

# Arthropods of Canadian Grasslands

Volume 3:  
*Biodiversity and  
Systematics*  
Part 1



Edited by  
**Héctor A. Cárcamo and Donna J. Giberson**



Biological Survey of Canada  
Commission biologique du Canada



1. Fraser River at Chilcotin R. junction, BC (Photo: Robert Cannings); 2. Valley slope grassland at Misery Mountain, near Peace River, AB (Photo: Chris Schmidt); 3. Ranch lands along Highway 21 south of Cypress Hills, SK (Photo: Penny MacKinnon). 4. West of Bindloss, along the Red Deer River valley, AB (Photo: Mark Oliver); 5. Grassland National Park (East Block), in SE Saskatchewan (Photo: Henri Goulet); 6. Near St.-Lazare, MB (NW of Brandon) (Photo: Cary Hamel, Nature Conservancy of Canada); 7. Near Gardenton, MB (south of Winnipeg) (Photo: Cary Hamel, Nature Conservancy of Canada); 8. Near Belleville, ON (Photo: Andy Hamilton).



# **Arthropods of Canadian Grasslands (Volume 3): Biodiversity and Systematics, Part 1**

*Edited by* **Héctor A. Cárcamo**  
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**Biological Survey of Canada**  
**Commission biologique du Canada**

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The Biological Survey of Canada is an incorporated not-for-profit group devoted to promoting biodiversity science in Canada, particularly with respect to the Arthropoda. It develops and coordinates national initiatives in systematics and faunistics.

The monograph series of the Biological Survey of Canada comprises invited, fully reviewed publications of record that are especially relevant to the fauna of Canada.

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## Preface

The Biological Survey of Canada (<http://www.biology.ualberta.ca/bsc/bschome.htm>) is a not-for-profit national organization that was established in 1977 to coordinate research on Canada's biota, particularly arthropods. Members of the Survey began planning the current book series, *Arthropods of Canadian Grasslands*, in the early 2000s to highlight the arthropods in grasslands, some of Canada's most endangered ecosystems. The arthropods, which include insects, mites, spiders, millipedes, and their relatives, contribute the bulk of animal diversity in most terrestrial habitats, but many groups remain poorly studied.

Many types of grasslands occur across Canada, but they reach their greatest expanse in the three Prairie Provinces. Other notable grassland regions occur in the interior of British Columbia, in the Peace River area of northern British Columbia and Alberta, and in parts of Yukon and southern Ontario. These regions and their characteristics are described in Volume 1 of this series, *Ecology and Interactions in Grassland Habitats* (Shorthouse and Floate 2010), which reviews the geological history, physical geography, and climatic features of Canadian grasslands. Volume 1 focuses on the ecological attributes and interactions of arthropods in natural grasslands and calls attention to the plight of disappearing grasslands and conservation efforts. Volume 2, *Inhabitants of a Changing Landscape* (Floate 2011), focuses on anthropogenic effects on grasslands and their arthropod fauna. It summarizes the fauna in modified grassland habitats such as agroecosystems and includes information on adventive (non-native) pest species, as well as those introduced for biological control. Both volumes are freely available online at <http://www.biology.ualberta.ca/bsc/english/publications.htm>. The volumes in this series are intended to reach a broad audience (e.g., scientists, students, naturalists, land use managers) in order to provide up-to-date information on arthropods, their habitats, and ecology for selected grasslands across the country. Therefore, authors were encouraged to define terminology and include images in their treatments of the fauna. However, readers will note considerable variation among chapters, reflecting the authors' interests and expertise.

Volume 3 was intended to bring the series to a close by providing a taxonomic summary, including checklists, for selected arthropod taxa that occur in grasslands. We planned to include groups about which very little is known (e.g., millipedes (Myriapoda), terrestrial isopods (Isopoda), and springtails (Collembola)), as well as better known groups (e.g., the butterflies and moths (Lepidoptera), dragonflies and damselflies (Odonata), and some of the beetles (Coleoptera)). Although only a subset of the arthropods is covered in this summary, it became clear early in the planning phase that a fourth volume would be needed to accommodate the 25 chapters covering over 8,000 species.

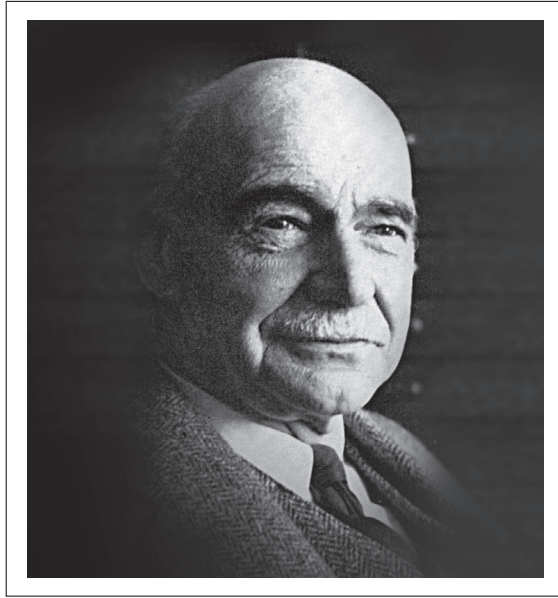
Volume 3 opens with an overview of the biogeography of arthropods of Canadian grasslands (Scudder), and specific biogeographical patterns make up a theme that is repeated through many of the chapters. The systematic section opens with an update on the status of a group of poorly known arthropods (Myriapoda and terrestrial Isopoda, Chapter 2 by Snyder), followed by some of the more common arachnids (plant-feeding mites by Beaulieu and Knee, Chapter 3, and spiders by Cárcamo *et al.*, Chapter 4). Chapter 5 bridges the arachnids and insects with a treatment of the ectosymbiont fauna (mites and lice) of birds (Galloway *et al.*). Chapter 6 (Lindo) covers a non-insect hexapod order, Collembola, and the rest of the chapters are then devoted to insects. Chapters 7 and 8 review two aquatic groups, the Plecoptera (Doddall and Giberson) and the Odonata (Cannings), respectively. Two iconic grassland herbivore groups are reviewed in Chapters 9 and 11 (grasshoppers by Miskelly and leafhoppers by Hamilton). The true bugs are covered in Chapter 10 (Scudder)

and the aphids in Chapter 12 (Footitt and Maw). Volume 3 closes with two chapters devoted to biting flies: black flies (Chapter 13 by Currie) and Culicidae, Ceratopogonidae, and Tabanidae (Chapter 14 by Lysyk and Galloway). Volume 4 (forthcoming) will focus on selected Coleoptera (beetles), Lepidoptera (moths and butterflies), other Diptera (robber flies, Asilidae), and Hymenoptera (bees, wasps, and ants).

The checklists throughout Volumes 3 and 4 are the core of each chapter, bringing together for the first time extensive lists of taxa that are associated with specific Canadian grasslands. Depending on the authors' expertise, some treatments are highly taxonomic and biogeographical in nature while others are more ecologically oriented. Chapter length varies considerably, depending on how well the taxa have been studied and the diversity of the group. Regardless of length, each chapter provides an up-to-date, accessible snapshot of the current diversity of each taxon that can be used as a baseline for further taxonomic investigation and environmental benchmarks, or as the basis for more ecological study. To improve the readability of the chapters, taxonomic authorities are presented only in checklist tables and omitted from the text (except for taxa not listed in tables). We hope that these volumes will highlight the fascinating diversity of the arthropods and their key ecological roles in Canadian grasslands and will allow them to become better known to a wide audience.

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**Fig. 1:** Edgar Harold Strickland (1889-1962). Photo from the Strickland Museum Collection, University of Alberta.

*The year 2013 was a landmark year for entomologists in the Canadian Prairies, since it marked 100 years of professional entomology in the region. Two influential entomologists began professional work on the Prairies in 1913: Edgar Strickland founded the Dominion Entomological Laboratory in Lethbridge and Norman Criddle was appointed as entomological field officer in Manitoba. These two scientists started an entomological legacy that would benefit several generations of Canadians. Therefore, we dedicate the two systematic entomology volumes in this book series to the memories of these men: Volume 3 to E.H. Strickland and Volume 4 to N. Criddle.*

## Dedication

### *Edgar Harold Strickland (1889-1962)*

In 1913, Edgar Harold Strickland (29 May 1889 – 31 May 1962) was sent west by the Dominion Department of Agriculture to establish a field laboratory at Lethbridge, Alberta, with an initial focus on controlling severe outbreaks of cutworms and wireworms that were occurring on the Prairies. Strickland, fresh from a master's degree from Harvard, was appointed as "Officer-in-Charge" of the new Dominion Entomological Laboratory and remained in that position until 1921 (with some time away to serve in the First World War). In 1922, he accepted a teaching position with the University of Alberta and moved to Edmonton, but continued to work in entomology.

When Strickland came to Alberta, he already had a diverse background in entomology. He attended Wye Agricultural College east of London, where he developed an interest in Diptera, particularly mosquitoes. After graduating in 1911, he was awarded a Carnegie studentship to study black fly parasites with W.M. Wheeler at Harvard University,



with a long-term goal of working in Africa on sleeping sickness; while at Harvard, he also developed a long-lasting interest in Hymenoptera. He went to Alberta to get field experience and was tasked with opening the first entomological laboratory in Alberta. He must have enjoyed the Prairies, as he stayed in Alberta for most of the rest of his working life, except for his service in World War I and a period when he moved between Ottawa and Lethbridge. He started his war service as a private, but later served as a lieutenant with the 1<sup>st</sup> Battalion, Canadian Machine Gun Corps, until he was wounded in 1918. In 1919, he returned to his entomological duties, continuing his work on prairie insect field crop pests, but also spending his winters in Ottawa working on stored product insects. His outstanding work did not go unnoticed, and in 1922 he was offered a position with the Faculty of Agriculture at the University of Alberta. He founded the Department of Entomology and remained its only faculty member until Brian Hocking joined him in 1946. He retired in 1952, and with his wife Alice, moved to Victoria, where he died in 1962 at the age of 73. They had two daughters and four grandchildren.

Strickland's entomological legacy is vast (see Hocking 1963, for a complete list of Strickland's contributions). Strickland published more than 60 scientific articles on a wide array of topics: cultural methods to manage crop and household pests, the distribution of black widow spiders, improved methods to store insects in vials, and the role of parasitoids and birds in natural control. In 1945, he published a visionary article questioning the environmental impacts of the widespread use of DDT. As an avid collector, he caught insects during and after work and identified them as well as he could, also depositing the specimens in the collections where he worked. He founded the insect collection at the University of Alberta that was later named in his honour; it now includes over a million specimens and features a "virtual museum" (<http://www.biology.ualberta.ca/facilities/strickland/>), which allows electronic access to prairie insect information. One of Strickland's greatest legacies was a series of seminal checklists on several important prairie groups. Their continuing importance is acknowledged in the references of several chapters in this series: Coleoptera (Elateridae), Biting Flies (Diptera), Hymenoptera (Ichneumonoidea and Braconidae), and Hemiptera. Another chapter, the Odonata, acknowledges the Strickland Virtual Museum.

His work was also recognized by his peers. In 1952, he was the first president of the Entomological Society of Alberta, he became an honorary member of the Entomological Society of Canada, and he was elected a fellow of the Entomological Society of America. In 1954, he was honoured by the University of Alberta with a doctor of science degree. Strickland's legacy spans beyond science. He is remembered both as an outstanding teacher and an accomplished soldier. As Hocking (1963) noted, Strickland's first-year entomology courses were the highlight in many students' careers because he mixed insect biology teachings with his philosophy of life. He was also a well-decorated soldier. Colonel Strickland, as he was known later, became a caring advocate for war veterans, a mentor to young faculty, and an anonymous philanthropist.

It is our honour to dedicate this book to the memory of Edgar H. Strickland.  
Héctor Cárcamo and Donna Giberson



**Fig. 2:** Strickland examining a yucca plant in the southern prairies. Photo from the Strickland Museum Collection, University of Alberta.

### ***Strickland's Checklists***

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We gratefully acknowledge the enthusiastic group of biology graduates from the University of Saskatchewan for their kind financial contribution through TRoutreach to help with the publication of Volume 3, and Iain Phillips for all his fund-raising efforts. Thank you TRoutreach!



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# Chapter 1

## An Introduction to the Biogeography of Canadian Grassland Arthropods

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**Abstract.** This chapter provides an introduction to the biogeography of the arthropods of Canadian grasslands, with examples mostly from the exopterygote insects. The origin of grasslands in North America is discussed, with emphasis on changes in the Quaternary period when most of Canada was glaciated and earlier grasslands were eliminated. Three main refugia for grassland insects reinvading Canadian habitats in the past 10,000 years are outlined. Examples are given for elements from open refugia in the south of the continent for the Great Plains and southwest for the Great Basin, with an East Beringian refugium highlighted for northern elements. Finally, three suture-zones (along the 100<sup>th</sup> meridian, along the Rocky Mountains, and across northern British Columbia and Alberta) where these three elements meet in Canada are discussed. With the projected climate change, it is expected that there will be dramatic changes in the distribution and composition of the grassland arthropod fauna in future.

### Introduction

Grassland ecosystems, in general dominated by members of the Poaceae, have rich herbaceous vegetation with few or no trees or shrubs (Moore 1964). Brink (1983), however, noted that there is no simple, single definition of grassland.

Although the current distribution of grasslands and their associated arthropods is attributed to both natural and anthropogenic forces, climate remains a dominant factor (McGinn 2010). Further, as noted by Mayr and O'Hara (1986), all current distribution patterns of flora and fauna are the result of the interplay of both historical and ecological factors. The most significant interval, and of fundamental importance for understanding the distribution of the Canadian arthropod fauna, is the Quaternary period (Pleistocene plus Holocene epoch), which started some 2.6 million years before present (mbp; International Commission on Stratigraphy 2013). It was the climatic fluctuations in the Quaternary that were primarily responsible for the communities and patterns of arthropod distributions that we observe today (Matthews 1979).

Most of Canada was glaciated 15,000 years bp,<sup>1</sup> and significant portions remained glaciated well into the Holocene (Matthews 1979). The Laurentide ice sheet extended over most of the prairies and the north-central and northeastern United States (Mickelson *et al.* 1983). The Cordilleran ice sheet covered interior British Columbia, with major ice lobes extending southward into Washington, Idaho, and Montana (Clague 1989). However, some coastal areas in British Columbia on the Queen Charlotte Islands (Haida Gwaii)

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<sup>1</sup> All dates cited are in radiocarbon years, following Matthews (1979).



and northern Vancouver Island evidently were unglaciated during the Wisconsin ice age (Heusser 1989), as judged by both geological and biological evidence. The latter evidence is indicated by both the vascular plants (Ogilvie 1989) and native earthworms (McKey-Fender *et al.* 1994). In Canada, extensive grasslands have attained their present distribution only in the past 10,000 years, since the last glaciation.

Six of Canada's ecozones have grasslands at present. The largest areas are in the Prairie Provinces and in the interior of British Columbia (Shorthouse 2010*a*, 2010*b*; Shorthouse and Larson 2010). Remnant grasslands also exist in northern British Columbia, Ontario, and the Yukon (Shorthouse 2010*b*). The grasslands in southern Ontario are considered to be remnants of the Prairie Peninsula that developed about 8,000 years ago (Transeau 1935; Wright 1968). Some of the isolated grassland areas in the interior of British Columbia may be remnants of grasslands that extended farther north in the Early Holocene (Hebda 2007). The grasslands in the unglaciated part of the Yukon are possible remnants of the Mammoth Steppe, or mosaic of plant communities that existed in the Late Pleistocene (Elias 1994; Schweger 1997). These are found today mostly on south-facing slopes dominated by xeric *Artemisia frigida* Willd. grass communities (Scudder 1997*a*). Lafontaine and Wood (1988) noted that *A. frigida* does not occur in dry tundra, but a few minute patches of *A. frigida* occur today on suitable steep river banks as far north as the arctic coast of the Yukon. However, the present Late Holocene fauna cannot be considered to be in a state of equilibrium (Matthews 1979). The Canadian grassland arthropod fauna are projected to experience dramatic ecological rearrangements and species range shifts when the climate regime changes in the future (Hamann and Wang 2006; Hebda 2007).

This chapter outlines the history of grassland ecosystems in Canada, providing some details of their occurrence over time, with emphasis on the post-colonization from refugia in the north and south of the continent. Mention is made of faunal interactions and the expectation of dramatic change in the future. Arthropods used as examples throughout the text are mostly from the exopterygote insects.

### Origin of Grasslands

With the Late Miocene uplift of the Rocky Mountains, there was increased aridity in the centre of the continent, resulting in the development of grasslands in the continental interior in the Late Miocene–Early Pliocene (6–5 mbp) (Axelrod 1985). Prior to the development of north–south geographical barriers in North America such as the Rocky Mountains, no rain-shadow effect on the North American continent existed, and so there was an absence of strong seasonal and annual aridity inland. Hence, grasslands were rare prior to 40 mbp (Ruddiman and Kutzbach 1991). Grasslands developed later west of the Rocky Mountains in the Late Pliocene (Leopold and Denton 1985; Heusser and King 1988).

In all instances, it was the associated climate change and resulting aridity from reduced precipitation that allowed the development of grasslands. This change resulted in ecosystems that could tolerate conditions where precipitation occurred in peak periods followed by annual stretches of drought (Brown 1985).

### Changes in the Quaternary

As a result of extensive late Wisconsin glaciations (Dillon 1956), the northern grasslands in Canada were obliterated, and it is proposed that the area was recolonized *de novo* (Howden 1969). The regional vegetation zones and their faunas on the continent at the time of the

Wisconsinan glacial maximum were either displaced southward or may have existed in plant communities with no current analogue. With the rapid warming in the Late Pleistocene and Early Holocene, grasslands redeveloped in the high plains on the continent, and these were completed, at least in Nebraska, by 10,000 years bp (Matthews 1979). With the peak of the warm Hypsithermal period (8,000–6,000 years bp) (or xerothermic interval in 10,000–7,000 BC), the grasslands expanded until 7,000 years bp, when subsequent cooling resulted in grassland retreat (Wright 1970; Ritchie 1976). However, this Hypsithermal grassland expansion did not occur at the same instant in all areas and sites (Matthews 1979). Of all the biomes of North America, the grasslands in particular seem to have fluctuated greatly during the Pleistocene (Hamilton 2006).

In the Rocky Mountain regions, postglacial warming started around 13,700 years bp in north-central Colorado (Short and Elias 1987), with the most rapid warming occurring after 11,500 years bp. Elias (1994) has noted that fossil evidence suggests that insects responded to major climatic change much faster than did the vegetation. Hence, it is possible that insect movement was quite dramatic during interglacial intervals.

