reflect their importance on nitrogen mineralization fluxes (Berg et al., 2001). Species within the top trophic positions have diets high in protein, as indicated by a high ^{15}N-enrichment, as light nitrogen is mainly excreted as waste (Peterson and Fry, 1987). As documented in the literature, organisms that have satisfied their protein requirements for tissue maintenance and energy needs (Chapman, 1988) excrete nitrogen containing-compounds such as ammonia and uric acid as wastes (Pant, 1988). Through this action, predatory mites play a central role in the mineralization of nitrogen in forest ecosystems.Calculations based on the food web model of Berg et al. (2001) estimated that predatory mites may contribute in average 25.3% of the total mineralization in the LFH horizons.

5.5. Future research

Over the years of doing my thesis research I have produced considerable information about mesostigmatan mites in northwestern boreal mixedwood forests from Alberta. The natural stands I studied allowed me to investigate the ecology of forest floor mesostigmatan mites during the boreal forest successional process. However, generalizations about community patterns must remain tentative. Further efforts are necessary to understand how diversity and community composition are affected by wildfire (Déchêne and Buddle, 2009). Additionally, many questions remain unanswered about the effects of variable retention

harvesting (Work et al., 2010; Pinzon et al., 2012) as well as about the effects of mosses and bryophytes on mesostigmatan biodiversity (Salmane and Brumelis, 2008; Caners et al., 2010).

Although I was able to report 46 morphospecies, only 17 of them were identified at the species level and many species could not be named because they are new to science (e.g., all the Uropodina). In Canada, the number of described mesostigmatid species is much lower than for Europe. This indicates that ecological studies in Canada are impeded by a lack of sufficient taxonomy. In spite of a wealth of taxonomic knowledge available in Europe, comprehensive taxonomic information is required for Canadian mesostigmatan mites as there are not many shared species between the two continents.

Stable isotope analysis is a powerful tool in soil ecology (Peterson and Fry, 1987; Gannes et al., 1997) and holds considerable promise as an indicator of feeding relationships and trophic positions in the food webs of mesostigmatan mites. However, a lack of sufficient experimental and theoretical studies of analytical procedures can hamper the interpretation of stable isotope ratios. In my study, I found that differences in size and abundance of the mites led to variations in their respective sample sizes. The use of small samples is a requirement for building the entire food web including all the species in the study area (e.g., tiny and less abundant mites) which can present difficulty in the measurements of $^{15}N/^{14}N$ ratios. Working with small sample sizes requires documenting the effectiveness of stable isotope analysis in the low permissible levels to achieve linearity within the detection window (communication from G.G. Hatch Stable

Isotope Laboratory, Ottawa). Furthermore, the relationships between body size and trophic position could be useful to investigate as they have been shown to be important in aquatic food webs, with little information available for soil food webs (Klarner et al., 2013).

Additional research regarding trophic positions and feeding behavior of mesostigmatan mites could be undertaken using fatty acid analysis since that neutral lipid fatty acid composition is directly influenced by diet, with storage lipids related to nutritional needs (Chamberlain et al., 2004; Chamberlain and Black, 2005; Chamberlain et al., 2005; Haubert et al., 2004). Finally, molecular analysis could be used to identify specific predator–prey links (Sheppard and Harwood, 2005; Heidemann et al., 2011) and to recognize the prey and predator relationships implicated within the trophic guilds and subguilds.

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Figure 5.1. Geographical distribution of species of the genus *Mixorzercon*.

APPENDIX

APPENDIX A1

Table A.1. Relative abundances of mesotigmatan mites from the forest floor in three naturally disturbed stands: deciduous, mixed and coniferous, at the northwestern boreal mixedwood forest of Alberta.