Grassland patterns varied during the Wisconsinan. Ross (1970) placed the tallgrass prairie on the Texas–Mexico border during the Wisconsinan maximum, but suggested that small patches of grassland may have survived elsewhere. Prairie grasslands developed as a discrete vegetation type on the Great Plains about 10,000 years bp and remained grassland throughout the Holocene (Baker and Waln 1985). However, this prairie grassland moved northward and eastward in the maximal warm period in the Early Holocene (Wright 1970; Holloway and Bryant 1985).

In the Early and Middle Wisconsinan, which occurred 100,000 to 30,000 years ago, before the last major expansion of continental ice sheets in North America, grasslands may have been more extensive than they are today. Hence, the Prairie Peninsula, which was an Early Wisconsinan projection of the tallgrass prairie into northeastern North America (Transeau 1935), is now represented only by remnants; there was a gradual demise of most of the Early Wisconsinan Prairie Peninsula during the Middle and Late Wisconsinan (Wright 1977). Hamilton (1994) noted that this Prairie Peninsula evidently extended into Ontario, with current remnants now on the Ojibway Prairie and Walpole Island. In the Chihuahuan Desert, Middle Wisconsinan records (45,600–24,100 years bp) indicate juniper-desert grassland assemblages, and Late Wisconsinan packrat midden records document desert grassland and desert scrub elements (Van Devender 1990). In the Mojave Desert, steppe shrubs were dominant between 18,000 and 15,000 years bp and gave way to succulent forbs and grasses about 12,000 years bp (Spaulding 1990). Steppe vegetation was dominant in the intermontane valleys of the Great Basin throughout the Wisconsinan (Thompson 1990). Thus steppe vegetation was present in eastern Washington in the Early Wisconsinan (Heusser and King 1988), prevailing during full glacial times (Barnosky *et al.* 1987; Whitlock and Bartlein 1997), and steppe, similar to the modern steppe of eastern Washington, was present in the southeastern Columbia Basin 3,300–2,300 years bp. In addition, cool, dry conditions, similar to that of the grassland region of Washington today, existed in the Puget Trough around 16,400 years bp (Barnosky *et al.* 1987).

Similarly, Clague *et al.* (1990) showed that grassland was dominant near Quesnel in British Columbia during the Middle Pleistocene. Cool shrub-herbaceous vegetation in which grasses and *Artemisia* were abundant occurred in south-central British Columbia as early as 13,000 years bp (Hebda and Heinrichs 2011: Fig. 2). From 10,000 to 8,000 years bp, almost all of the lower elevation areas within southern British Columbia were covered by sage-grassland (Hebda 1982). Indeed, grasslands likely extended well north of today's

range in the southern interior of British Columbia from 6,800 to 6,600 years bp (Mathewes and King 1989), but retreated afterward, such that the present largely forested vegetation of the interior was established between 4,000 and 2,000 years bp (Hebda 1995).

Giterman *et al.* (1982) reported that xeric steppe vegetation first appeared in the lower Kolyma basin of West Beringia in the Early Pleistocene, and Guthrie (1985, 1990) considered that an arid steppe (Mammoth Steppe) dominated East Beringia in the Late Pleistocene. However, recent research suggests that this region was not covered in a uniform ecosystem at this time, but was most likely a mosaic of plant communities that included abundant *Artemisia* and grasses (Elias 1994; Schweger 1997).

### Northern Grassland Arthropods

Hamilton and Whitcomb (2010) noted that the insect faunas of Canadian grasslands are not simple extensions of those that exist today in the south-central United States, as had been claimed by Oman (1949). Rather, the insect biodiversity of the northern grasslands differs in composition and ecology from those of unglaciated sites both on the Great Plains and on the adjacent desert plains of the southwestern part of the United States. The arthropods of the Canadian grasslands have to adapt to the specific weather and climate patterns of the north, outlined by McGinn (2010), and make adjustments in their seasonal phenology and host specificity (Hamilton and Whitcomb 2010). Not all southern species have been able to make the appropriate adaptations, and so the northern grassland faunas are less rich when compared with the more southern biotas. In some groups, like the leafhoppers, the fauna of the Canadian grasslands is unexpectedly diverse, although the reasons for this are not entirely clear (Hamilton and Whitcomb 2010; and see Hamilton, Chapter 11, this volume). Further, a large percentage of northern leafhopper species seem to disperse too slowly to have filled their host's geographical range in the 10,000 years since deglaciation (Hamilton and Whitcomb 2010). Grassland-like habitats occurred well before this in southern British Columbia (Hebda and Heinrichs 2011), but they may not have been suitable for many current grassland species.

The ability to avoid freezing temperature and winter desiccation and the power of dispersal are major factors in determining the distribution of various species. The ability to survive over winter is an important seasonal adaptation for northern insects (Danks 1978). Dispersal mechanisms, both active and passive, are important insect adaptations (Johnson 1969). Hamilton and Whitcomb (2010) stressed the different dispersal abilities of various leafhoppers and planthoppers and noted how these abilities influence their biogeography. Danks *et al.* (1997) noted that most insects are relatively mobile, allowing them to respond fairly quickly to the changed postglacial conditions of access and habitat suitability. Therefore, widely distributed species, most of which have high dispersal ability, show little evidence of their biogeographical origins. Ball and Currie (1997) noted that the ground beetle species that are widely distributed in North America do not provide decisive evidence about their origins, and this is true for most taxa. For example, in wide-ranging terrestrial Heteroptera species in the Prairies Ecozone (see Chapter 10), deciphering their origin is a problem. Of the 46 Nearctic (including Beringian) species of terrestrial bugs listed by Scudder (see Chapter 10), 44 (96%) occur in grassland habitats in the Yukon (Scudder 1997b), and 38 (83%) occur in the main grassland areas of British Columbia that were depicted by Scudder (2010). It is not possible at present to determine where these species originated in the post-Pleistocene. Some of the species now in the Yukon might have had remnant populations that survived the Pleistocene *in situ*, but only detailed intraspecific genetic analyses will resolve their history and biogeography.

Likewise, of the 162 Nearctic (excluding Beringian) terrestrial species of Heteroptera listed in the Prairies Ecozone by Scudder (see Chapter 10), at least 88 (54%) also occur in the grasslands of British Columbia. All of these evidently survived the Pleistocene in refugia south of the Cordilleran and Laurentide ice sheets, but it is not clear for most of them whether this was in the Great Plains area and/or the Great Basin area.

It is species with limited distribution and usually poor dispersal ability that are best suited to biogeographical analysis. When they have a known and limited host preference, especially if monophagous, the biogeographical interpretations have greater reliability. Unfortunately, these conditions are not met in a vast number of the northern grassland insects.

### Refugia for Grassland Insects<sup>2</sup>

There are three primary refugia areas for the insects that colonized the Canadian grasslands in the Quaternary period (Fig. 1). The largest refugial areas for grassland arthropods in the Quaternary were undoubtedly in the south in the United States. However, Hamilton (2002) identified at least nine glacial-era refugia close to the ice front in the Pacific Northwest. Hamilton (2006) suggested that a number of flightless leafhoppers could have survived on steep, south-facing slopes in canyons where summer insolation raised local temperatures close to those of modern springtime.

The tallgrass prairies probably had a refugium on the Gulf Coast during the Wisconsinan maximum (as postulated by Ross 1970), while the shortgrass prairie component survived on the high plains of Texas and New Mexico. The latter is the most distinctive component today in the Great Plains biogeographical element.

A refugium in the southwest must have been the source of many species that colonized the Great Basin and associated grassland areas. This refugium was the remnant of late Wisconsinan steppe vegetation that prevailed in the southwestern deserts (Spaulding 1990; Van Devender 1990) and gave rise to the desert grasslands of today (Humphrey 1953, 1958). Many grassland insects now only found west of the Rocky Mountains seem to have been derived from this refugium.

Slater and Knop (1969) concluded that milkweed bugs of the *Lygaeus kalmii* Stål complex are of Sonoran origin on the basis of the geographical variation in North American populations. They stated that dispersal of the *Lygaeus* eastward from the Mexican Plateau must have taken place during at least two distinct periods and that complete or nearly complete isolation of the various populations had occurred at some time in the past. During glacial advances, the cool southeast may have possessed populations isolated from those of the west and southwest.

The East Beringian region, which remained unglaciated throughout the Pleistocene, constituted an important refugium for many grassland arthropods. Because of its supposed steppe-like characteristics, East Beringia must have been a refugium for Old World species that traversed the Beringian Land Bridge. Ross (1970) also considered it to be a refugium for many insects displaced from the high plains of western North America when these areas were revegetated by spruce forests that migrated northward with cooling.

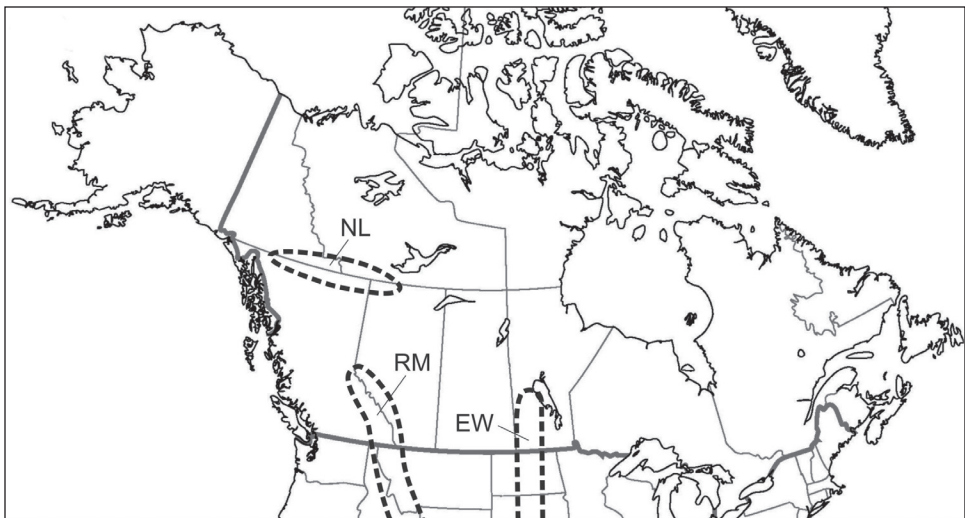
There was probably a corridor in the northern Rocky Mountain foothills connecting this East Beringian refugium to the mid-continent by 10,000 years bp (Reeves 1973).

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<sup>2</sup> Arthropods that occur in arctic, alpine, and other high-elevation areas, as well as those in coastal grassland habitats, are not included.



**Fig. 1.** Map of North America showing suggested grassland refugia for future Canadian ecosystem elements at the time of maximum Wisconsinan glaciation. EB = East Beringian refugium; GB = Great Basin refugium; GP = Great Plains refugium.



**Fig. 2.** Map of Canada and adjacent United States showing suggested suture-zones for Canadian grassland arthropod fauna. EW = eastern-western suture-zone; NL = northern latitudes suture-zone; RM = Rocky Mountains suture-zone.

An ice-free corridor existed between the Pleistocene ice sheets at various times (Reeves 1973; Rutter 1980; Schweger 1989; Burns 1990), but this was evidently a variable and intermittent entity that existed only in narrow windows of Quaternary time (Schweger 1989). It could have channelled the movement of insects in the north–south direction, or a south–north direction, but its characteristics probably varied over time and thus served to modulate any insect movement (Schweger 1989).

Undoubtedly, the Beringium refugium contained grassland elements that can now be found in the unglaciated areas of the Yukon and the grasslands on warm south-facing slopes. Nevertheless, not all of the northern warm steppe grassland insects, north and west of the Cordilleran–Laurentide ice sheet complex, arose from this refugial source. Lafontaine and Wood (1988) concluded that although 15 species of noctuid moths in the grasslands of the Yukon are disjuncts of more southern species, they are not Beringian remnants, but have instead invaded Beringia recently from the south.

Scudder (1993) suggested that some of the seed-feeding, xeric steppe-inhabiting lygaeoid Heteroptera may have survived the Late Pleistocene in a northern Beringian refugium, as well as in refugia to the south. Such a scenario was suggested by the fact that species such as *Crophius ramosus* Barber, *Emblethis vicarius* Horváth, *Kolenetrus plenus* (Distant), and *Slaterobius insignis* (Uhler) have what appear to be bicentric, tricentric, or quadricentric ranges (Scudder 1993). Lattin (1964) also suggested a dual northern Beringian and southern refugial origin for the xeric steppe-inhabiting scutellerid *Vanduzeeina borealis* Van Duzee. Preliminary intraspecific genetic studies of the big-eyed bug, *Geocoris bullatus* (Say), showed that although this species now has a broad Nearctic (including Beringia) distribution, and one might assume that it had a southern refugial origin, the species actually seems to be composed of two genetic stocks, one of northern and one of southern origin (Scudder 1993). However, further molecular studies are needed to confirm these preliminary results.

## Grassland Faunal Elements

Endemic species are the most instructive grassland elements because they provide, in most cases, convincing and direct evidence of their biogeographical origin. However, there are few reliable endemic grassland arthropod taxa in the Canadian fauna in most groups (but see Hamilton, Chapter 11). In addition, many may appear as endemics because of a lack of study elsewhere. The occurrence of apparent endemics in previously glaciated areas poses significant biogeographical explanatory problems.

### *Great Plains Elements*

The many species of grass-feeding insects that are now confined to the prairie grasslands are undoubtedly southern refugial elements. Vickery and Scudder (1987) listed over 28 species of Orthoptera that are now confined to the prairie grassland, and these were mapped by Vickery and Kevan (1986). While many of these, such as *Amphitornus coloradus* (Thomas), *Aulocara femoratum* Scudder, *Cordillacris crenulata* (Bruner), *Encoptolophus costalis* (Scudder), *Eritettix simplex tricarinatus* (Thomas), *Mermiria bivittata maculipennis* Bruner, *Opeia obscura* (Thomas), *Philbostroma quadrimaculatum* (Thomas), and *Trimerotropis latifasciata* Scudder, are grass feeders, others such as *Hypochlora alba* (Dodge) and *Melanoplus bowditchi canus* Hebard feed on *Atriplex* species. *Schistocerca emarginata* (Scudder) does not feed extensively upon grasses, and others are definitely forb feeders (Vickery and Kevan 1986). While *Cordillacris crenulatus* and *Mermiria bivittata*

*maculipennis* just reach into Canada on the prairies, others such as *Aulocara femoratum* move into the prairie grasslands, and species such as *Philbostruma quadrimaculatum* and *Encoptolophus costalis* are more widely distributed, with the latter reaching the Peace River area (Vickery and Kevan 1986).

In the Heteroptera, a group of 21 terrestrial species of the Prairies Ecozone were identified by Scudder (see Chapter 10) as a Great Plains element, and these undoubtedly survived the Pleistocene south of the ice front. Of these, the endemic *Orectoderus montanus* Kelton and *Trigonotylus canadensis* Kelton are grass-feeding species, while others such as *Chlamydatus artemisiae* Kelton and *Labopidea brooski* Kelton feed on *Atriplex* species.

Hamilton (2005b) showed that grassland-endemic “short-horned” bugs are common on the prairies and there are regional hotspots with high biodiversity. The Qu’Appelle coulee where it meets the canyon of the South Saskatchewan River is the area recognized as the most important hotspot. Hamilton (2005a) showed that leafhoppers and planthoppers, particularly species that are monophagous on a single grass species, are good indicators of native grassland ecosystems, and they persist in relict grasslands. Hamilton (2005a) then showed that such eastern Homoptera provide evidence of long-lost tallgrass prairies in Manitoba. Hamilton (1994) used leafhopper evidence to trace remnants of the Prairie Peninsula in southern Ontario, and Paiero *et al.* (2010) have described the insects of the Ojibway Prairie, a tallgrass remnant.

In the Acari, a few endemic oribatid species have been reported. Behan-Pelletier (1993) described *Eueremaeus aridulus* as an endemic in the grasslands of Alberta and Saskatchewan, and *Oribatella pawnee* Behan-Pelletier & Walter is evidently a Great Plains endemic (Behan-Pelletier and Walter 2012).

### **Great Basin Elements**

This element, derived from the refugium that must have existed in the southwestern deserts, is a major component in the intermontane grassland insect fauna in British Columbia. Such elements are clearly evident in some of the exopterygote insects.

Several grassland orthopteroid species in the Western Cordilleran (excluding Beringian) category in the Montane Cordillera Ecozone are Great Basin elements in the interior grasslands of British Columbia (Scudder and Vickery 2011). These include *Metator nevadensis* (Bruner), which is a grass feeder; *Melanoplus ruggelesi* Gurney, which feeds on *Artemisia* sp.; and *Psoloessa delicatula buckelli* Rehn, which inhabits sagebrush habitats (Vickery and Kevan 1986). Another notable Great Basin component, rather rare in British Columbia, is the ground-dwelling mantid *Litaneutria minor* (Scudder). Although it is a predator, in Canada it is confined to the bunchgrass habitat in the South Okanagan (Cannings 1987), but has a range that extends to North Dakota and south to Mexico (Vickery and Kevan 1986).

Great Basin elements were included by Scudder (2011) in the insects categorized in the Montane Cordillera Ecozone as belonging to the Western Cordilleran (excluding Beringia) geographical pattern. Of the 210 terrestrial Heteroptera placed in this category, 121 are plant bugs (Miridae), many of which are predaceous. However, there are at least 38 taxa that are clearly Great Basin elements (Table 1). While some of these feed on grasses, others rely on *Artemisia* spp., *Purshia tridentata* (Pursh) DC (Rosaceae), *Ribes cereum* Dougl. (Grossulariaceae), and other plants as breeding hosts. Additional species appear to be endemic, such as *Dichaetocoris gillespiei* Schwartz & Scudder, which breeds on *Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae), and *Melanotrichus robineau* Schwartz & Scudder, which is probably associated with native Brassicaceae,

**Table 1.** Some Great Basin plant bug species in the intermontane grasslands in the British Columbia interior.

Species	Breeding Host
<i>Aurantioicoris cuneotinctus</i> (Van Duzee)	<i>Purshia tridentata</i> (Pursh) (DC [Rosaceae])
<i>Ceratocapsus cunealis</i> Henry	<i>Artemisia tridentata</i> Nutt. [Asteraceae]
<i>Chlamydatus brevicornis</i> Knight	<i>Artemisia tridentata</i>
<i>C. schuhi</i> Knight	<i>Leptodactylon pungens</i> (Torr.) Nutt. [Polemoniaceae]
<i>Deraeocoris bakeri</i> Knight	<i>Artemisia tridentata</i> , <i>Ericameria nauseolus</i> (Pall.) Nesom & Baird [Asteraceae]
<i>D. fulgidus</i> Van Duzee	<i>Purshia tridentata</i>
<i>D. schwartzii</i> (Uhler)	<i>Artemisia tridentata</i>
<i>Europiella unipuncta</i> Knight	<i>Artemisia tridentata</i>
<i>Ilnacorella argentata</i> Knight	<i>Balsamorhiza</i> sp. [Asteraceae]
<i>Irbisia pacifica</i> (Uhler)	grasses [Poaceae]
<i>I. serrata</i> Bliven	grasses
<i>I. shulli</i> Knight	grasses
<i>Knightomiroides ponderosae</i> Stonedahl & Schwartz	<i>Pinus ponderosa</i> Dougl. [Pinaceae]
<i>Lopidea nigridea nigridea</i> Uhler	<i>Artemisia tridentata</i>
<i>Microlophus rivalis</i> (Knight)	<i>Ribes</i> sp. [Grossulariaceae], <i>Rubus</i> sp. [Rosaceae]
<i>Macrotylus multipunctatus</i> Van Duzee	<i>Lupinus</i> sp. [Fabaceae]
<i>Melanotrichus vestitus</i> (Uhler)	<i>Phacelia linearis</i> (Pursh) Holz. [Hydrophyllaceae]
<i>Neurocolpus longirostris</i> Knight	Unknown
<i>Oligotylus nigerrimus</i> (Van Duzee)	<i>Ceanothus</i> sp. [Rhamnaceae]
<i>Orectoderus arcuatus</i> Knight	<i>Artemisia tridentata</i>
<i>Orthotylus contrastus</i> Van Duzee	<i>Populus</i> sp. [Salicaceae]
<i>Parthenicus brindleyi</i> Knight	<i>Physocarpus malveceus</i> (Greene) Kuntze [Rosaceae]
<i>P. pallidicollis</i> Van Duzee	<i>Purshia tridentata</i>
<i>P. sabulosus</i> Van Duzee	<i>Artemisia</i> sp.
<i>P. thibodeauii</i> Schwartz & Scudder	Unknown
<i>Phytocoris californicus</i> Knight	<i>Ceanothus</i> sp.
<i>P. plenus</i> Van Duzee	Unknown
<i>P. purshiae</i> Stonedahl	<i>Purshia tridentata</i>
<i>P. rostratus</i> Knight	Unknown
<i>P. strigosus</i> Knight	<i>Ericameria nauseolus</i>
<i>Pilophorus stonedahli</i> Schuh & Schwartz	<i>Pinus ponderosa</i>
<i>Plagiognathus ribesi</i> Kelton	<i>Ribes cereum</i> Dougl.
<i>Pronotocrepis clavicornis</i> Knight	<i>Ribes cereum</i>
<i>Pseudopsallus occidentalis</i> Stonedahl & Schwartz	Unknown
<i>Slaterocoris pilosus</i> Kelton	<i>Artemisia</i> spp.
<i>S. robustus</i> (Uhler)	<i>Artemisia tridentata</i>
<i>Teleorhinus cyaneus</i> Uhler	<i>Ceanothus</i> sp.
<i>Tupiocoris agilis</i> (Uhler)	<i>Ipomopsis aggregata</i> (Pursh) V. Grant
<i>T. elongates</i> (Van Duzee)	<i>Ribes</i> sp., etc.
<i>Tuxedo cruralis</i> (Van Duzee)	<i>Ceanothus</i> spp.



but has also been collected on *Lepidium perfoliatum* L., *Sisymbrium altissimum* L., and *S. loeselii* L. (Brassicaceae).

Hamilton (2011) found that southern populations of leafhoppers, which are mainly of Great Basin origin, may still be invading British Columbia from the south. He found that the South Okanagan has a distinctive semi-desert fauna that feeds on arid-adapted plants such as sagebrush *Artemisia tridentata* Nutt., antelope brush *Purshia tridentata*, and sand dropseed *Sporobolus cryptandrus* (Torr.) Gray. The South Okanagan has the richest grassland fauna that represents the northern extension of the Great Basin fauna, but lacks many species characteristics of central Washington and adjacent Idaho.

Endemic insects provide important information about faunal origins. The bristletail *Mesomachilis canadensis* Sturm is a Pacific Northwest endemic, known from British Columbia and Oregon (M.L. Bowser, *in litt.*), that clearly is a Great Basin element in the grasslands of the British Columbia interior. Likewise, the cicadellid genus *Errhomus* Oman, which has large, flightless females with limited vagility, is of southwest origin and endemic to the Pacific Northwest (Hamilton and Zack 1999). Only *Errhomus calvus* Oman has a range that extends into the previously glaciated areas in the grasslands of the British Columbia interior (Hamilton and Zack 1999). While most species of *Errhomus* are associated with and dependent on balsamroot, *Balsamorhiza sagittata* (Pursh) Nutt., *E. calvus* is evidently polyphagous, often being associated with more common forbs (Hamilton and Zack 1999).

Hamilton (2002), in a study of Pacific Northwest grassland Homoptera, concluded that 120 of the 241 species of Cicadellidae, Delphacidae, and Caliscidae were endemic. He suggested that only six taxa postdated the retreat of the glaciers and postulated that there had been nine main glacial refugia in the area. However, most of these were not in British Columbia. Species apparently endemic to the interior grasslands of British Columbia include *Ceratagallia okanaganana* Hamilton from Osoyoos (Hamilton 1998b) and *Hebecephalus planaria* Hamilton collected 10 km northeast of Douglas Lake on *Poa pratensis* L. (Poaceae) (Hamilton 1998a).

Other examples of Great Basin elements in the British Columbia interior can be found in the Coleoptera, Lepidoptera, and Diptera. Anderson (2011) identified 14 western arid species of weevils that are confined to the dry grassland valleys in the South Okanagan. These include *Anthonomus albus* Hatch, *Cercopidius artemisiae* (Pierce), *Cylindrocopturus helianthus* (Hatch), *Omius erectus* Hatch, *O. saccatus* (LeConte), *Ophryastes cinarensis* (Pierce), *Stamoderes lanei* (Van Dyke), and *Tychius semisquamosus* LeConte. In addition, the apparent endemic weevil *Ceutorhynchus opertus* Brown (Scudder and Cannings 1994) and some potentially rare tenebrionids occur in southern interior British Columbia grasslands (Hlady 1990; Scudder 1991, 1994). One of these tenebrionid species, *Eleodes obscurus sulcipennis* Mannerheim, is reported to have recently moved northward into the Okanagan (Cannings and Scudder 2009). Lafontaine and Troubridge (2011) identified several Great Basin butterflies with ranges that extend into the grasslands in the interior of British Columbia, and the distribution of these butterflies was mapped by Guppy and Shepard (2001). Included are the sandhill skipper *Polites sabuleti* (Boisduval), with larvae that feed on grasses, and the Behr's hairstreak *Satyrrium behrii* (Edward), with larvae dependent on their only food plant, *Purshia tridentata* (James and Nunnallee 2011). Other notable interior grassland species in British Columbia include the Great Basin endemic spider *Synageles leechi* Cutler, known only from British Columbia (West *et al.* 1984; Cutler 1987; Scudder 1994), and the endemic asilid *Efferia okanaganana* Cannings (Cannings 2011).

### ***Beringian Elements***

These grassland elements survived the Pleistocene in unglaciated Beringia and are found today in East Beringia on warm south-facing grassland slopes and immediately adjacent areas. Few seem to have dispersed far outside of East Beringia since the retreat of the Pleistocene glaciers.

Fortunately, there has been a great deal of research on Pleistocene fossil insect deposits in the Beringian refugium (Matthews 1975, 1979; Elias 1994), with most emphasis on the Coleoptera (Morgan and Morgan 1980; Morgan *et al.* 1983; Schwert and Ashworth 1988). This has allowed Anderson (1984, 1997), for example, to show that the endemic brachypterous weevil *Connatichela artemisiae* Anderson was present in Beringia during Middle Wisconsinan times and occurs today on dry, south-facing grassland slopes with *Artemisia*, where the larvae feed on the roots of *A. frigida*. The weevil *Vitavitus thulius* Kissinger found in Pliocene deposits in Alaska (Matthews 1977), Early Wisconsinan deposits in the Kolyma basin in Siberia, and at Cape Deceit in Alaska (Matthews 1974; Morgan *et al.* 1983), as well as elsewhere,<sup>3</sup> is now restricted to the Yukon and Northwest Territories (Kissinger 1973), where it occurs on many south-facing grassland slopes with *Artemisia* (Scudder 1993). This weevil, which is evidently parthenogenetic (Anderson 1997), suggests that some Beringian grassland elements must have moved south at the onset of glaciation, but failed to survive outside of Beringia.

Hamilton (1997) reported five species of leafhoppers endemic to the Beringian area that now occur exclusively within the Yukon River drainage system. He thus suggested that the Yukon River and its main tributary valleys may have served as a refugium for leafhoppers. The Pelly and Lapie rivers, tributaries of the Yukon River, form a single valley system with steep, warm, south-facing slopes that support a sagebrush-grass community that is the habitat for the endemic *Artemisia*-feeding *Empoasca nigroscuta* Gillette & Baker and *Chlorita nearctica* Hamilton (Hamilton 1997, 1998c).

There are other examples of Beringian elements as well. Footitt and Maw (1997) found the aphid *Uroleucon simile* (Hille Ris Lambers) to be a Palearctic–East Beringian species that occurs across the Palearctic and East Beringia; it is recorded from Alaska and the Yukon, having been collected on *Erigeron* sp. at Dawson City. In addition, Vickery (1997) reported one orthopteroid species, *Bruneria yukonensis* Vickery, as endemic in the Yukon, being collected on grassy slopes at Lake Laberge, Sheep Mountain, Aishihik River, and Sulphur Lake.

### **Suture-Zones for Grassland Insects**

Remington (1968) developed the concept of suture-zones as an appropriate term to use for belts of interfaunal or interfloral linkage. Such zones represent overlap between major biotic assemblages, including some pairs of species that hybridize in the zone. He depicted six major suture-zones in North America and listed the main taxa involved in each. Among the insects, he listed examples from the Lepidoptera, but none of the grassland insects. However, three main suture-zones can be recognized for Canadian grassland arthropods (Fig. 2).

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<sup>3</sup> Middle Wisconsinan deposits in the Bell and Old Crow area of the Yukon (Matthews 1975; Morlan and Matthews 1983), Holocene deposits in the Mackenzie Valley, and Early Wisconsinan samples from Minnesota (Ashworth 1980), together with Holocene samples from Brampton, Ontario, and from Cambridge Bridge, Vermont (Morgan *et al.* 1983).

The most evident suture-zone in Canada is that termed the eastern (humid)-western (arid) suture-zone (Scudder 1979), which runs north–south in the vicinity of the 100th meridian. Here the western Canadian grassland biota meets the eastern biota, and it is the line of separation recognized for eastern Canadian and western Canadian elements (Scudder, see Chapter 10).

Parshley (1923) and Slater and Knop (1969) showed that the two subspecies of the lesser milkweed bug *Lygaeus kalmii* Stål meet and now intergrade along the 100th meridian, and Slater and Knop (1969) noted that the faunal break at this meridian is a significant zoogeographical phenomenon, correlated with a sharp decline in rainfall as one moves from east to west. Significantly for grassland insects, this phenomenon correlates with the western boundary of the tallgrass prairie, where it meets the mixed and shortgrass prairie (Scudder 1979), and where Hamilton (2005a) documented the approximate limit for the occurrence of eastern tallgrass prairie leafhoppers.

The area of the 100th meridian is also the boundary for the occurrence of many western grassland species, such as the scutellerid *Homaemus aeneifrons consors* Uhler; the eastern subspecies *H. aeneifrons aeneifrons* (Say) occurs east of this line (Scudder, see Chapter 10). Scudder (Chapter 10) recognized 34 terrestrial Heteroptera taxa in the eastern Nearctic category of bugs in the Prairies Ecozone, although few of these feed on grasses or other plants in grassland habitats. Nevertheless, of special interest is the occurrence of the Poaceae-feeding blissid bug *Ischnodemus hesperius* Parshley, found abundantly in the tallgrass prairie remnant at the St. Charles Rifle Range near Winnipeg (habitat described by Roughley *et al.* 2010). *Ischnodemus hesperius* does not occur farther west.

Howden (1969) noted that the major mountain ranges in North America are largely oriented north–south and that this has had a discernible influence on the insect fauna, directing south to north movement. The Rocky Mountains have tended to keep southern refugial elements apart. However, the Rocky Mountains are in essence another suture-zone, where prairie grassland insects may meet the intermontane grassland insects.

There have been only a few routes for faunal movement between prairie and intermontane grasslands. Hamilton (2002) noted movement of Homoptera into the Pacific Northwest grassland had occurred across at least nine mountain passes on the continental divide and that three of these passes still provide continuous grassland connections between the prairies and the intermontane grasslands. However, no more than 14 slow-moving prairie Homoptera species have surmounted any one pass. The main passes in Canada in the past were the Crowsnest Pass at 1,400 m and the Yellowhead Pass at 1,200 m between Alberta and British Columbia, the Kicking Horse Pass at 1,700 m in British Columbia, and a pass at 700 m near Summit Lake on the Crooked River north of Prince George, British Columbia, referred to as the “Crooked River Pass” (Hamilton 2002). The latter and the Crowsnest Pass seem to have been the most important transit routes for leafhoppers in the past, but why the movement occurred in just one direction and what governs the permeability of these routes is not clear. Hamilton (2002) lists six Homoptera that seem to have moved through the Crooked River Pass and five that seem to have traversed the Crowsnest Pass. The species cited as probably moving north–south through the Crooked River Pass include the caliscelid *Bruchomorpha beameri* Doering and the cicadellids *Auridius ordinatus* (Ball), *Ceratagallia viator* Hamilton, *Elymana circius* Hamilton, *Pinumius sexmaculatus* (Gillette & Baker), and *Latalus intermedius* Ross & Hamilton. The five that moved east–west through the Crowsnest Pass are *Bruchomorpha beameri* and the cicadellids *Amblysellus wyomus* Kramer, *Auridius helvus* (DeLong), *Ceratagallia viator*, and *Rosenus cruciatus* (Osborn & Ball). The Crowsnest Pass still provides a continuous grassland connection between the prairies and

the intermontane grasslands in British Columbia and no doubt today still provides for east to west migration. Recent movement is suggested for several Heteroptera. These include the mirid *Lygus solidaginis* (Kelton), a prairie species, which in British Columbia is recorded only from Dutch Creek (Schwartz & Footitt 1998), and the mirid *Ilnacora albifrons* Knight, a species that occurs east to Ontario but is known only from Elko in British Columbia. In addition, two other prairie Heteroptera have evidently moved into British Columbia via the Crowsnest Pass: the mirid *Sixeonotus rostratus* Knight, recently collected in the Bull River Valley in British Columbia (Scudder 2013), and the rhyarochromid *Zeridoneus costalis* (Van Duzee), which has been collected at Wasa (Scudder 1986). *Zeridoneus costalis* also occurs in the grasslands of the Peace River in British Columbia (Scudder 1986), which are continuous with the prairies of the Great Plains (Scudder 1993).

Other Heteroptera extend east across Canada, but just reach into British Columbia in the Peace River grasslands. These include the mirids *Ceratocapsus nigricephalus* Knight recorded from Charlie Lake and *Labops brooksi* Slater collected at Rolla.

There may also be a suture-zone across northern British Columbia and Alberta where Beringian elements come in contact with the intermontane and/or the prairie fauna. This may not be as evident today, because there are no low-elevation grasslands now connecting these grassland areas (Scudder 1993). The current Beringian species do not seem to have moved far out of Beringia. However, in the past, especially during the Early Holocene (10,000–8,000 years bp), when southern grasslands may have extended much farther north than today (Hebda 1995), this suture-zone may have been more evident. Even the prairie grasslands of the Peace River area of British Columbia may have extended much farther north in the past, since open *Artemisia* and Poaceae herbaceous communities occurred at Lac Gill Blanc before 10,000 years bp (Hebda 1995).

Scudder (1993) noted that the intermontane grasslands of interior British Columbia likely extended well north of today's range during the driest part of the Holocene, which in the southern interior of British Columbia occurred 10,500 to 8,500 years bp (Mathewes and King 1989; Hebda 1995, 2007). In addition, modelling by Hamann and Wang (2006) of potential effects of climate change on ecosystems in British Columbia indicates that with modest warming in the future, grasslands can be expected to move north. Hamann and Wang (2006) used a model prepared by the Canadian Centre for Climate Modelling and Analysis (the Coupled Global Climate Model, a gas general circulation model using the 1992a Emission Scenario) and showed in their map for 2085, which is an average for 2071–2100, that some grassland areas would approach the Yukon border. Conservative Royal British Columbia Museum models suggest that South Okanagan climates may occur near the Yukon border by 2080 as well (Hebda 2007). Although the rate of climate change may exceed the ability of most species to disperse and adjust their range to new conditions (Austin *et al.* 2008), it can be expected that in future, a northern suture-zone may become more important and more clearly defined.

In conclusion, while there have been remarkable changes in the grasslands of Canada over the past 10,000 years, and the distribution of the arthropod fauna shows the clear interplay of historical and ecological factors, this fauna is not in a state of equilibrium. With projected climate change scenarios, it is to be expected that there will be dramatic changes in the distribution and composition of the grassland arthropod fauna in the future. In particular, with future grassland expansion on both sides of the Rocky Mountains, there could be renewed grassland connections. This could well result in much more faunal movement between prairie and intermontane grasslands in future. The consequences of such movement are impossible to predict.

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## Chapter 2

# Myriapoda and Terrestrial Isopoda of the Prairies of Canada

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**Abstract.** Myriapods and terrestrial isopods play important roles in numerous ecosystem processes, especially decomposition, and in the structure of soil food webs. This chapter discusses five focal taxa, specifically the terrestrial Isopoda (commonly known as pill bugs, sow bugs, roly-polys, woodlice, or slaters) and the four classes of the Myriapoda: Diplopoda (millipedes), Chilopoda (centipedes), Paurpoda, and Symphyla (sometimes called garden centipedes). After a brief review is given for each taxon's phylogenetic position, global diversity, and ecological role, current knowledge of species diversity in the Canadian prairies is summarized. Biodiversity of these five groups is relatively low in the prairies of Canada. Terrestrial isopods have yet to be discovered in Alberta, Saskatchewan, or Manitoba. Diplopoda are represented by 10 species, while six species of Chilopoda are known or suspected from the prairies. The Canadian pauropod fauna consists of two species that may be present in the prairies. Twenty-three species of Symphyla are known elsewhere in Canada, but none are known from the Prairie Provinces. Little research on these taxa has been done in this region and much remains to be discovered, likely including species that are new to science. In addition to diversity and distribution studies, future research directions should include studies of the biology and ecology of these species.