Sp. code	Family	Genus	Species	Deciduous	Mixed	Coniferous
	Suborder Sejida					
Sejus	Sejidae	*Sejus*	sp.	0.66(0.5)	0.29 (0.1)	0.0 (0.0)
	Suborder Monogynaspida Cohort Uropodina Subcohort Uropodiae					
Diny1	Dinychidae	*Dinychus*	sp.1	0.04(004)	0.0 (0.0)	3.70(3.7)
Diny2		*Dinychus*	sp.2	0.0 (0.0)	0.0 (0.0)	3.39(2.1)
Diny3		*Dinychus*	sp.3	0.0 (0.0)	0.0 (0.0)	0.50(0.5)
Diny4		*Dinychus*	sp.4	0.0 (0.0)	0.08(0.1)	4.01(2.1)
Iphidi	Dithinozerconidae	*Iphidinychus*	sp.	0.0 (0.0)	0.0 (0.0)	0.40(0.4)
Trachy	Trachytidae	*Trachytes*	sp.	3.44(1.1)	3.73(1.5)	8.52(3.0)
Uroobo	Urodinychidae	*Uroobovella*	sp.	0.44(0.4)	0.0 (0.0)	0.0 (0.0)
	Cohort Gamasina Subcohort Epicriiae					
Boreo	Zerconidae	*Boreozercon*	*emendi* (Díaz & Ujvári, 2010)	0.0 (0.0)	0.05(0.05)	3.07(1.6)
Malber		*Mixozercon*	*albertaensis* (Díaz & Ujvári, 2010)	5.03(1.9)	2.87(1.0)	2.60(2.3)
Mboreal		*Mixozercon*	*borealis* (Díaz & Ujvári, 2010)	0.66(0.4)	2.63(1.6)	1.22(0.8)
Mjason		*Mixozercon*	*jasoniana* (Díaz & Ujvári, 2010)	2.93(2.8)	3.62(2.6)	0.40(0.4)
Para		*Parazercon*	*radiatus* (Berlese, 1910)	8.18(1.9)	4.59(1.4)	13.15(4.1)
Skeiro		*Skeironozercon*	*tricavus* (Błaszak, 1982)	26.01(7.1)	29.63(4.9)	31.30(8.2)
Zalask		*Zercon*	*alaskaensis* (Sellnick,1958)	4.79(2.7)	2.83(1.1)	3.30(1.0)
Zcolumb		*Zercon*	*columbianus* (Berlese, 1910)	0.0 (0.0)	0.0 (0.0)	0.58(0.3)
Zmichae		*Zercon*	*michaeli* (Halašková, 1977)	0.0 (0.0)	0.0 (0.0)	0.32(0.3)
Copro	Coprozerconidae	nr.*Coprozercon*	sp.	0.83(0.5)	1.79(0.7)	2.41(0.8)

Continuation Table A.1

Sp. code	Family	Genus	Species	Deciduous	Mixed	Coniferous
	Subcohort Dermanyssiae					
Epicri	Ameroseiidae	*Epicriopsis*	sp.	0.0 (0.0)	0.07(0.1)	0.14(0.1)
Amero		*Ameroseius*	nr. *mariehigginsae*	0.0 (0.0)	0.07(0.1)	0.0 (0.0)
Arctocet	Ascidae	*Arctoseius*	cetratus (Sellnick, 1940)	1.80(1.0)	4.80(1.9)	2.22(1.9)
Arctosem		*Arctoseius*	semiscissus (Berlese, 1892)	1.22(0.6)	3.04(1.0)	2.59(0.8)
Arcto1		*Arctoseius*	sp.1	1.89(1.2)	1.13(0.6)	1.18(0.4)
Arcto2		*Arctoseius*	sp.2	2.25(0.6)	0.95(0.4)	2.24(0.8)
Arcto3		*Arctoseius*	sp.3	1.07(1.0)	0.56(0.3)	2.64(1.8)
Arcto4		*Arctoseius*	sp.4	0.0 (0.0)	0.61(0.6)	0.10(0.1)
Arcto5		*Arctoseius*	sp.5	0.39(0.4)	0.07(0.1)	0.32(0.3)
Asca		*Asca*	*garmani* (Hurlbutt, 1963)	6.62(1.7)	4.39(1.8)	4.33(1.7)
Iphido		*Iphidozercon*	sp.	0.0 (0.0)	0.0 (0.0)	0.14(0.1)
Zercono1		*Zerconopsis*	sp.1	0.72(0.5)	0.24(0.1)	0.32(0.2)
Zercono2		*Zerconopsis*	sp.2	0.15(0.1)	0.0 (0.0)	0.0 (0.0)
Dendro1	Digamasellidae	*Dendrolaelaps*	sp.1	11.77(4.4)	13.32(5.9)	0.0 (0.0)
Dendro2		*Dendrolaelaps*	sp.2	0.19(0.2)	3.10(1.3)	2.10(1.8)
Dendro3		*Dendrolaelaps*	sp.3	1.69(1.4)	3.30(2.5)	0.07(0.1)
Dendro4		*Dendrolaelaps*	sp.4	0.06(0.1)	0.0 (0.0)	0.0 (0.0)
Dendro5		*Dendrolaelaps*	sp.5	0.0 (0.0)	3.04(2.5)	1.85(1.9)
Haemo	Haemogamasidae	*Haemogamasus*	*pontiger* (Berlese, 1904)	0.0 (0.0)	0.35(0.3)	0.0 (0.0)
Hypo	Laelapidae	*Hypoaspis*	nr. *giffordi*	0.0 (0.0)	0.35(0.3)	0.0 (0.0)
Procto1	Melicharidae	*Proctolaelaps*	sp.1	0.0 (0.0)	0.39(0.3)	0.65(0.4)
Procto2		*Proctolaelaps*	sp.2	0.0 (0.0)	0.69(0.5)	0.0 (0.0)
Procto3		*Proctolaelaps*	sp.3	0.19(0.2)	0.76(0.5)	0.0 (0.0)
Procto4		*Proctolaelaps*	sp.4	0.0 (0.0)	0.24(0.2)	0.07(0.1)
Zygo	Pachylaelapidae	*Zygoseius*	*furciger* (Berlese, 1916)	0.07(0.1)	0.0 (0.0)	0.0 (0.0)
Ambly	Phytoseiidae	*Amblyseius*	*krantzi* (Chant, 1959)	0.11(0.1)	0.20(0.1)	0.0 (0.0)
Typhlo		*Typhlodromips*	*ojibwa* (Chant & Hansell, 1971)	0.0 (0.0)	0.07(0.1)	0.0 (0.0)
Gama	Rhodacaridae	*Gamasellus*	*vibrissatus* (Emberson, 1967)	16.79(3.2)	6.15(2.4)	0.17(0.2)
Total†	**16**	**25**	**46**	**28**	**35**	**33**