**Résumé.** Les myriapodes et les isopodes terrestres jouent un rôle important dans de nombreux processus écosystémiques— notamment la décomposition— ainsi que dans la structure des chaînes alimentaires du sol. Ce chapitre traite de cinq taxons principaux : les isopodes terrestres (communément appelés cloportes) et les quatre classes de myriapodes : diplopedes (mille-pattes), chilopodes (scolopendres), pauropodes et symphyles (parfois appelés scolopendres des jardins). Après un bref examen de la position phylogénique de chaque taxon, de sa diversité mondiale et de son rôle écologique, le chapitre résume nos connaissances actuelles sur les espèces de ces cinq groupes relativement peu diversifiés des prairies canadiennes. Aucun isopode terrestre n'a été observé à ce jour en Alberta, en Saskatchewan ni au Manitoba. Les diplopedes sont représentés par 10 espèces, et six espèces de chilopodes sont présentes dans les prairies ou soupçonnées de l'être. La faune des pauropodes canadiens compte deux espèces qui pourraient être présentes dans les Prairies. Vingt-trois espèces de symphyles sont connues ailleurs au Canada, mais aucune n'a été observée dans les provinces des Prairies. Ces taxons n'ont fait l'objet de peu de recherches dans la région, et il reste encore beaucoup à découvrir à leur sujet, y compris probablement de nouvelles espèces non décrites. En plus de se pencher sur la diversité et sur la répartition de ces insectes, les recherches futures devraient porter également sur leur biologie et leur écologie.

## Introduction

There is no doubt that arthropod biodiversity is critically important ecologically and economically on local to global scales. While insects (subphylum Hexapoda, class Insecta) comprise the vast majority of arthropod diversity, other extant subphyla (Chelicerata, Crustacea, and Myriapoda) contribute to ecosystem functioning through many avenues. Many species in these groups contribute to ecosystem processes, such as decomposition, while others play important roles in food web dynamics (Coleman *et al.* 2004). I summarize

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what is known about the diversity, distribution, and ecology of five focal taxa of soil-dwelling, non-insect arthropods in the Canadian prairies. Four of these taxa comprise the Myriapoda: the major groups of the class Diplopoda (millipedes) and the class Chilopoda (centipedes), as well as the less well-known classes Pauropoda (pauropods) and Symphyla (symphylans, sometimes called garden centipedes). In addition, I will discuss the terrestrial Isopoda (class Crustacea: order Isopoda: suborder Oniscidea), which go by many common names (e.g., pill bugs, sow bugs, roly-polys, woodlice, slaters), but herein are simply called isopods. Most isopod species have similar niches to millipedes and thus are appropriate to discuss here.

Oniscidea forms a monophyletic group of isopods with slightly more than 3,600 species described (Schmidt 2008). The group is primarily terrestrial with some littoral species. Isopods are the only crustaceans that have been evolutionarily successful in terrestrial environments and are one of two crustacean groups (the second being Amphipoda) that include species capable of living their entire life away from water (Hopkin 1991). Isopods have two critical adaptations to terrestrial life where the major barrier for colonization from aquatic environments is the low moisture content of air. First, eggs and first instar young are reared in a marsupium, or brood pouch, which maintains a moist environment. Second, the pleopods, the appendages toward the posterior end of the body, have been modified into lungs (sometimes called pseudotracheae) and a nitrogenous waste excretion system that conserves water (Hopkin 1991; Oliver and Meehan 1993). However, isopods are still quite prone to desiccation and are thus found in moist soil, in leaf litter, in or under logs, and in riparian areas. Many isopod species are synanthropic (Jass and Klausmeier 2001), benefiting from the moist habitats around buildings.

Myriapoda likely forms a monophyletic group, but placement of Myriapoda within the Arthropoda is uncertain, as are relationships among Diplopoda, Chilopoda, Symphyla, and Pauropoda within Myriapoda (Sierwald and Bond 2007; Shear and Edgecombe 2009). These four taxa have very different ecological roles. Millipedes, like isopods, are important detritivores, fragmenting leaf litter and making it increasingly available for microbial decomposers (Cárcamo *et al.* 2000). Centipedes are important predators in many ecosystems, consuming many kinds of invertebrates (Giribet *et al.* 1999). Some centipedes are large enough to consume vertebrates and some will occasionally ingest detritus (Coleman *et al.* 2004; Mercurio 2010). Pauropoda consume fungi and detritus, or may be predaceous (Scheller 1990; Coleman *et al.* 2004). Symphyla are omnivorous and may be best known as pests in greenhouses (Edwards 1990; Coleman *et al.* 2004). Little is known about the biology and ecology of Pauropoda and Symphyla, in part because both taxa are tiny, pale soil dwellers with little diversity relative to taxa such as millipedes or insects. Globally, Pauropoda has about 500 described species (Scheller 1990) while Symphyla has about 200 (Scheller and Adis 1996); in comparison, there are over 12,000 millipede (Sierwald and Bond 2007) and over 3,000 centipede species (Giribet *et al.* 1999).

There have been few taxonomic or biodiversity studies on the focal taxa in Canada. Those that included the Prairies Ecozone (also called Palliser's Triangle), a triangular region dominated by grasslands that stretches across southern Alberta, Saskatchewan, and Manitoba (Shorthouse and Larson 2010), are listed in Table 1. Relatively few studies have been conducted on myriapods and isopods of the prairies. Only one of these studies (Scheller 1984) includes identification keys to the fauna. However, Kevan and Scudder (1989) is a good general identification resource for the Myriapoda of Canada, at least to the family level.

**Table 1.** Taxonomic or biodiversity studies of the focal taxa covering the Canadian prairies.

<b>Taxon</b>	<b>Geographical Coverage; Comments</b>	<b>Reference</b>
Isopoda	Canada and continental USA	Jass and Klausmeier 2001
Diplopoda	Canada and Alaska	Behan-Pelletier 1993
	Central Canada (Rocky Mountains to eastern Lake Superior); includes summary of entire Canadian fauna	Shelley 2002
Chilopoda	Canada and Alaska	Kevan 1983
	Canada, Alaska, presence/absence in USA	Behan-Pelletier 1993
	Canada, USA, and Greenland	Mercurio 2010
Paupoda	Canada	Scheller 1984
	Canada, Alaska, presence/absence in USA	Behan-Pelletier 1993
Symphyla	Canada; species diversity estimate only	Scheller 1979
	Side note on Canadian Symphyla	Kevan 1983
	Canada; review of previous papers	Behan-Pelletier 1993

A lack of taxonomic research is not surprising because of the limited diversity present in the region. These groups are all particularly sensitive to moisture levels and would thus be expected to be depauperate in more xeric regions (e.g., grasslands). In addition, biodiversity is further reduced in the northern latitudes (Golovatch and Kime 2009).

### Diversity in Canadian Prairies

#### ***Isopods (Class Crustacea: Order Isopoda: Suborder Oniscidea)***

No terrestrial isopods have been reported from the Prairie Provinces of Alberta, Saskatchewan, and Manitoba (Jass and Klausmeier 2001). Many isopod species in North America are non-native and synanthropic, and they may be expected to occur in developed or disturbed areas within this region. However, the limited growing season and aridity make a fairly hostile environment even for invaders that are successful elsewhere. Few native isopods are found in the centre of the continent, that is, from the Rocky Mountains to the Mississippi River, north of Texas (Jass and Klausmeier 2000, 2001). Only a few introduced isopod species are known in the states that border the Prairies: Montana (four species), North Dakota (zero species, South Dakota also zero), and Minnesota (eight species) (Jass and Klausmeier 2001).

#### ***Millipedes (Class Diplopoda)***

Shelley (2002) provides the most recent and thorough summary of the Canadian millipede fauna. Table 2 lists the 10 millipede species known from Canadian grasslands. It is interesting to note that 4 of the 10 species are introduced, and none are endemic to the region.

A complete listing of the Canadian fauna and potential species in Canadian grasslands can also be found in Shelley (2002), but little has been published on this topic in the last decade (but see Shelley 2007; Shelley and Smith 2011). One noteworthy addition is the genus *Scytonotus* C. L. Koch 1847 (Polydesmida: Polydesmidae), now known from one sample from Jasper National Park (Shelley 2007). This suggests the possibility that *Scytonotus* may exist in the Canadian grasslands, or in adjacent forested habitats.

In a similar situation is *Austrotyla borealis* Shear 1971 (Chordeumatida: Conotylidae), which is only known from the type locality in Jasper National Park (Hoffman 1999; Shelley 2002).

Several additional millipede species may be found in Canadian grasslands but have not been reported. *Polyxenus lagurus* (Linnaeus 1758) (Polyxenida, Polyxenidae), one of Shelley's (2002) potential species for central Canada, was recorded as existing in Alberta by Behan-Pelletier (1993). Behan-Pelletier (1993) also reported *Brunsonia atrolineata* (Bollman 1893) (Chordeumatida: Conotylidae) (as *Conotyla atrolineata*) from Alberta. Unfortunately, no locality data were published in this review of the fauna and these records are unconfirmed. Behan-Pelletier (1993) report *Parajulus perditus* Chamberlin 1920 (Julida: Parajulidae) (as *Bollmaniulus perditus*) from Alberta; this species is of uncertain validity (Hoffman 1999; Shelley 2002) and is not included in Table 2.

**Table 2.** Diplopoda (millipedes) known from Canadian grasslands (Shelley 2002). *Species checklist available at: <http://dx.doi.org/10.5886/672d42kv>*

Taxon	Comments
Julida	
Julidae	
<i>Cylindroiulus latestriatus</i> (Curtis 1845)	Introduced European species. Only reported from Edmonton but likely widespread in developed areas.
Blaniulidae	
<i>Archiboreoiulus pallidus</i> (Brade-Birks 1920)	Introduced European species.
<i>Nopoiulus kochii</i> (Gervais 1847)	Introduced European species. Only reported from Edmonton but may be widespread in developed areas.
Nemasomatidae	
<i>Orinisobates expressus</i> (Chamberlin 1941)	While included in Shelley's list for Canada with a record for Alberta, was omitted from the central Canada list.
Parajulidae	
<i>Aniulus garius</i> (Chamberlin 1912)	
<i>Oriulus venustus</i> (Wood 1864)	
Chordeumatida	
Caseyidae	
<i>Underwoodia iuloides</i> (Harger 1872)	
<i>Underwoodia tida</i> Chamberlin 1925	
Conotylidae	
<i>Brunsonia albertana</i> (Chamberlin 1920)	Shelley suggested that this species can be found on the western edge of the prairies, and further west.
Polydesmida	
Polydesmidae	
<i>Polydesmus inconstans</i> Latzel 1884	Introduced European species. Only reported from Edmonton but likely widespread in developed areas.

**Centipedes (Class Chilopoda)**

The Canadian centipede fauna is very poorly studied. A preliminary survey was assembled (Kevan 1983), but limited research has been published since. Kevan's (1983) literature review recorded 70 species from Canada and Alaska, but only 30 were recorded from Canada. Five species from Kevan's (1983) list are thought to occur in Canadian grasslands (Table 3). A sixth, *Scolopocryptops rubiginosus* L. Koch 1878 (Scolopendrida: Cryptopidae), was listed as unconfirmed (Kevan 1983; Behan-Pelletier 1993; Mercurio 2010), but Shelley (1992) determined that Scolopendromorpha were limited to British Columbia and Ontario. Introductions and greenhouse records of other Scolopendromorpha are listed by Kevan (1983), but none of these records apply to the prairies.

Other species have been listed as unconfirmed or are uncertain. For example, *Taiyuna occidentalis* (Geophilida: Chilenophilidae) was also listed as unconfirmed from the region (Kevan 1983); Behan-Pelletier (1993) reports this species from British Columbia only. Kevan (1983) also appeared to have reservations about *Lithobius forficatus* (Lithobiida: Lithobiidae) and similar species (see Table 3). Lastly, Behan-Pelletier (1993) reports *Paobius albertanus* (Lithobiida: Lithobiidae) from Alberta, but this is the only Lithobiidae they report from Alberta, Saskatchewan, and Manitoba. The reasons for the discrepancies between the checklists of Kevan (1983) and Behan-Pelletier (1993) are unclear.

**Table 3.** Chilopoda (centipedes) known or suspected from Canadian grasslands. *Species checklist available at: <http://dx.doi.org/10.5886/672d42kv>*

Taxon	Comments	References
Geophilomorpha Dignathodontidae		
<i>Strigamia chionophila</i> Wood 1862	Collected in Fort Whyte, Manitoba, for an experiment; also reported from Alberta.	Aitchison 1979; Mercurio 2010
Chilenophilidae		
<i>Taiyuna occidentalis</i> (Meinert 1886)	Kevan reports as unconfirmed from southern Manitoba, with several question marks.	Kevan 1983
Lithobiomorpha Henicopidae		
<i>Lamyctes fulvicornis</i> Meinert 1868	Collected in Fort Whyte, Manitoba, for an experiment. Introduced to some areas? See Kevan 1983.	Aitchison 1979; Kevan 1983
Lithobiidae		
<i>Paobius albertanus</i> Chamberlin 1922	Type locality in Alberta, but exact location is uncertain. The original description lists "the Spring Lakes Trip" (presumably a reference to lakes near Edmonton). However, Mercurio (2010) notes that the holotype label reads "Canada: Albert, Rauff[?], Alba" which I interpret as Banff, Alberta, the collector's home town.	Behan-Pelletier 1993; Mercurio 2010
<i>Lithobius forficatus</i> (Linnaeus 1758)	Introduced. Range probably "across southern Canada but may be confused with other species" (Kevan 1983).	Kevan 1983
Scutigermorpha Scutigerae		
<i>Scutigera coleoptrata</i> (Linnaeus 1758)	Introduced. Known from Saskatchewan and Alberta. Probably present inside buildings throughout North America.	Kevan 1983



The most recent summary of the centipede fauna in North America is an annotated catalogue published by Mercurio (2010) that lists, in addition to the incorrect *S. rubiginosus* record from Manitoba listed above, *P. albertanus* and *Strigamia chionophila* (Lithobiida: Lithobiidae) from Alberta and no centipedes from Saskatchewan. Other species listed above (Table 3) are not found in his province-level lists.

### ***Pauropods (Class Pauropoda)***

No species of Pauropoda are known from the Prairie Provinces of Alberta, Saskatchewan, and Manitoba, or in the neighbouring states to the south, Montana and North Dakota (Scheller 1984). Twenty-three species are known from elsewhere in Canada—with most of the diversity in Ontario, Québec, and British Columbia—and many more are predicted (Scheller 1984). Scheller's (1984) publication represents the first (and only?) published records of Canadian Pauropoda, although they are summarized by Behan-Pelletier (1993).

### ***Symphylans (Class Symphyla)***

Only two species have been reported from Canada, although up to 10 species are predicted to be discovered (Scheller 1979). *Scutigereilla immaculata* (Newport 1884) (Symphyla: Scutigereillidae), an introduced species, is known across Canada, including Alberta, although not specifically from the prairies (Scheller 1979; Kevan 1983; Behan-Pelletier 1993). *Symphylella vulgaris* (Hanson 1903) (Symphyla: Scolopendrellidae) has also been reported from Québec (Kevan 1983; Behan-Pelletier 1993).

## **Research Priorities**

Overall, taxonomy of these groups is in poor shape. Primarily because of the efforts of Hoffman, Shelley, and Shear, much of North American millipede taxonomy has undergone recent revision and the Canadian fauna has been mostly discerned. The other taxa are, however, in much worse shape. Few taxonomists are studying centipedes or isopods in North America, and few taxonomists globally are studying the North American fauna. Only a handful of people in the world study Pauropoda and/or Symphyla. Scheller has recently described species from Canada, the United States, and other countries, but no other researcher appears to be actively studying the North American fauna (Shear and Edgecombe 2009).

There are undoubtedly additional species of these five taxa in Canadian grasslands, both new to Canada and new to science (Scheller 1979, 1984; Kevan 1983); many of these may already be collected and are stored in museum collections. For non-insect arthropods, "knowledge of the diversity. . . still is very incomplete" (Behan-Pelletier 1993: 11) and taxonomy must be a research priority in order to facilitate full discovery of the biodiversity of the region. Determination of the geographical range of each species is another research priority that can go hand-in-hand with biodiversity discovery. This distribution information will be an important piece of conservation strategies for this region. Lastly, being little-studied and highly cryptic, the basic biology and ecology of most species within these groups are virtually unknown. Investigations in these areas are important to understanding the role of these species in grassland ecosystem functioning.

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## Chapter 3

# Plant-feeding Mites of the Canadian Prairies

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**Abstract.** The diversity of plant-feeding mites of the Canadian Prairies Ecozone is reviewed using the literature and collection records. At least 101 species of strictly phytophagous mites (Trombidiformes: 57 Eriophyoidea, 41 Tetranychoidae, three Tarsonemidae) and five presumed moss feeders (four Stigmaeidae, one Cryptognathidae) are present in the ecozone. In addition, species from at least two genera (Astigmata: *Rhizoglyphus*, *Tyrophagus*) that are primarily fungivorous can feed facultatively on plants, and approximately 40 species from several genera live in stored plant products, feeding on grains or associated fungi. A diversity of mites from at least 11 families in three orders (Mesostigmata, Trombidiformes, Sarcoptiformes) feed facultatively or obligatorily on floral products (pollen or nectar), including 15 species that are obligate associates of bees, mostly *Bombus* species. On the basis of records from the United States and the dearth of distribution and host association records for Canada, we predict the diversity of strict phytophages in the Canadian Prairies Ecozone to be at least 200 species. While many species (29) are associated with Poaceae (true grasses), we suspect that the poorer records for other plant families (e.g., Fabaceae (pea family), Asteraceae (aster or daisy family), Cyperaceae (sedges), Brassicaceae (crucifers)) common in the Prairies Ecozone merely reflect a lower collecting effort. At least 11 species were recorded on field cereal crops (including three fungivorous *Siteroptes* spp. (Siteroptidae), vectors of fungal pathogens), 11 on fruit crops, six from greenhouses (and three predicted to occur), six on weeds, nine on conifers, and 27 species on other hardwood trees and shrubs, including many urban ornamental plants. The biology and distribution of nearly all of these potential pests, and other species on native or naturalized hosts, are poorly documented. Their taxonomy is also poorly understood, since about two-thirds of the species are undescribed or have uncertain identities. Efforts targeting the taxonomy and biology of plant-feeding mites of the Canadian Prairies are needed to better understand, protect, control, and exploit the plant-associated mites of this region.

**Résumé.** La diversité des acariens phytophages de l'écozone des Prairies canadiennes est revue en utilisant la littérature et les données de récoltes disponibles. Au moins 101 espèces d'acariens strictement phytophages (Trombidiformes : 57 Eriophyoidea, 41 Tetranychoidae, trois Tarsonemidae) et cinq qui se nourrissent présumément de mousse (quatre Stigmaeidae, un Cryptognathidae) sont présentes dans les Prairies. En outre, les espèces provenant d'au moins deux genres (Astigmata : *Rhizoglyphus*, *Tyrophagus*) principalement fongivores peuvent facultativement se nourrir de plantes, et environ 40 espèces appartenant à plusieurs genres vivent dans les produits végétaux entreposés, se nourrissant de grains ou de champignons qui leurs sont associés. Une diversité d'acariens appartenant à au moins 11 familles de trois ordres (Mesostigmata, Trombidiformes, Sarcoptiformes) se nourrissent facultativement ou obligatoirement de produits floraux (pollen ou nectar), dont 15 espèces qui sont strictement associées aux abeilles, principalement à des espèces de *Bombus*. D'après les données sur les espèces présentes aux États-Unis, et considérant le manque de données sur la répartition géographique et les plantes-hôtes pour les espèces canadiennes, nous estimons que la diversité des phytophages strictes dans l'écozone des Prairies canadiennes est d'au moins 200 espèces. Alors que de nombreuses espèces (29) sont associées à des Poaceae (graminées vraies), nous soupçonnons que le peu de données disponibles pour d'autres familles de plantes (par exemple les Fabaceae (famille des pois), Asteraceae (famille des asters et des marguerites), Cyperaceae (laïches), et Brassicaceae (crucifères)) communes dans l'écozone des Prairies ne font que refléter un faible effort de

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récolte. Au moins 11 espèces ont été recensées sur des cultures de céréales (y compris trois espèces de *Siteroptes* (Siteroptidae) fongivores, vectrices de pathogènes fongiques), 11 sur des cultures fruitières, six dans les serres (et trois autres possibles pour la région), six sur des mauvaises herbes, neuf sur des conifères et 27 espèces sur d'autres arbres et arbustes feuillus, dont de nombreuses plantes ornementales en milieu urbain. La biologie et la distribution de la quasi-totalité de ces ravageurs potentiels sont peu connues, ainsi que celles d'autres espèces sur des hôtes indigènes ou naturalisées. Leur taxonomie est également mal comprise, puisqu'environ le deux tiers des espèces sont non décrites ou ont une identité incertaine. La recherche portant sur la taxonomie et la biologie des acariens phytophages des Prairies canadiennes doit être favorisée davantage afin de mieux comprendre, protéger, contrôler et exploiter les acariens associés aux plantes de cette région.

## Introduction

The Prairies Ecozone of Canada comprises a diverse set of habitats, where roughly 1,300 vascular and non-vascular plant species occur, either naturally or after unintentional introduction or escape from cultivation (Looman and Best 1987). Essentially all of these plants have mites using their leaves, stems, flowers, buds, bark, and roots as their foraging, reproducing, and sheltering grounds for part or all of their life cycle. Plant-associated mites include fungivores, saprophages, predators, parasites, phytophages, and omnivores and are a diverse group, though less diverse taxonomically than the mite faunas of soil and litter (Walter and Proctor 1999; Walter 2004). Phytophagy<sup>1</sup> evolved independently in several mite lineages (Krantz and Lindquist 1979; Lindquist 1998). However, major evolutionary radiations of phytophagy on vascular plants occurred in only two lineages of mites, both within the order Trombidiformes (Prostigmata): the Tetranychoida and the Eriophyoidea. Each superfamily comprises about 2,000 and 4,000 described species, respectively, which are all presumed to be strict phytophages, or “plant parasites” (Walter 2004; Mesa *et al.* 2009; de Lillo and Skoracka 2010; Migeon and Dorkeld 2013). Other prostigmatic mite taxa include essentially obligate phytophagous species: at least seven genera of Tarsonemidae, two genera of Penthaleidae, and one genus of Stigmaeidae. Representatives of all of these taxa occur in the Canadian Prairies Ecozone. Feeding on live plant tissues is exceptional in other mite groups and is mostly restricted to fungivorous or predatory forms that feed facultatively on plant tissues or on floral products—pollen and nectar.<sup>1</sup>

Mites can be detrimental to agriculture. They include pests of pome and stone fruits, berries, cereals, stored grains and other food products, vegetables, and ornamentals, as well as parasites that can drastically affect the health and populations of livestock (e.g., cattle ticks) or key pollinators (e.g., varroa mites on honey bees) (Helle and Sabelis 1985b; Lindquist *et al.* 1996; Sammataro *et al.* 2000; Lysyk 2011). Fortunately, many mites are also beneficial to agriculture, either directly or indirectly, by contributing to terrestrial and aquatic food chains and to nutrient cycling (Behan-Pelletier 1999), or by acting as biocontrol agents of crop pests and of weeds (Gerson *et al.* 2003). In sustainable agriculture systems based on the moderate use of softer (less toxic) chemical pesticides, predatory mite communities may play an important role in biological control, although

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<sup>1</sup> *Phytophagy* is here defined as feeding on a live plant substrate rather than consuming whole plants or plant parts (*herbivory*; Krantz and Lindquist 1979) (analogous to a parasite feeding on an animal host). In addition, we consider feeding on pollen and nectar to be a form of phytophagy in the broad sense, though distinct from feeding on live plant tissues. Although trombidiform and sarcoptiform mites commonly feed on microscopic algae, lichen, and especially fungi, this is not considered phytophagy here, nor is it treated in any detail, except where pests (of field crops or stored products) are concerned.

they are not often well understood or exploited (Bostanian *et al.* 2006; Beaulieu and Weeks 2007). Similarly, phytophagous mites that attack crop plants or weeds are understudied and often overlooked. Mites therefore may affect plants, particularly crops, more than we think because the symptoms produced are often subtle and overlooked, or mistaken for a nutrient deficiency or disease (Kane *et al.* 2012), and because mites are too small to be readily associated with observed symptoms. Even with fairly obvious symptoms, mites may still be deemed inoffensive. For example, the eriophyid mite *Vasates aceriscrumena* is a common pest for the sugar maple industry, but is not considered significant beyond disfiguring maple leaves, despite the fact that the spindle-shaped galls (0.5 mm long) that it induces on the leaves can sometimes cover entire trees (Patankar *et al.* 2012). However, it has been recently shown that the presence of these galls on a leaf can reduce leaf photosynthesis by 30 to 60% and that the presence of only a few galls can compromise gas exchange across the entire leaf (Patankar *et al.* 2011); tree growth and maple syrup yields may suffer similar drops, without anyone noticing. Can this be the case for crops in the Prairies or elsewhere in Canada? Given our limited knowledge of plant-feeding mites in the Prairies, we think it is certainly possible.

The existing information on plant-associated mites in the Prairies Ecozone, specifically grasslands, is minimal, and similar to that reported for grassland soil mites (Behan-Pelletier and Kanashiro 2010). Very few taxonomic surveys have been published, although the key to insect and mite galls of prairie trees and shrubs by Wong *et al.* (1977) is a major exception. Some brief accounts of plant-feeding mites in the Prairies have been presented within broader taxonomic or geographical contexts (Macnay and Creelman 1958; Lindquist *et al.* 1979; Ives and Wong 1988; Hiratsuka *et al.* 1995). In addition, interesting biological studies conducted on the poplar bud gall mite (Crane and Hiratsuka 1994; Kalischuk *et al.* 1997) and some bee-associated mites (*Parasitellus* spp., Richards and Richards 1976) in central and southwestern Alberta, respectively, have added to the knowledge of mites of the Prairies. Surprisingly little is known about pest species in the Prairies Ecozone. The biology of some mite pests of fruits that occur in the Prairies have been studied, but more largely in eastern Canada, British Columbia, or overseas (e.g., *Tetranychus schoenei*, Cagle 1943; *Bryobia rubrioculus*, Anderson and Morgan 1958; *Panonychus ulmi*, Herbert 1981, Lester *et al.* 1999; cf. Table 1). Although a few pests of field cereal crops and their diseases have been investigated (e.g., *Aceria tosichella*, Slykhuis 1956; *Tetranychus sinhai*, Wallace and Sinha 1965; *Siteroptes*, Arnott and Bergis 1967), they still remain poorly understood. By comparison, the taxonomic and ecological knowledge base for pests of pastures and cereals in other countries is starting to improve because of a recent increase in focused research (e.g., Australia: Halliday 2005; Arthur *et al.* 2011; Hill *et al.* 2012; Poland: Skoracka 2004; Skoracka and Kuczynski 2006). Further, mites associated with stored grains and oilseeds—an artificial habitat within grasslands (White *et al.* 2011)—were studied in detail by Sinha and others (e.g., Sinha 1963, 1964b, 1979; Sinha and Wallace 1966; White *et al.* 1979; Barker 1983). In contrast to those phytophagous mites, the dynamics and ecology of mites in stored grains are fairly well understood and, notwithstanding possible revision of some species concepts, useful identification tools are available for stored-product mites (e.g., Hughes 1976; Smiley 1991).

Here we describe and make some predictions on the diversity of plant-feeding mite groups (obligate and facultative) of the Canadian Prairies Ecozone, using the literature, unpublished surveys of mites (preserved in the Canadian National Collection of Insects, Arachnids and Nematodes (CNC)), and our own observations. We first summarize the main difficulties associated with taxonomic research on plant-feeding mites and conclude

**Table 1.** Mites feeding on vascular plants, mosses, floral products (pollen, nectar), or stored products in the Prairies Ecozone in Alberta (AB), Saskatchewan (SK), and Manitoba (MB), or from elsewhere in Canada (as a comparative reference; indicated under “Canada”), and their hosts, based on Canadian National Collection of Insects, Arachnids and Nematodes (CNC) specimens (indicated by +), the literature ((+)), or predictions of occurrence ((+)). Some fungivores that represent potential pests of crops/stored products as contaminants or vectors of plant pathogens are also included. (See key at end of table for other symbols).

Higher Taxa	Species	AB	SK	MB	Canada	Hosts, Habitats, Symptoms, Remarks (Selected Sources)
<b>Superorder Parasitiformes</b>						
<b>Order Mesostigmata: Suborder Monogynaspida</b>						
Ascoidea						
Ameroseiidae						
	<i>Ameroseius, Klemania</i> spp. <sup>(lit,pr,sp?)</sup>	+	+	+	+	Soil-litter, stored products, bracket fungi, animal nests
Melicharidae						
	<i>Proctolaelaps bombophilus</i> (Westerboet) <sup>(sp)</sup>	+				Bumble bee associates (also found in rodent nests elsewhere); probably feed on pollen stored in the nests (Lindquist <i>et al.</i> 2009; Klimov and OConnor 2004)
	<i>Proctolaelaps longanalis</i> (West.)	+				
	<i>Proctolaelaps longisetosus</i> (West.)	+	+	+	+	
	<i>Proctolaelaps ornatus</i> (West.)	+				
	<i>Proctolaelaps</i> spp. <sup>pr, lit, sp(?)</sup>	+	+	+	+	Soil-litter, corticolous habitats, stored products, nests
Dermanyssoida						
Laelapidae						
	<i>Melittiphis alvearius</i> (Berlese) <sup>(sp)</sup>			+	+	Honeybee hives (recorded in AB and SK, North of the Prairies Ecozone) (Crozier 1989)
	<i>Pneumolaelaps</i> nr <i>bombicolens</i> (Canestrini) <sup>(sp,pr)</sup>			+	+	Obligate associates of bumble bees ( <i>Bombus</i> spp.); some records from honeybee nests (records from Alberta are mostly from Prairie Bluff Mountain, near the western edge of the Prairies Ecozone) (Hunter and Husband 1973; Royce and Krantz 1989; Klimov and OConnor 2004)
	<i>P. longanalis</i> Hunter and Husband	(+)			+	
	<i>P. richardsi</i> Hunter and Husband	(+)				
	<i>P. sinhai</i> Hunter and Husband	(+)			+	
Parasitoidea						
Parasitidae						
	<i>Parasitellus hobbsi</i> (Richards) <sup>(sp,pr)</sup>	(+)			(+)	Obligate associates of bumble bees ( <i>Bombus</i> spp.); some records from honeybee hives (records from Alberta are from Prairie Bluff Mountain; Richards 1976; Richards and Richards 1976; Klimov and OConnor 2004)
	<i>P. favius</i> (Richards)	(+)	+	+	+	
	<i>P. inquinobombus</i> (Richards)	(+)				
	<i>P. pertheccatus</i> (Richards)	(+)	+	+	+	





Higher Taxa	Species	AB	SK	MB	Canada	Hosts, Habitats, Symptoms, Remarks (Selected Sources)
	<i>Aceria malherbae</i> Nuzzaci	(+)			(+)	Introduced for the control of field bindweed (leaf curling) (McClay and De Clerck-Floate 2013)
	<i>Aceria</i> nr <i>matricariae</i> Petanovic, Boczek, and Shi	+				Scentless chamomille ( <i>Matricaria perforata</i> Mérat, weed), witch's broom symptoms (V. Carney pers. comm.)
	<i>Aceria negundi</i> (Hodgkiss)	—(?)			+	<i>Acer negundo</i> L., whitish leaf erinea below, swellings above (Wong <i>et al.</i> 1977)
	<i>Aceria</i> cf. <i>neoartemisiae</i> (Keifer)	+	+	+		Pasture sage ( <i>Artemisia frigida</i> Willd.), white sagebrush ( <i>A. neoartemisiae</i> causes erineum and distorted flowers) (Fig. 2A)
	<i>Aceria parapopuli</i> (Keifer)	+	+	(+)	+	'Poplar bud gall mite'; woody proliferation around buds of <i>Populus</i> spp. and hybrids (Ives and Wong 1988; Crane and Hiratsuka 1994; Kalischuk <i>et al.</i> 1997)
	? <i>Aceria parulmi</i> Keifer	—(Δ?)			+	American elm ( <i>Ulmus americana</i> L.); finger-like galls on upper leaf surface (Ives and Wong 1988 (galls mentioned as caused by <i>A. ulmi</i> ))
	? <i>Aceria querci</i> (Garman)	—(Δ?)				<i>Quercus macrocarpa</i> Michx.; blisterlike galls on upper leaf surface, erinea underneath (Wong <i>et al.</i> 1977 (as <i>Eriophyes</i> sp.))
	<i>Aceria tosichella</i> Keifer sp. complex	+	+	+*	+	'Wheat curl mite'; wheat, Kentucky bluegrass (Slykhuus 1980; Skoracka <i>et al.</i> 2012)
	<i>Aceria ulmi</i> (Garman)	—(?)			(+)	Elms; inquiline in other mite galls (e.g. possibly caused by <i>A. parulmi</i> , see above) (J. Amrine pers. comm.; Rose and Lindquist 1997; Ives and Wong 1988; Hiratsuka <i>et al.</i> 1995)
	? <i>Aceria</i> (= <i>Eriophyes</i> ) <i>viburni</i> (Connold)	(Δ)				<i>Viburnum</i> sp.; erinose leaf patches (Amrine and de Lillo 2006; Walter and Latonas 2012)
	<i>Aceria</i> sp. 1		+			<i>Solidago</i> cf. <i>canadensis</i> L.
	<i>Aceria</i> sp. 2			+		Dotted blazingstar ( <i>Liatris punctata</i> Hook.)
	<i>Aculodes</i> nr <i>janboceki</i> Skoracka	+				Kentucky blue grass ( <i>Poa pratensis</i> )
	<i>Aculodes</i> nr <i>mckenziei</i> (Keifer)			+		Foxtail barley ( <i>A. mckenziei</i> is on cereals and grasses)
	<i>Aculodes</i> sp. 1			+		Sand reedgrass ( <i>Calamovilfa longifolia</i> Hook. (Scribn.))
	<i>Aculops</i> nr <i>hamátus</i> Liro			+		Wild mint ( <i>Mentha arvensis</i> L.)
	<i>Aculops lycopersici</i> (Tryon)	—	[+]		+	'Tomato russet mite' (greenhouses; on Solanaceae) (Zhang 2003)
	nr <i>Aculops</i> sp. 1		+			Spear willow
	<i>Aculus schlechtendali</i> (Nalepa)	—	[+]		+	'Apple rust mite' (minor apple pest)
	<i>Aculus</i> sp. 1		+			<i>Fraxinus pennsylvanica</i> Marsh. in a nursery

<i>Calepitrimerus nr achilleae</i> Roivammen	+			Yarrow ( <i>C. achilleae</i> is vagrant among leaf hairs)
<i>Calepitrimerus baileyi</i> Keifer	(+)	+		Crabapple, rolled and distorted leaves (Creelman 1971)
<i>Calepitrimerus nr cariniferus</i> Keifer	+			White sagebrush ( <i>Artemisia ludoviciana</i> Nutt.)
<i>Cecidophyes rouhollahi</i> Craemer	+?			Introduced for control of <i>Galium</i> spp.; probably not established, since no sign of overwinter survival (McClay 2013)
<i>Cecidophyopsis hendersoni</i> (Keifer)	+	+		<i>Yucca</i> sp. (can cause leaf browning)
<i>Epitimerus trilobus</i> (Napella)	(+)			<i>Sambucus racemosa</i> L., deformed leaves (Walter and Latonas 2012)
<i>Eriophyes laevis</i> (Nalepa)	—	(?)	—	Small beadlike galls on <i>Alnus</i> leaves (Wong <i>et al.</i> 1977)
<i>Eriophyes cf. prunicurmena</i> (Walsh)/ <i>emarginatae</i> Keifer	+	Δ	+	Chokecherry ( <i>Prunus virginiana</i> L.), small pocket or short spindle galls on leaf upper surface (Fig. 1A) (Wong <i>et al.</i> 1977; Ives and Wong 1988)
<i>Eriophyes pyri</i> (Pagenstecher)	(+)		+	'Pear leaf blister mite' (reddish swellings on leaves) (Macnay and Creelman 1958)
<i>Eriophyes nr similis</i> Nalepa	+			Plum; spindle galls on lower leaf surface (Fig. 1B) (Ives and Wong 1988 (as <i>E. nr padi</i> ); M. Dolinski pers. comm.)
<i>Eriophyes</i> sp.	—	(?)	—	<i>Amelanchier alnifolia</i> Nutt.; nipplelike galls on leaf underside, erineae above (Wong <i>et al.</i> 1977 (as <i>E. cerasicrumena</i> (Walsh))
<i>Leipothrix</i> sp. 1		+		<i>Galium cf. boreale</i> L.
<i>Leipothrix</i> sp. 2		+		Greenhouse tomatoes
? <i>Phyllocoptes didelphis</i> Keifer	Δ		+	Trembling aspen (Fig. 1C-D), erineum on lower leaf surface, bulging above, saclike (mentioned as <i>Eriophyes</i> sp. in: Ives and Wong 1988; Hiratsuka <i>et al.</i> 1995)
<i>Tetra cf. lobulifera</i> (Keifer)			+	'Cottonwood leafcurl mite'; trembling aspen (Coyle and Amrine 2004)
<i>Tetra nr nielseni</i> Keifer			+	American elm ( <i>T. nielseni</i> causes leaf browning)
<i>Tetra</i> sp. 1		+		Wild licorice ( <i>Glycyrrhiza lepidota</i> Nutt. (Pursh.)) (Fig. 2B)
<i>Vasates quadrripedes</i> Shimer sp. complex	+		+	'Maple bladder gall mite'; <i>Acer saccharinum</i> L., <i>Acer</i> spp. (Wong <i>et al.</i> 1977; Ives and Wong 1988)
Eriophyiidae sp.	—	(?)	—	<i>Corylus cornuta</i> , yellow erineae on upper leaf surface (as <i>Eriophyes</i> sp.) (Wong <i>et al.</i> 1977)
Eriophyiidae spp.	—	(?)	—	<i>Betula</i> spp., leaf erineae and aborted buds (as <i>Eriophyes</i> ) (Wong <i>et al.</i> 1977)
Eriophyiidae spp.	—	(?)	—	<i>Ulmus americanus</i> and <i>Ulmus</i> sp., globose or pouchlike leaf galls (as <i>Eriophyes</i> spp.) (Wong <i>et al.</i> 1977)