Note: relative abundances values are means (n = 9) and standard error given in parentheses.
† Total number of families, genera or species recorded.

Appendix A2

Views of the places where the forest floor samples were collected.

Coniferous-dominated stand by white spruce (*Picea glauca*)

Horizons of the forest floor from a sample in a coniferous stand

Deciduous-dominated stand by aspen (*Populus tremuloides*)

Horizons of the forest floor from a sample in a deciduous stand

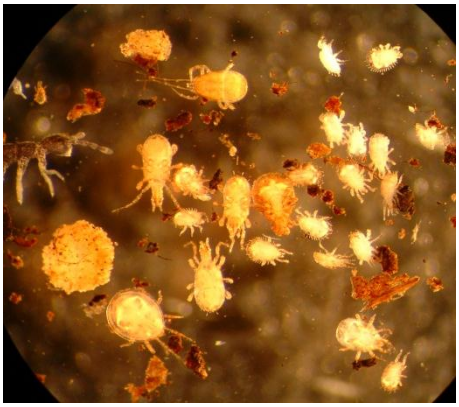
Note: L (litter), F (fermentation), and H (humified) horizons.

Appendix A3

Extraction of mites from the forest floor using the Tullgren method.

Forest floor microarthropods collected into 70% ethanol

Sample of forest floor

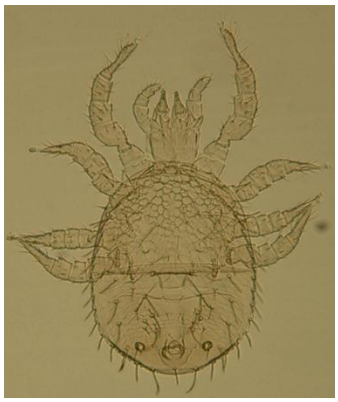


View of mesostigmatan mites from an extracted sample

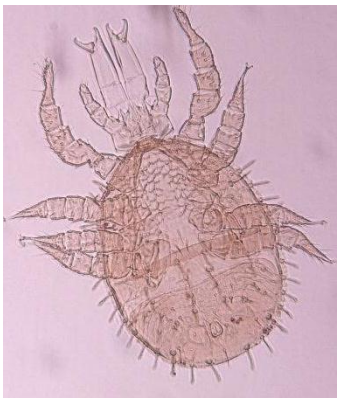
Appendix A4

Mesostigmatan species and morphospecies found in the forest floor of boreal mixedwood forests in northwestern Alberta.