Higher Taxa	Species	AB	SK	MB	Canada	Hosts, Habitats, Symptoms, Remarks (Selected Sources)
	?Eriophyidae spp.	—	(?)	—	—	<i>Salix</i> spp., various leaf galls (as <i>Eriophyes</i> spp.) (Wong <i>et al.</i> 1977)
Phytoptidae						
	<i>Nalepella halounga</i> Keifer	+			+	White spruce in a nursery (causes browning of needles) (Marshall and Lindquist 1972)
	<i>Nalepella tsugifoliae</i> Keifer		+		+	Blue spruce ( <i>Picea pungens</i> Engelm.) in a nursery (also on eastern hemlock elsewhere; browning of needles)
	<i>Nalepella</i> spp.		+		+	Spruces ( <i>Picea</i> spp.)
	<i>Oziella yuccae</i> (Keifer)	(+)				<i>Yucca</i> sp., causing leaf blight (Steiner 1982)
	? <i>Phytoptus abnormis</i> Garman	—	(?)	—	+	<i>Tilia americana</i> L.; club-shaped galls on upper leaf surface (Wong <i>et al.</i> 1977)
	<i>Setoptus nr flexilis</i> Keifer	+*				under needle sheaths of a pine tree
	<i>Trisetacus gemmavittatus</i> Styer, Nielsen, and Balderston	+			+	'Pine rosette mite'; <i>Pinus bankstiana</i> Lamb.; aborted buds and stunted needles (Ives and Wong 1988)
Erythraeoidea (Parasitengonina)						
Erythraeidae						
	<i>Balaustium</i> spp. <sup>pr,po,ph</sup>	+	+	+	+	Plants and litter
Eupodoidea (Eupodides)						
Penthaeidae						
	<i>Penthaleus major</i> (Dugès) <sup>ph</sup>	—	[+]	—	+	'Winter grain mite'; pest of pasture and cereals; records from British Columbia, eastern Canada, and South Dakota (Streu and Gingrich 1972)
Pygmephoroida (Heterostigmatina)						
Siteroptidae						
	<i>Siteroptes avenae</i> (Müller) <sup>u</sup>	+		+	+	Wheat, barley, Kentucky bluegrass (vector of <i>Fusarium</i> to cereals and of carnation bud rot) (Fig. 3A-C) (Suski 1973; Zhang 2003)
	<i>Siteroptes cerealium</i> (Kirchner)			+	+	
	<i>Siteroptes nr reniformis</i> Krantz		+		+	Wheat, barley (vector of <i>Nigrospora</i> ; Fig. 3D) (Laemmlein and Hall 1973)
Raphignathoidea (Raphignathina)						
Cryptognathidae <sup>ph?</sup>						
	<i>Favognathus</i> sp.	(+)				Litter (suspected to feed on moss) (Waller and Latonas 2012)

Stigmaeidae							
<i>Eustigmaeus frigida</i> (Habeeb) <sup>ph(manuscript?)</sup>	(+)	(+)	(+)	(+)	(+)	Moss, wood and soil in meadow and boggy habitats (Gerson 1972; Walter and Latonas 2012; D. Walter pers. comm.)	
<i>E. gersoni</i> Wood	(+)	(+)	(+)	(+)	(+)	Soil where mosses and algal masses were present	
<i>E. rhodomela</i> (Koch)	(+)	(+)	(+)	(+)	(+)	Soil (elsewhere: mosses in open soils)	
<i>E. segnis</i> (Koch)	(+)	(+)	(+)	(+)	(+)	Spruce litter, aspen litter	
Tarsonemoidea (Heterostigmatina)							
Tarsonemidae							
<i>Phytonemus</i> (= <i>Stenotarsonemus</i> , = <i>Tarsonemus</i> ) <i>pallidus</i> (Banks) <sup>ph</sup>	(+)	(+)	(+)	(+)	(+)	'Cyclamen mite' or 'strawberry mite', strawberries, ornamentals (Bird and Mitchener 1954; Zhang 2003)	
<i>Polyphagotarsonemus latus</i> (Banks) <sup>ph</sup>	—	[+]	—	—	—	'Broad mite' (polyphagous pest of greenhouses)	
<i>Stenotarsonemus</i> spp. <sup>ph</sup>	+	+	+	+	+	Prairie grass and sod (mainly Poaceae associates)	
<i>Tarsonemus granarius</i> Lindquist <sup>tu</sup>	+	+	+	+	+	Stored wheat and oats (Lindquist 1972; Sinha 1979)	
<i>Tarsonemus</i> spp. <sup>tu(wsp?)</sup>	+	+	+	+	+	Litter and plants, stored grains	
Tetranychoida (Raphignathina) <sup>ph</sup>							
Linotetrinidae							
<i>Linotetrans</i> nr <i>cylindricus</i> sensu Baker	+	+	+	+	+	Grassland soil (Fig. 4B) (Baker 1953; Lindquist <i>et al.</i> 1979)	
Tenuipalpidae							
<i>Aegyptobia nomus</i> Pritchard and Baker	+	+	+	+	+	(Mesa <i>et al.</i> 2009; Beard <i>et al.</i> 2012 <i>et</i> ) Salgrass ( <i>Distichlis stricta</i> Torr. (Rydb.)) (witch's broom symptoms) (Crocker <i>et al.</i> 1982)	
<i>Aegyptobia</i> ( <i>macswaini</i> group) sp. A	+	+	+	+	+	<i>Opuntia</i> sp.	
<i>Aegyptobia</i> ( <i>tragardhi</i> group) sp. B	+	+	+	+	+	Juniper and underlying litter	
<i>Brevipalpus phoenicis</i> (Geijskes) sp. complex	+*	+	+	+	+	Palms (pest of greenhouse ornamentals)	
<i>Brevipalpus</i> ( <i>portalis</i> group) sp. A	+	+	+	+	+	<i>Mentha arvensis</i> , <i>Lycopus asper</i> Greene	
<i>Brevipalpus</i> ( <i>cuneatus</i> group) sp. A	+	+	+	+	+	<i>Cirsium</i> sp.	
<i>Brevipalpus</i> ( <i>cuneatus</i> group) sp. B	+	+	+	+	+	Dotted blazingstar ( <i>Liatris punctata</i> )	
<i>Brevipalpus</i> ( <i>cuneatus</i> group) sp. C	+	+	+	+	+	Stiff goldenrod ( <i>Solidago rigida</i> L.)	

Higher Taxa	Species	AB	SK	MB	Canada	Hosts, Habitats, Symptoms, Remarks (Selected Sources)	
	<i>Brevipalpus (cuneatus group) sp. D</i>			+		Red osier dogwood ( <i>Cornus sericea</i> L.)	
	<i>Dolichotetranychus cf. carnea</i> Banks	+				Saltgrass (Khanjani <i>et al.</i> 2011)	
	<i>Dolichotetranychus nr salinas</i> Pritchard and Baker	+				Grass and sod	
	<i>Dolichotetranychus n. sp. A</i>	+				Grass and sod (Fig. 4A)	
	<i>Pentamerismus n. sp. nr erythreus</i> (Ewing)	+				Juniper and underlying litter (Khanjani and Gotoh 2008)	
	Tetranychidae						
	<i>Bryobia praetiosa</i> Koch sp. complex	+	+	+	+	(Baker and Tuttle 1994) 'Clover mite'; pest of pasture, lawns and buildings (Morgan and Anderson 1957; Anderson and Morgan 1958)	
	<i>Bryobia n. sp. 1 (praetiosa sp. complex)</i>	+	+			Cultivated timothy ( <i>Phleum pratense</i> L.) (Fig. 2C)	
	<i>Bryobia rubrioculatus</i> (Scheuten)	—	(+)	—	+	'Brown mite'; minor pest of fruit trees ( <i>Malus</i> , <i>Prunus</i> spp.; Macnay and Creelman 1958; Herbert 1965)	
	<i>Eotetranychus frosti</i> (McGregor)	+			+	<i>Rubus cf. idaeus</i> L. (elsewhere: <i>Rubus</i> , <i>Rosa</i> spp.)	
	<i>Eotetranychus populi</i> (Koch)	+	+		+	<i>Populus</i> spp. (pest of poplars and willows; Jeppson <i>et al.</i> 1975)	
	<i>Eotetranychus cf. potentillae</i> Tuttle and Baker	+				<i>Potentilla</i> sp.	
	<i>Eotetranychus sp. 1</i>	+				Poaceae sp.	
	<i>Monoceronychus n. sp. nr aristidae</i> Tuttle and Baker	+				Grass sod; <i>Opuntia</i> sp.	
	<i>M. n. sp. nr aristoides</i> Tuttle and Baker	+				Winter wheat (Fig. 4C)	
	<i>M. nr bouteloua</i> Baker and Tuttle	+				Grass sod	
	<i>Neopetrobia nr dubinini</i> Wainstein	+				Grass sod	
	<i>N. nr mcgregori</i> (Pritchard and Baker)	+				Grass and sod	
	<i>Oligonychus laricis</i> Reeves		+			<i>Larix sibirica</i> Ledeb. ( <i>Larix</i> spp. elsewhere)	
	<i>Oligonychus milleri</i> (McGregor)	+			+	<i>Pinus contorta</i> Dougl. ( <i>Pinus</i> spp. elsewhere) (Landwehr and Allen 1982)	
	<i>Oligonychus pratensis</i> (Banks)	+	+			'Banks grass mite'; wheat, turfgrass (Kentucky bluegrass) (elsewhere also a pest of corn and sorghum) (Margolies 1987)	

<i>Oligonychus ununguis</i> (Jacobi)	+	+	+	+	'Spruce spider mite'; pest of conifers (Ives and Wong 1988)
<i>Panonychus citri</i> (McGregor)	(+)				'Citrus red mite'; ornamental plants (Steiner 1982; Steiner and Elliot 1987)
<i>Panonychus ulmi</i> (Koch)				[+]	'European red mite'; fruit tree ( <i>Malus</i> , <i>Prunus</i> ) pest
<i>Petrobia latens</i> (Müller)	+	+	+	+	'Brown wheat mite'; barley, winter wheat, alfalfa (Smidansky and Carroll 1996)
<i>Schizotetranychus celtidis</i> McGregor	+				Grass and sod
<i>Schizotetranychus</i> cf. <i>elymus</i> McGregor	+				Winter wheat, grass and sod
<i>Schizotetranychus schizopus</i> (Zacher)	+				Willows ( <i>Salix</i> spp.) (Duncan and Lindquist 1989)
<i>Schizotetranychus</i> nr <i>shizopus</i>		+			Willow
<i>Tetranychus mcdanieli</i> McGregor	+	+	+	+	'McDaniel spider mite'; raspberries, <i>Rubus</i> spp., red currants, apple, plum, Caragana, herbs (also on <i>Amelanchier alnifolia</i> , K. Fry pers. comm.) (Roy <i>et al.</i> 1999)
<i>Tetranychus pacificus</i> McGregor	+	(+)	(+)	+	Fruit trees ( <i>Malus</i> , <i>Prunus</i> spp.), black currants (Macnay and Creelman 1958)
<i>Tetranychus schoeneti</i> McGregor	+			+	Wild strawberries (elsewhere: several Rosaceae; elms) (Cagle 1943; Szezepeaniec <i>et al.</i> 2011)
<i>Tetranychus sinhai</i> Baker	+			+	Barley, wheat, rye, corn (Wallace and Sinha 1965)
<i>Tetranychus urticae</i> (Koch)	+	+	+	+	'Two-spotted spider mite'; alfalfa, peas, ornamental flowers, fruit trees, small fruit crops, wheat
Tuckerellidae					
<i>Tuckerella hypoterra</i> McDaniel and Morihiro				[+?]	Recorded from grass sod in South Dakota (McDaniel and Bolen 1982)
Tydeoidea (Eupodides) <sup>(supr,po,ph?)</sup>					8 species in stored grains; also on foliage and tree bark (Momen and Sinhai 1991)
<b>Order Sarcoptiformes: Suborder Oribatida</b>					
<b>Cohort Asigmatina</b>					(Sinha 1963; Sinha 1964b; Hughes 1976; O'Connor 2009)
Acaroidea					
Acaridae					
<i>Acarus farris</i> (Oud.) <sup>(s,gr)</sup>	+	+	+	+	'Grain mites'; stored grains (can feed on cereal endosperm) and other plant or animal products (e.g. flour, cheese)
<i>Acarus immobilis</i> Griffiths	+	+	+	+	
<i>Acarus siro</i> L.	+	+	+	+	
<i>Acotyledon</i> and <i>Neoacotyledon</i> spp.	+	+	+	+	Stored grains (also in vertebrate nests)
<i>Aleuroglyphus ovatus</i> (Troupeau) <sup>(s,gr)</sup>	+	+	+	+	'Brownlegged grain mite'; stored plant products

Higher Taxa	Species	AB	SK	MB	Canada	Hosts, Habitats, Symptoms, Remarks (Selected Sources)
	<i>Kuzinia laevis</i> (Dujardin) <sup>po,lu</sup>			+	+	<i>Bombus terricola</i> Kirby (obligate associate of bumble bees) (Klimov and OConnor 2004)
	<i>Mycetoglyphus fungivorus</i> (Oud.) <sup>lu(ph)</sup>			+	+	Barley field, stored grains, agricultural soil (Nakao 1989 (feeding on spinach))
	<i>Rhizoglyphus robini</i> Claparède <sup>lu,ph</sup>	+	+	+*	+	'Bulb mites'; bulbs, onions, canola roots, soil, litter (Diaz <i>et al.</i> 2000; Fan and Zhang 2004)
	<i>Rhizoglyphus</i> spp.			+	+	Bulbs, soil
	<i>Sancassania anomala</i> (Nesbitt) <sup>lu</sup>			+	+	Stored grains, decaying vegetation, soil
	<i>Sancassania berlessei</i> (Michael) sp. complex			+	+	Stored grains, mushroom beds
	<i>Tyrophagus entomophagus</i> (Laboulbène and Robin) <sup>lu</sup>	—	(+)	—	+	Stored products (Sinha 1964 <i>b</i> )
	<i>Tyrolichus casei</i> (Oud.) <sup>lu</sup>			+		'Cheese mite'; stored products, bee brood
	<i>Tyrophagus permiciosus</i> Zakhvatkin <sup>lu(ph,gr)</sup>	+	+	+	+	Stored grains, indoor plant, soil, honey bee nest (Fan and Zhang 2007)
	<i>Tyrophagus putrescentiae</i> (Schrank)	+	+	+	+	'Mould mite'; stored products, diseased plants (Zhang 2003; Fan and Zhang 2007)
	<i>Tyrophagus similis</i> (Volgin)	+			+	Pasture, stored barley
Suidasiidae						
	<i>Suidasia nesbitti</i> Hughes <sup>lu</sup>			+	+	'Scaly grain mite'; stored products
	<i>Tortonia</i> spp. <sup>po</sup>	+		+	+	Cleptoparasites in nests of leafcutter bees and mason bees (Megachilidae), alfalfa foliage (Klimov and OConnor 2004; Walter and Latonas 2012)
Gycophagoidea						
Aërogllyphidae						
	<i>Aërogllyphus robustus</i> (Banks) <sup>lu(ger)</sup>	+		+	+	Stored grains, vespid wasp nest (Sinha 1966 <i>a</i> )
Chortoglyphidae						
	<i>Chortoglyphus arcuatus</i> (Troupeau) <sup>lu</sup>			+*	+	Stored grains
Glycophagidae						
	<i>Ctenoglyphus plumiger</i> (Koch) <sup>lu</sup>	—	(+)	—	+	Stored grains, hay stacks
	<i>Glycophagus domesticus</i> (DeGeer) <sup>lu(ger)</sup>	+*	+	+	+	Stored grains, bee hives

<i>Glycyphagus (Lepidoglyphus) destructor</i> (Schränk) <sup>(u,gr)</sup>	(+)	+	+	+	'Long-haired mite'; stored grains and other food products
<i>Glycyphagus (L.) michaeli</i> (Oud.)		+		+	Stored grains
<i>Gohieria fusca</i> (Oud.) <sup>(u)</sup>		(+)	+	+	'Brown flour mite'; stored grains (Sinha 1974)
Hemiscaroptoidea					
Carpoglyphidae					
<i>Carpoglyphus lactis</i> (L.) <sup>(u,po)</sup>	+		+	+	'Dried-fruit mite'; honey bee hives (typically on products with high sugar content) (Sinha 1966b)
Hemisarcopidae					
<i>Namacarus minutus</i> Oud. <sup>(u)</sup>		+		+	Stored wheat (elsewhere: in vertebrate nests) (Sinha 1974)
Winterschmidtidae					
<i>Acalvolia squamata</i> (Oud.) <sup>(u)</sup>		+		+	On grain-infesting insects (beetles, psocids) (Barker 1993)
<i>Procalvolia cf. zacheri</i> (Oud.) <sup>(u)</sup>		+	+	+	Stored grains
<b><i>Oribatida sensu stricto</i></b> <sup>(u,po,pr)</sup>		+	+	+	Essentially fungivores-detritivores in soil and on plants; some spp. occasional in mouldy grains and baled hay; facultative phytophagy rare (Norton and Behan-Pelletier 2009; Behan-Pelletier and Kanashiro 2010)
Hydrozetoidea					
Hydrozetidae					
<i>Hydrozetes</i> spp. <sup>(ph)</sup>	(+)	+		+	Immatures burrow within duckweed ( <i>Lemma</i> spp.) (Walter <i>et al.</i> 2013)

**KEY:**

Feeding habits as follows (indicated after taxa names):

ph – feeds on live tissues of vascular plants or mosses (phytophage)

ne – nectar

po – pollen

fu – fungi

gr – stored grains

pr – predators

Feeding habits indicated within parentheses represent facultative behavior, or suspected behavior based on limited observations.