Zerconidae



Skeironozercon tricavus



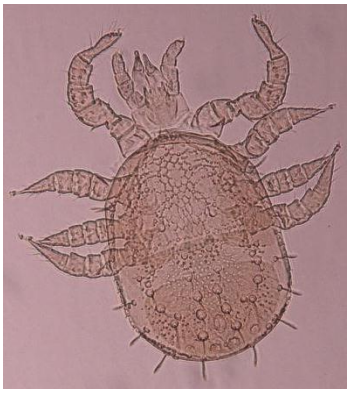
Parazercon radiatus

Zercon alaskaensis

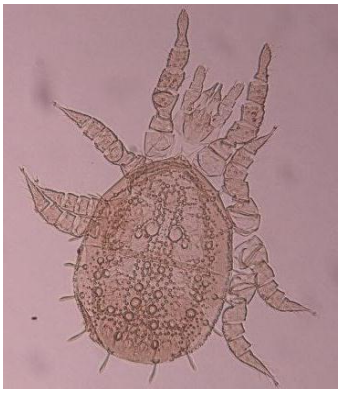
Zercon michaeli

Zercon columbianus

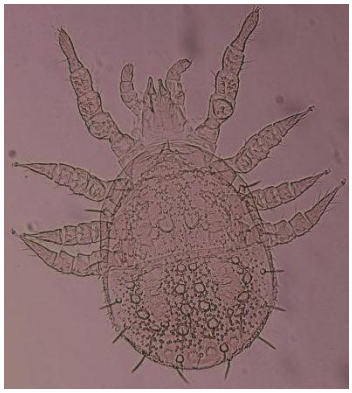
Boreozercon emendi



Mixozercon albertaensis



Mixozercon jasoniana



Mixozercon borealis

Note: Pink mites were dyed with Rose Bengal.

Ascidae

Arctoseius cetratus

Arctoseius semiscissus

***Arctoseius* sp1**

***Arctoseius* sp3**

***Arctoseius* sp4**

***Arctoseius* sp5**

Asca garmani

***Zerconopsis* sp1**

***Iphidozercon* sp.**

Note: Pink mites were dyed with Rose Bengal.

Digamasellidae, Haemogamasidae and Laelapidae

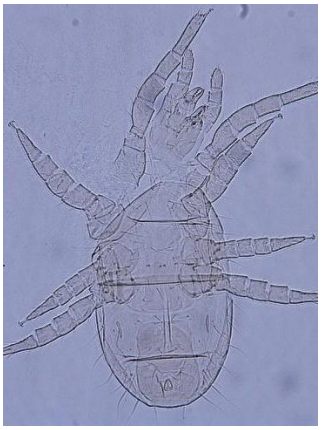
***Dendrolaelaps* sp1 (deutonymph)**

***Dendrolaelaps* sp2**

***Dendrolaelaps* sp2 (♂)**

***Dendrolaelaps* sp3**

***Dendrolaelaps* sp4 (♂)**



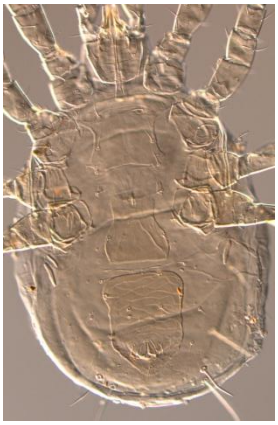
***Dendrolaelaps* sp5**

Haemogamasus pontiger

Hypoaspis* nr. *giffordi

Note: Pink mites were dyed with Rose Bengal.

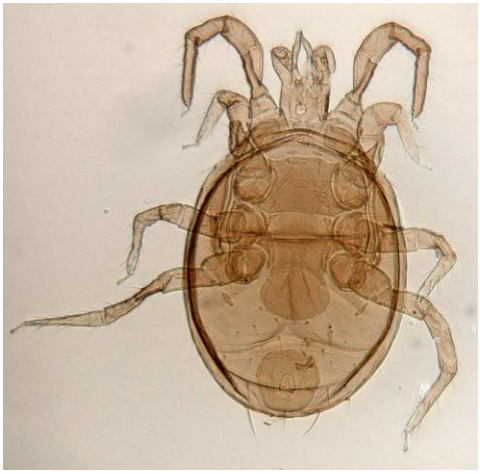
Phytoseiidae, Pachylaelapidae and Melicharidae



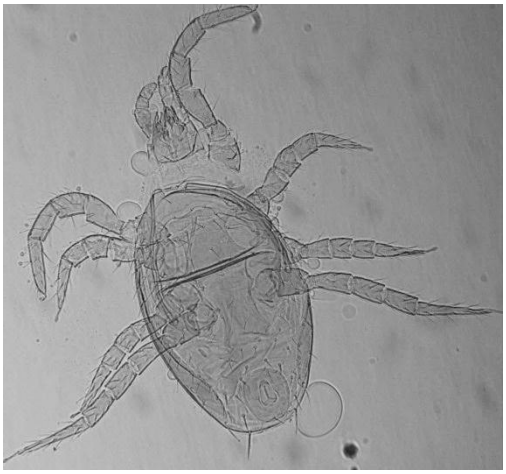
Typhlodromips ojibwa

Amblyseius krantzi

Zygoseius furciger



***Proctolaelaps* sp1**



***Proctolaelaps* sp2**

***Proctolaelaps* sp3**

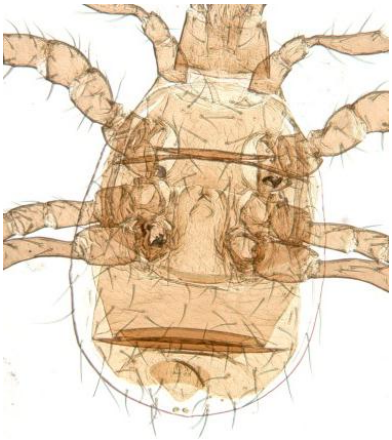
***Proctolaelaps* sp4**

Rhodacaridae, Ameroseiidae, Veigaiidae and Sejidae

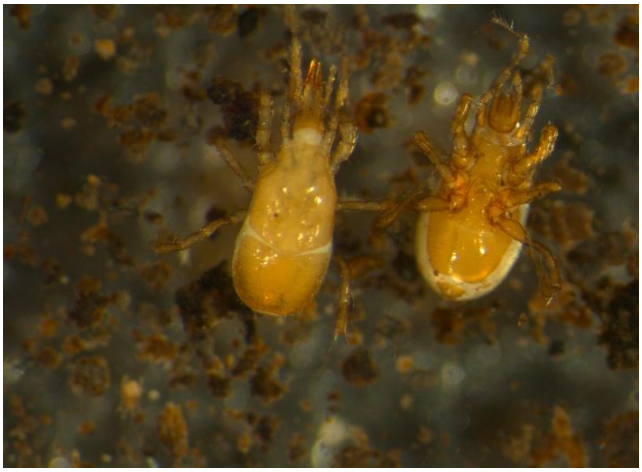
Gamasellus vibrissatus

***Epicriopsis* sp.**

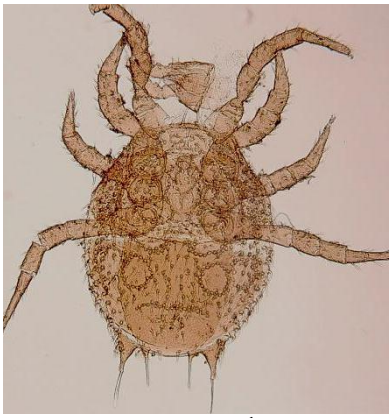
Ameroseius* nr. *mariehigginsae



Veigaia kochi

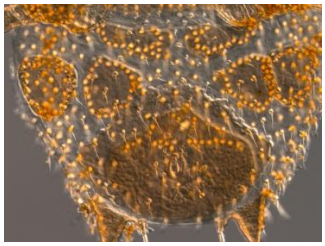


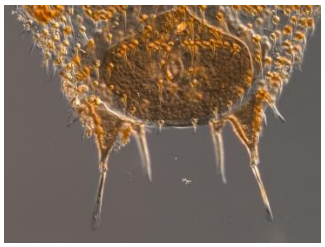
Veigaia kochi



***Sejus* sp. (♂)**

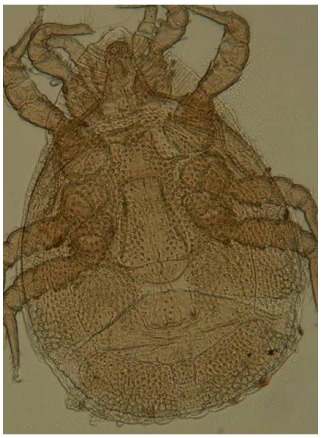
***Sejus* sp.**





Note: Pink mites were dyed with Rose Bengal.