Other symbols:

? – indicates uncertainty about species identity, feeding habit, or province in which species occurs

Δ – species identity is based on plant symptoms (gall type)

\* – specimens were identified by Evert Lindquist or Ian Smith, and not retained at the CNC

Most species recorded from the CNC were collected and identified by the authors (many Tetranychoida and Eriophyoidea), or verified by them in the case of previous identifications made by others. When consistent across a genus or higher taxa, feeding habits and literature sources are indicated only once. Strictly predatory or parasitic mites in stored products are excluded here.



with a discussion of the key aspects of their dispersal potential and invasiveness within the context of current intense international trade and global climate change. Given the pivotal role of agriculture in the Prairie Provinces, we also highlight some of the (potential) pest species of crops and stored products and the diseases that they may transmit.

### Taxonomic and Biological Hurdles

Plant-feeding mites are small, mostly 0.1–0.8 mm long, and are often unnoticed in the field or incorrectly identified. Accurate identifications of mites are made difficult not only by their small size, but also by the need for specialized equipment and training. Although families and some genera can be identified with a hand lens on the basis of their general shape, colour, and behaviour, this is usually impossible for species identification. An important exception are well-known gall-inducing eriophyoids, which can be identified by using the host plant and associated damage, because each species typically causes a specific type of gall on a single host. For most other mites, accurate species identification requires examination at 400× or 1,000× magnification, using a compound microscope equipped with phase contrast or differential interference contrast technology. Even with a suitable microscope and acarological experience, many taxa cannot be identified to species or even genus (see Table 1). This is due to a general lack of keys to genera and species, inadequate species descriptions, poorly defined generic concepts, and too many species remaining undescribed.

The difficult taxonomy of mites is complicated by their reproductive patterns. Most plant-feeding mite groups are arrhenotokous, in which unfertilized eggs hatch into haploid males and fertilized eggs into diploid females (Norton *et al.* 1993; Lindquist 1998), giving rise to field sex ratios of one male to three or more females. Unfortunately, for many genera of spider mites (Tetranychidae), the (rarer) males are required to confirm identity because the females of closely related species can be nearly identical (Baker and Tuttle 1994). Moreover, the critical feature for species recognition is the shape of the aedeagus in a perfectly lateral view; this orientation is difficult to achieve during slide mounting and often leaves room for some taxonomic doubt. In the case of thelytokous (all-female) species, the male characters are not even available for study. However, this may result from endosymbiotic *Wolbachia* or *Cardinium* bacteria that feminize males (common among bryobiine spider mites and *Brevipalpus* spp. (Tenuipalpidae); Weeks *et al.* 2001; Ros *et al.* 2008). Another problem faced when working with a certain group of mites (Eriophyoidea) is that many species exhibit two morphologically distinct types of females (a protogyne, representing females of one or more summer generations, and a deutogyne, which emerge in mid- or late summer). The deutogyne will seek refuge for aestivating and/or overwintering (e.g., under tree bark scales) until early spring when she begins laying eggs that develop into protogynes. The two (conspecific) morphs may be (wrongly) assigned to different species or even genera (Jeppson *et al.* 1975), although the forms can generally be correctly associated with each other with experience and good sample sizes.

Molecular markers represent an invaluable complementary tool to alleviate these problems associated with morphological identifications by strengthening species (and generic) concepts and clarifying complexes of morphologically similar species or the conspecificity of variable populations (e.g., Gotoh *et al.* 2009; Skoracka *et al.* 2012). However, species-level markers have been developed for perhaps only 50 species of spider mites (e.g., de Mendonça *et al.* 2011; Matsuda *et al.* 2012) and for fewer tenuipalps and eriophyoids (Mata *et al.* 2010; Navajas and Navia 2010), and so the groundwork for

assigning DNA bar codes to species is yet to be done. Moreover, molecular work on mites can be a daunting task since specimens can easily be lost during DNA extraction, and the extreme small size of some eriophyoids, 0.1–0.3 mm long, may require the use of several specimens for a single extraction.

The list of species of Eriophyoidea, Tetranychidae, and Tenuipalpidae recorded from the Prairies Ecozone (Table 1) shows the lack of taxonomic and distributional data. Only 32% (18 of 57 species) of eriophyoids are identified to species with relative certainty, and most species have few locality records. One-third (9 of 27 species) of tetranychid species are undescribed or have uncertain identity, and approximately one-third (~6 of 18) of the named species listed have not been mentioned in the literature for Canada. Four tetranychids were previously recorded only from Arizona (*Eotetranychus potentillae*, *Monoceronychus boutelouae*, *Schizotetranychus celtidis*) or Florida (*Neopetrobia mcgregori*), and two undescribed species (*Monoceronychus* n. sp. nr *aristidae*, *M.* n. sp. nr *aristoides*) have their closest known relatives (*M. aristidae*, *M. aristoides*) recorded only from Arizona (Baker and Tuttle 1994). Among the 13 tenuipalpid species recorded from the Prairies Ecozone, only one could be identified with certainty (*Aegyptobia nomus*), and several others likely represent undescribed species (Table 1).

The host range of most species is based on only a few collecting records, and the biology is based on predictions made from limited knowledge of related pest species. When a mite is noticed in the field, it is sometimes assumed (wrongly) to be a cosmopolitan or common pest (e.g., the “two-spotted spider mite” on greenhouse plants, or the “wheat curl mite” on cereals), but such incorrect assumptions of identities can result in poor pest management decisions (Huber *et al.* 2002) that lead to both crop and economic losses.

Determination of the feeding habits of a mite, and of the associated plant symptoms, is difficult. The main diets of many taxa remain uncertain (e.g., genera of tydeoids, tarsonemids, stigmatids, eupodids), sometimes because the results of a few studies conflict, for example, when a previously assumed predator may behave as a fungivore or phytophage, or vice versa (Krantz and Lindquist 1979; Walter 1987b; Walter *et al.* 2009). Similarly, feeding habits have sometimes been observed to differ broadly between congeneric species, and even conspecific life stages (e.g., Evans 1992; MacLennan *et al.* 1998; Halliday 2001). In those cases, categorizing a species or genus into a broad feeding group (e.g., predator or fungivore) is impossible. Even well-known predators such as the phytoseiids commonly feed on pollen and nectar, and some apparently feed on leaf tissues (Ader *et al.* 2012), as is also suspected for other “predators” (*Zetzellia*, Santos 1991; *Balaustium*, Arthur *et al.* 2011). Many fungivorous astigmatic mites also feed on live plant tissues or on cereal grains (Sinha 1979; Zhang 2003). Omnivory, or a non-specialized diet, is therefore more common than was assumed in the past (Walter 1987b). In many cases, however, proper experiments to elucidate feeding habits are simply lacking (e.g., Lesna *et al.* 2009), and distinctive dietary preferences and adaptations may truly exist between related genera and species (Krantz and Lindquist 1979; Walter and Ikonen 1989; McMurtry and Croft 1997; Beard and Walter 2001).

In the field, host plant damage is difficult to notice unless a dense population is present, because most plant-feeding mites feed on one or a few plant cells at a time by piercing the epidermis and ingesting the cell contents (Lindquist 1998; Beard *et al.* 2012b). However, the feeding activity of mites can cause conspicuous or drastic effects, such as stunting of plants, galling, leaf chlorosis, bronzing, cracking, and necrosis, though the mechanisms for these effects are poorly understood. In some cases, the damage involves toxins in the mites’ saliva, or viruses or other pathogens that may be transmitted by the mite

(Tomczyk and Kropczyńska 1985; Westphal and Manson 1996; Childers *et al.* 2003a); distinguishing viral symptoms from the effects of the mite phytotoxins can be difficult and time-consuming because of their similarity (e.g., *Brevipalpus* feeding and citrus leprosis symptoms; Childers *et al.* 2003a). Moreover, determining whether a pathogen's main vector is a mite or a co-occurring phytophagous pest can be problematic (e.g., *Siteroptes* and silver top of grasses; see below). Fortunately, the small size of mites together with their usually rapid development and high fecundity provide one advantage: they are relatively easy to culture and study in the laboratory (Walter 1987b; Gerson *et al.* 2003; Sobhian *et al.* 2004).

### Parasitiformes: Order Mesostigmata

In the superorder Parasitiformes, which includes the ticks (Ixodida) and the diverse mesostigmatic mites, feeding on live plant tissues appears to be rare except for pollen and nectar feeding in some groups (Lindquist *et al.* 2009; but see Ader *et al.* 2012). Non-parasitic Mesostigmata are predominantly predators, with fungivory—obligate or facultative—exhibited by some species in a few families. Some of these fungivores may feed opportunistically on pollen, for example, species of *Ameroseius*, *Kleemanina* (Ameroseiidae), and *Proctolaelaps* (Melicharidae), which have representatives in litter and plant-associated habitats (e.g., bracket fungi, bark beetle galleries) in the Prairies (Evans and Till 1979; Lindquist *et al.* 2009) (Table 1). Some *Kleemanina*, *Proctolaelaps*, and a few uropodoids (e.g., *Trichouropoda* (= *Leiodinychus*) *orbicularis*) can infest stored food products, where they feed on moulds (Hughes 1976). Facultative feeding on pollen and plant exudates is also common for predatory mites in the family Phytoseiidae. These include most of the acarine biocontrol agents that are used to manage mite (e.g., spider mites, eriophyoids) and insect pests (e.g., thrips; Gerson *et al.* 2003). Such plant-produced resources are particularly important for species used in biological control since they can sustain populations when prey is scarce, and indeed many predatory species can be reared solely on a pollen diet (e.g., *Euseius* spp., McMurtry and Croft 1997). Some experiments indicate that certain phytoseiids also feed directly on leaf tissue, although without significant damage to the plant (Nomikou *et al.* 2003; Ader *et al.* 2012). At least 30 species of phytoseiids are recorded from the Prairie Provinces (Chant and Hansell 1971; Chant *et al.* 1974; de Moraes *et al.* 2004; Table 1), and many may feed opportunistically on pollen and extra-floral nectar.

Some mesostigmatic mites are pollen-feeding cleptoparasites of apid bees. Four species of *Proctolaelaps* are associated with bumble bees (*Bombus* spp.) and probably feed on pollen stored in their nests (Lindquist *et al.* 2009; Table 1), similarly to certain members of Laelapidae and Parasitidae. *Melittiphis alvearius* (Laelapidae), sometimes called the “pollen mite” (Knihinicki and Halliday 1995), was introduced to North America from New Zealand in 1985 in bee packages (Davis and McRory 1987; Crozier 1989) and has since become established in North America, including the Canadian Prairie Provinces. It feeds on pollen in honey bee hives (Gibbins and van Toor 1990; Eickwort 1994). At least three species of *Pneumolaelaps* (Laelapidae) and four of *Parasitellus* (previously *Parasitus* spp.; Parasitidae) are associated with bumble bees in the Prairie Provinces (Hunter and Husband 1973) and can be fairly common in their nests (Richards and Richards 1976; Crozier 1989). *Pneumolaelaps* and *Parasitellus* feed on the nectar coating and surface compounds of pollen grains and possibly also prey or scavenge on injured or dead bees and other invertebrates in the nest, including mites (Costa 1966; Richards 1976; Royce and Krantz 1989; Koulianos and Schwarz 1999). All of these pollen-feeding mites disperse

phoretically (the term given to organisms that can be transported from one place to another on other species) on their bee hosts, but, although they feed on their hosts' provisions, their impact appears to be of little or no concern to apiculture. In fact, *Parasitellus* may even be beneficial to bumble bees by feeding on their parasitic nematodes (Schousboe 1987). Other mesostigmatans occur in beehives in Canada, but are parasites (e.g., *Varroa destructor* Anderson and Trueman, Williams *et al.* 2009), predators of microarthropods, or have unknown feeding habits (Eickwort 1994).

In contrast to the mites associated with bees, the pollen- and nectar-feeding ameroseiids and melicharids that are associated with hummingbirds and other flower-visiting animals in warmer regions (e.g., Velazquez and Ornelas 2010) appear to be absent from Canada. Personal observations (WK) suggest that none of those pollen-feeding mite groups are associated with hummingbirds in Alberta.

### **Acariformes: Order Trombidiformes (Suborder Prostigmata)**

In Trombidiformes, two superfamilies are entirely composed of obligate plant feeders (Eriophyoidea, Tetranychoidae), and three families (Tarsonemidae, Penthalpidae, Stigmaeidae) have at least some members that primarily or exclusively feed on plants. In addition, other trombidiform mites (e.g., Tydeoidea) may feed facultatively on plant tissues, or at least on pollen or plant exudates, including many otherwise predatory mites (e.g., some Anystidae, Stigmaeidae, and Erythraeidae). However, the feeding habits of other families are largely unknown, and phytophagy has not yet been entirely excluded for these mites (e.g., Homocaligidae, Kethley 1990). Cryptognathid mites, at least one species of which occurs in the Prairies Ecozone, may feed on mosses (Table 1), as may the moss-dwelling penthalodids (Krantz and Lindquist 1979), though other penthalodids are suspected predators or microbivores (Strandtmann 1971; Walter *et al.* 2009).

#### ***Anystidae (Anystina: Anystoidea)***

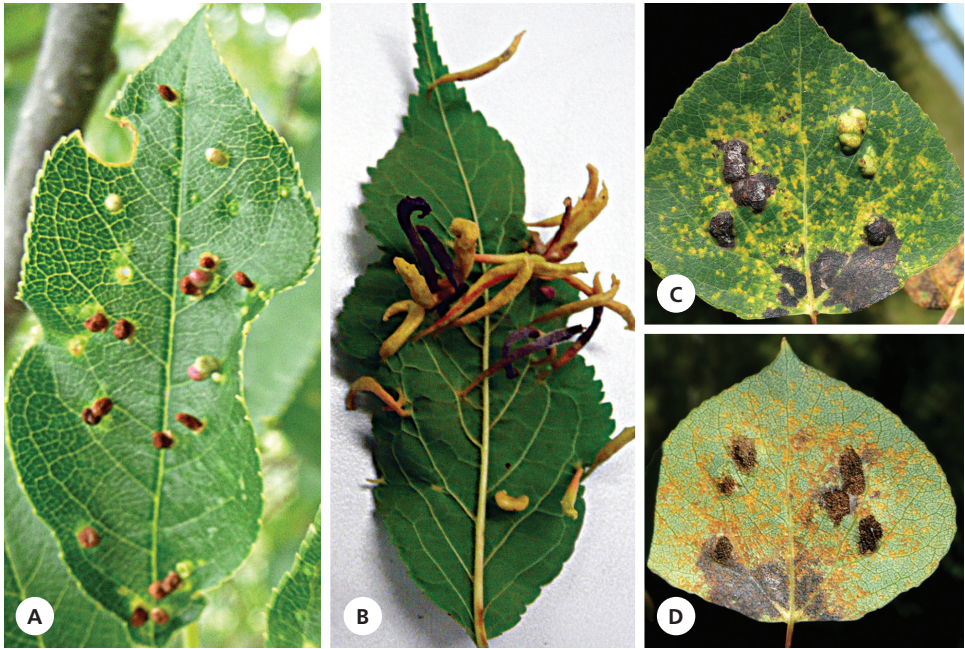
*Anystis* (whirligig) mites are red, large, very fast moving spider-like mites that are commonly seen on plant surfaces and buildings. Although they are aggressive predators of small arthropods, *Anystis* spp. have been observed feeding on exudates of extra-floral nectaries (Pemberton 1993). One species occurs in the Prairies Ecozone: *Anystis baccharum* (= *Anystis agilis* (Banks)), which is an important agent for biocontrol of orchard mite and insect pests (Laurin and Bostanian 2007; Table 1). *Anystis* species have also been occasionally recorded to bite people (Southcott 1978).

#### ***Eriophyoidea (Eupodides)***

Eriophyoid mites are intriguing biologically and are often referred to as “gall mites,” since over a quarter of the ~4,000 described species induce some form of galls on their host plant (de Lillo and Skoracka 2010). Indeed, their name<sup>2</sup> originates from the galls that they induce on the host plant, often in the shape of hair-like excrescences or outgrowths (erinea; Fig. 1D). These galls provide protection to the mites against harsh microclimates and predators. In addition to erinea, eriophyoids induce all sorts of “enclosed” galls that protrude on one side of a leaf and open narrowly on the other side (e.g., spindle-, bead-, and pocket-like

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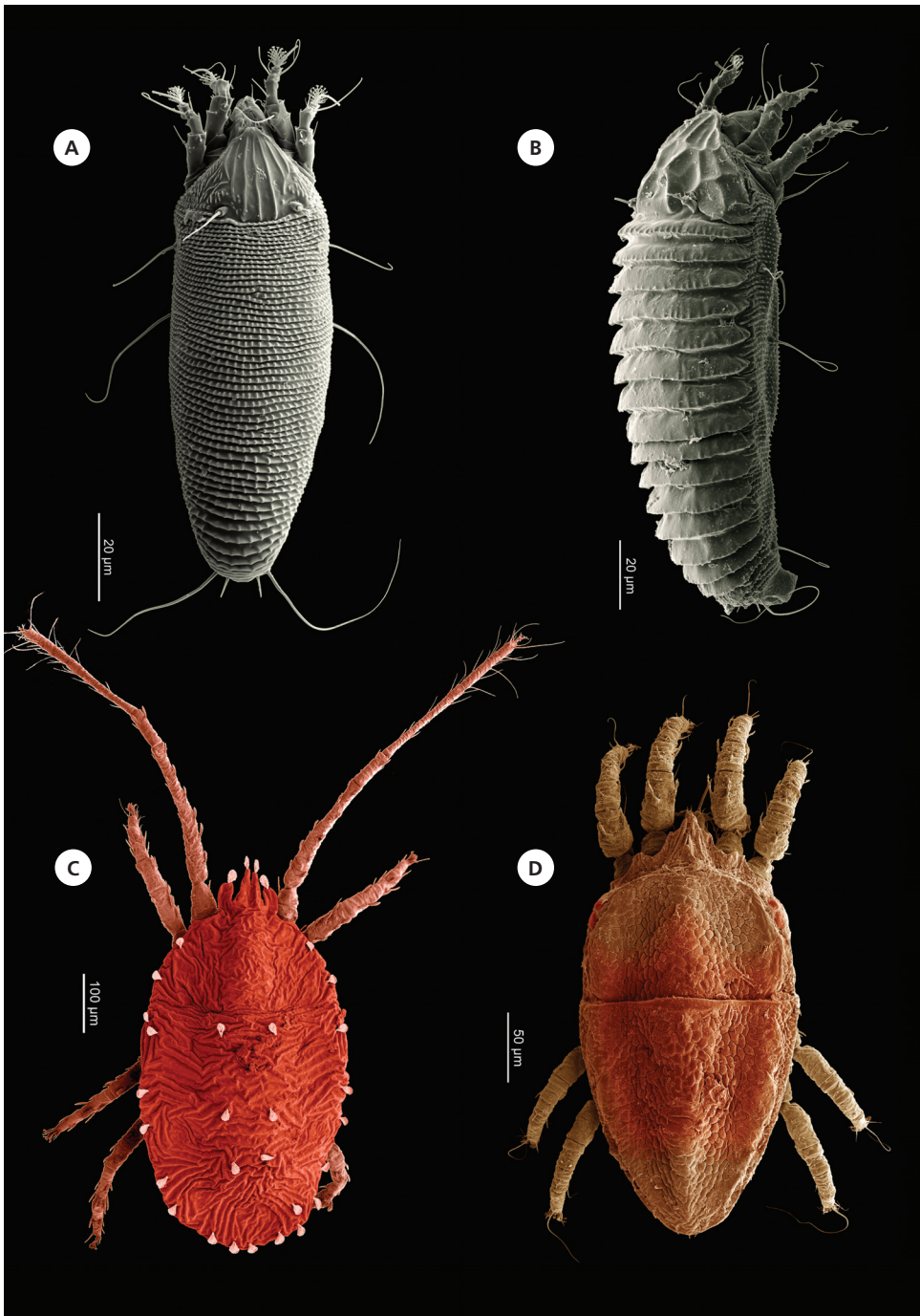
<sup>2</sup> The Greek root “erion” means *wool*; “phyes” means *grower, maker*, as from the genus *Eriophyes* (Amrine *et al.* 2003).