Uropodinas



***Trachytes* sp.**

***Trachytes* sp. (deutonymph)**

***Trachytes* sp. (larva)**

***Iphidinychus* sp.**

***Dinychus* sp3**

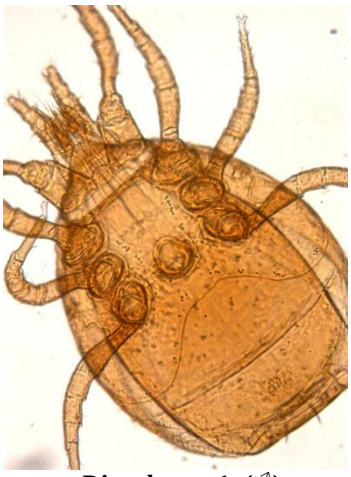
***Dinychus* sp4 (♂)**

***Uroobovella* sp. (♀)**

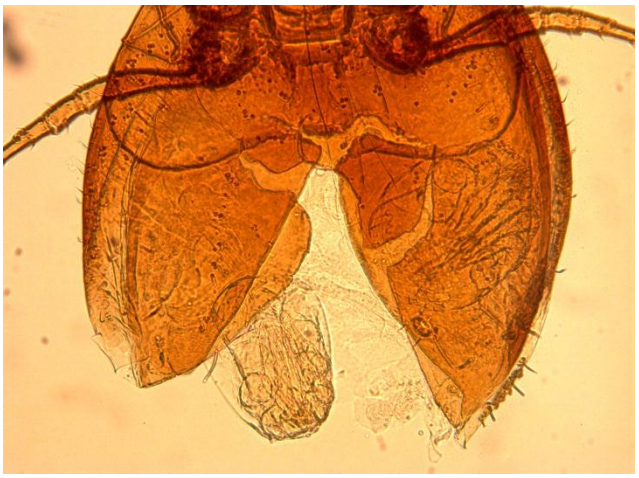
***Uroobovella* sp. (♂)**

***Uroobovella* sp. (deutonymph)**

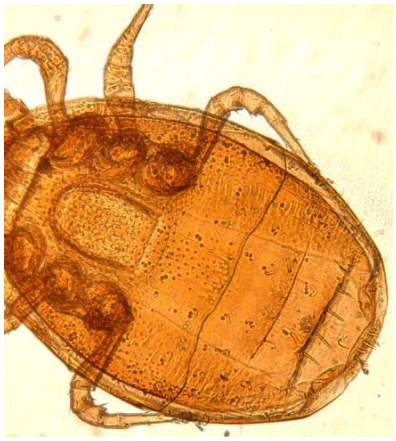
Uropodinas



***Dinychus* sp1 (♂)**



***Dinychus* sp1 eggs**



***Dinychus* sp2**

***Dinychus* (protonymph)**

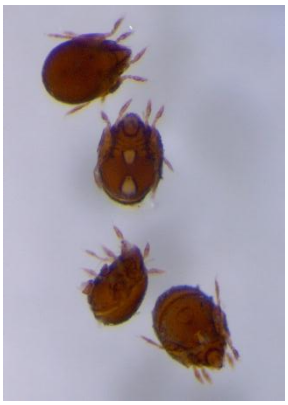
***Dinychus* (larva)**

Appendix A5

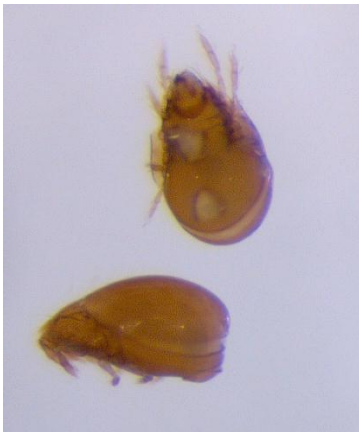
Oribatid mites analyzed with the stable isotope ^{15}N.

Phthiracarus boresetosus

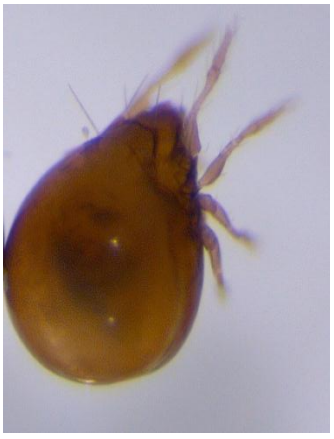
Eremaeus sp.



Propelops* nr. *alaskensis



Scheloribates pallidulus



***Pilogalumna* sp.**

***Ceratozetes* sp.**

Epidamaeus sp.

Oribatid mites feeding on an dead millipede larva