**Fig. 1.** Some eriophyid-induced galls. A, Short nail galls on *Prunus virginiana* induced by *Eriophyes* cf. *prunicrumena/emarginatae* (species names may be synonymous). B, Spindle galls on plum, sheltering *Eriophyes* nr *similis*. C, Pocket galls with D, erinea (old, darkened) beneath *Populus tremuloides* leaves, probably induced by *Phyllocoptes didelphis*.

galls; Fig. 1A–C), as well as various other deformations and abnormal growth patterns in inflorescences, buds, and stems. The non-galling eriophyoids are referred to as “free-living” or vagrant, and feed on the leaf surface, causing rusting, silverying, or bronzing (Westphal and Manson 1996). Eriophyoids also have intriguingly reduced morphology. They not only include the smallest of all mites, but they also have only two pairs of legs and a much reduced number of setae on the body and legs (Fig. 2A and B) (Lindquist 1996).

The actual diversity of eriophyoids in the Prairies Ecozone is probably much higher than the ~57 species recorded (Table 1) (see Lindquist *et al.* 1979 for overall Canadian estimates). Given that there are ~1,300 plant species in the Prairies Ecozone (Looman and Best 1987), that most eriophyoids are host specific to one or a few related plant species (de Lillo and Skoracka 2010), and that a large proportion of plant species may have one or more eriophyoid associates, we predict that a few hundred species of eriophyoids occur in the Prairies. Two additional points can support this prediction. Besides the species listed in Table 1, another approximately 100 eriophyoid species are recorded in the United States from plant species that also occur in the Canadian Prairies (Baker *et al.* 1996). In addition, some plant families are clearly underrepresented in terms of eriophyoid associates. For example, one species, presumably undescribed (*Tetra* sp. 1), was found on wild licorice (Fabaceae) in Saskatchewan (Fig. 2B; Table 1). This is the only eriophyoid recorded from Fabaceae in the Prairies. Worldwide, over 200 eriophyoid species are currently associated with fabaceous hosts, and this represents only about 5% of the entire known diversity of Eriophyoidea (Amrine and Stasny 1994; Amrine and de Lillo 2012). As Fabaceae is one of the most diverse



**Fig. 2.** Scanning electron micrographs of phytophagous mites (females). A, *Aceria* cf. *neoartemisiae* (Eriophyidae) from white sagebrush. B, *Tetra* sp. 1 (Eriophyidae) from wild licorice. C, *Bryobia* n. sp. 1 (*praetiosa* sp. complex) (Tetranychidae) from a timothy field. D, *Brevipalpus* (*portalis* group) sp. A (Tenuipalpidae) from wild mint. Specimens on the micrographs were colorized according to natural colours; the two eriophyids are probably white and semi-translucent naturally.

plant families in the ecozone (Looman and Best 1987), there certainly must be several more species present on members of this plant family in the Canadian Prairies Ecozone.

Eriophyoids are currently classified into three families, two of which are recorded in the Prairies Ecozone (Diptilomiopidae is not yet recorded). Six eriophyid species from three genera (*Abacarus*, *Aceria*, and *Aculodes*) are recorded from Poaceae in the ecozone (Table 1). At least two of these species occur on native grasses, while the others are on introduced grasses or cereals, and some species are important pests. For example, of the grass-associated eriophyoids, the wheat curl mite, *Aceria tosichella* (or members of its species complex), is the most problematic for Canadian agriculture. This mite transmits the wheat streak mosaic virus (WSMV) to wheat throughout the Prairies and secondarily to other cereals and grasses elsewhere (Slykhuis 1956; Oldfield and Proeseler 1996; Gavloski and Meers 2011). For example, corn grown near winter wheat in Ontario is also affected by the virus, thus favouring the perpetuation of the WSMV year-round (Gates 1970). Feeding by the wheat curl mite on corn also causes kernel red streak, apparently due to toxins in the mite saliva, but does not result in measurable yield losses (Styer and Nault 1996; Liu *et al.* 2005). In Alberta and Ohio, *A. tosichella* also transmits the pathogen of wheat spot mosaic to wheat and other crops such as corn, as well as to wild grasses (Slykhuis 1956; Oldfield and Proeseler 1996). The *A. tosichella* complex is also associated with the high plains disease, caused by the wheat mosaic virus (distinct from WSMV, but possibly identical to the wheat spot mosaic virus), which affects many cereals and some grasses in the United States and South America (Navia *et al.* 2013). The cereal rust mite, *Abacarus hystrix*, transmits rye grass mosaic virus, a serious disease of ryegrasses (*Lolium* spp.) in cultivated grasslands and pastures, as well as the Agropyron mosaic virus to various grasses, including wheat. However, the latter has less impact on crop yield than WSMV (Slykhuis 1962; Slykhuis 1980; Frost and Ridland 1996). Both *A. tosichella* and *A. hystrix* appear to represent complexes of cryptic species with narrow host ranges (Skoracka *et al.* 2002, 2012; Skoracka and Dabert 2010), but further testing is needed to clarify this in North America (Frost and Ridland 1996). *Aculodes mckenziei* is another common species occurring on wheat and various grasses (Nault and Styer 1969; Skoracka 2004) and it (or a very similar species) occurs in the Prairies Ecozone (Table 1).

Eriophyoids are also present on a number of other plants in the ecozone. Five eriophyoid species occur on fruit crops in the Rosaceae (*Malus*, *Prunus*, and *Amelanchier* spp.; Fig. 1A and B) (an additional species is suspected to occur, *Aculus schlechtendali*). The Asteraceae host a further six eriophyoid species, including two on yarrow and one on Canada thistle, which we collected at sites across all three Prairie Provinces. Although we noticed no symptoms, *Aceria anthocoptes* appears to be widespread on Canada thistle, a noxious weed, and may potentially be useful in Canada thistle control (Rancic *et al.* 2006; Michels *et al.* 2008). Aspens and poplars (*Populus*) represent the plant genus with the most eriophyoid species (four) in the Prairies Ecozone, including mites inducing leaf curling, leaf erineae (Fig. 1C and D), and bud galls or large cauliflower-shaped woody proliferations (*Aceria parapopuli*) that disfigure poplars. A total of 19 eriophyoids are recorded on other hardwood trees (*Acer* spp. 3 mite spp., *Betula*  $\geq 1$ , *Fraxinus* 3, *Quercus* 1, *Tilia* 1, *Ulmus*  $\geq 3$ ) and shrubs (*Alnus* 2, *Corylus* 1, *Eleagnus* 1, *Salix*  $\geq 1$ , *Sambucus* 1, *Viburnum* 1). At least four eriophyoid species, all Phytoptidae, are recorded from conifers (Table 1). Some of these (e.g., *Nalepella* and *Trisetacus* spp.) have received some attention in Canada and elsewhere because of the damage they cause to the foliage of various conifers during serious infestations (Marshall and Lindquist 1972; Smith 1984; Ives and Wong 1988).

In addition to the Canada thistle rust mite and two species on yarrow (*Aceria* nr *kiefferi*, *Calepitrimerus* nr *achilleae*), three other species (*Aceria malherbae*, *Aceria* nr *matricariae*, *Aculodes* nr *mckenziei*) are present on weeds (field bindweed, scentless chamomile, and foxtail barley, respectively), the first two of which probably have specific associations (e.g., Craemer 1995). *Cecidophyes rouhollahi* seemingly did not survive Albertan winters after its introduction to control cleavers and false cleavers (*Galium* spp.) (McClay 2013).

#### ***Erythraeidae (Parasitengonina: Erythraeoidea)***

*Balaustium* species are conspicuous red mites that commonly walk on picnic tables, walls, or other sunlit surfaces (Hedges *et al.* 2012). *Balaustium* mites usually forage on vegetation and prey aggressively on small arthropods, thereby contributing to the control of mite and insect pests of orchards. They are known to supplement their diet with pollen from flowers (Cadogan and Laing 1977; Welbourn 1995) and in high numbers can incidentally bite humans (Newell 1963). Some species are also considered capable of feeding on live plant tissues (Newell 1963), and *B. medicagoensis* Meyer and Ryke was reported as a pest damaging field crops in Australia (Halliday 2001; Arthur *et al.* 2011). No plant damage from *Balaustium* has been reported in the Prairies or elsewhere in Canada. Other members of Erythraeidae occur in the Prairies Ecozone (Behan-Pelletier and Kanashiro 2010), but are not known to feed on plant material.

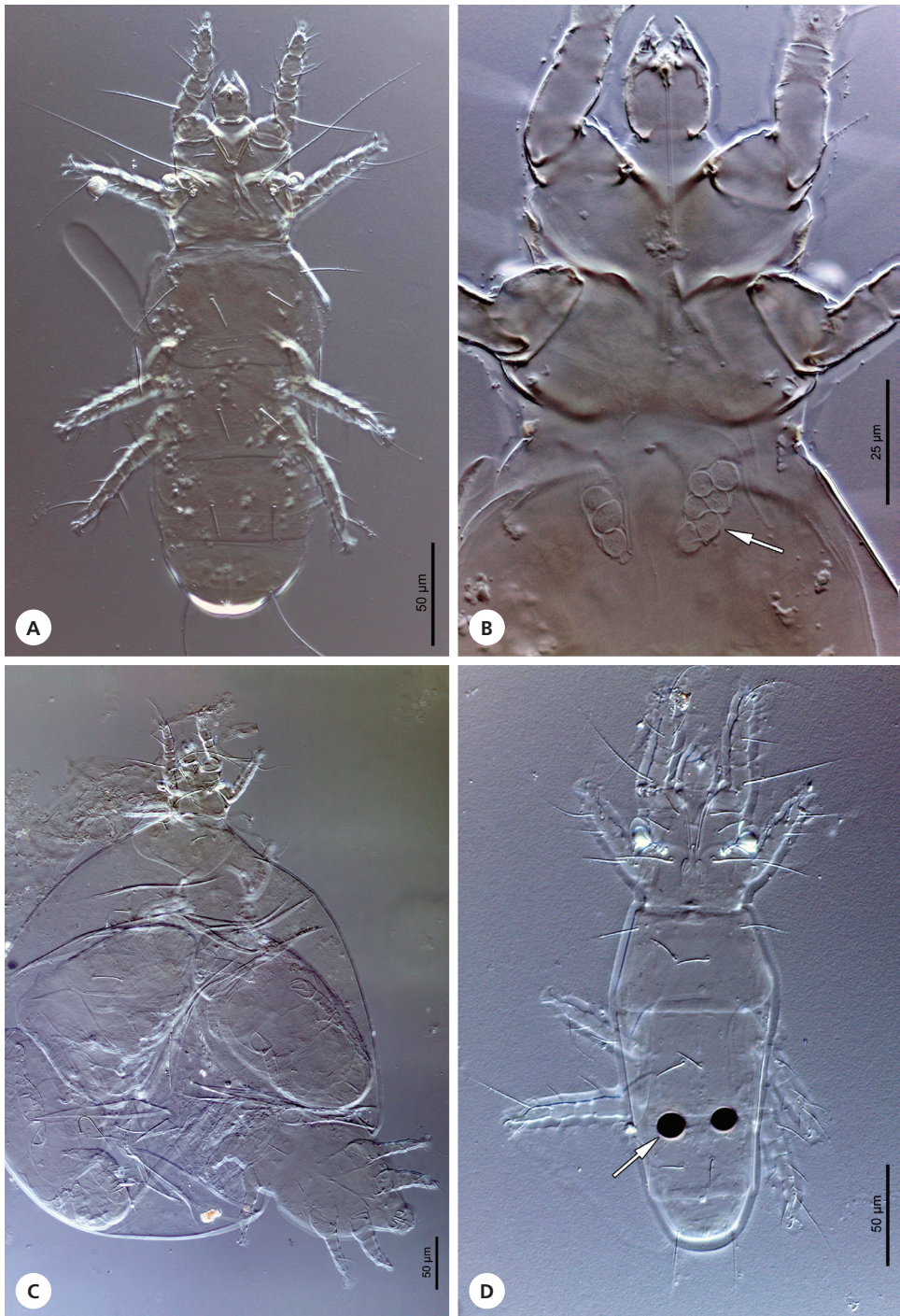
#### ***Penthaleidae (Eupodides: Eupodoidea)***

No member of this family has been reported in the Prairies Ecozone, but *Penthaleus major*, the winter grain mite (also pea mite or blue oat mite), is predicted to occur. This species is a widespread pest of pasture plants and cereals in temperate regions (Umina *et al.* 2004). Its common names originate from a propensity to feed on cool-season crops, including peas, alfalfa, lupines, oats, wheat, barley, and canola. It can also infest peanuts, vegetables, and ornamental plants in greenhouses (Jeppson *et al.* 1975; Zhang 2003). Records of *P. major* in British Columbia, eastern Canada (Qin and Halliday 1996; Table 1), and South Dakota (Middlekauff and Pritchard 1949; Streu and Gingrich 1972) indicate that *P. major* may occur in the Canadian Prairies. Wallace and Mahon (1971) suggested that *P. major* could probably survive in most areas in both hemispheres between 25° and 50–55° latitudes. It is also recorded as a summer pest of pastures and hay fields as far north as northern Norway, Iceland, and southwest Greenland (Hallas and Gudleifsson 2004; Umina *et al.* 2004). *Halotydeus destructor* (the red-legged earth mite) is known only from South Africa, Australia, and New Zealand, where it is a pest of field crops and pastures. However, the central west coast of North America, from San Diego to Vancouver, is considered climatically suitable for the potential establishment of *H. destructor* (Wallace and Mahon 1971).

#### ***Siteroptidae (Heterostigmatina: Pygmephoroidea)***

Although fungivorous, *Siteroptes* species (Fig. 3A–D) are of interest to agriculture since they carry and disseminate fungal spores (e.g., *Fusarium*, *Nigrospora*, *Botrytis* spp.) that cause serious diseases to cereals (e.g., possibly silver top of wheat, barley, rye, and oats) and perennial grasses (e.g., fescue) (Holmes *et al.* 1961; Suski 1973; Lindquist 1985). At least three species of *Siteroptes* occur in the Prairies Ecozone (Table 1). The mite–fungi relationships appear to be species specific and mutualistic, since studies indicate that each mite species needs a specific fungus to feed and develop on, while the mite in turn benefits the fungus by enhancing dispersal and stimulating growth (Laemmlein and Hall 1973; Su *et al.* 1981; Walter *et al.* 2009). Adult females of these mites have specialized organs,





**Fig. 3.** Fungivorous mites vectoring fungal pathogens of cereals. A, *Siteroptes avenae* female. B, Paired sporothecae (arrow) of *S. avenae* showing several *Fusarium* fungal spores. C, Physogastric *S. avenae* female, containing four larvae that were about ready to emerge. D, *Siteroptes nr reniformis* showing paired sporothecae (arrow), each containing a single *Nigrospora* spore.

sporothecae, which are invaginated sacs dedicated to transporting fungal spores (Fig. 3B and D). Although some research suggests that *Fusarium* and *Siteroptes* species (*S. avenae* and/or *S. cerealium*) are not, respectively, the main cause and vector of silver top of cereals in North America (Hardison 1959; Arnott and Bergis 1967, suggesting feeding by mirids as the causal agent), the close mite–fungi relationship indicates that *Siteroptes* species are potential vectors of various fungal diseases. *Siteroptes reniformis* appears to be the main vector of *Nigrospora oryzae*, a pathogen causing lint rot of cotton in California, and may also vector other types of *Nigrospora* rot affecting sorghum, corn, and wheat (Laemmlen and Hall 1973) (Fig. 3D). *Siteroptes* and their associated fungi may also affect other plants such as ornamentals, including orchids (Staal 1989) and carnations, to which they are reported to transmit central bud rot (Cooper 1940; Zhang 2003).

### ***Stigmaeidae (Raphignathina: Raphignathoidea)***

Although raphignathoid mites are generally considered predaceous (Walter *et al.* 2009), one genus of Stigmaeidae, *Eustigmaeus*, has at least some phytophagous members, feeding on mosses (Gerson 1972). Four species of *Eustigmaeus* have been recorded from the Prairies Ecozone (Table 1). In addition, the adult females may be both phoretic and ectoparasitic on Diptera (e.g., phlebotomine sandflies in warmer regions; Zhang and Gerson 1995) (Lindquist 1998; Walter and Latonas 2012). It is possible that the immature stages of these parasitic *Eustigmaeus* spp. feed on bryophytes or other substrates.

Another sort of dietary flexibility was shown in two other stigmaeids, *Agistemus fleschneri* (Summers) and *Zetzellia mali* (Ewing). While otherwise known as predators of other mite pests in apple orchards of British Columbia and eastern Canada (Downing and Arrand 1976; Thistlewood *et al.* 2013), both mites are known to feed on pollen as an alternative food source. In addition, *A. fleschneri* can be reared on pollen alone (Thistlewood *et al.* 1996), but *Z. mali* is also known to feed on yeast and has been observed probing apple and grape leaf tissue (Santos 1991). We have not found any records of these genera in the Prairies Ecozone to date.

### ***Tarsonemidae (Heterostigmatina: Tarsonemoidea)***

Tarsonemids are a taxonomically and ecologically diverse group that includes insect parasites (e.g., honey bee tracheal mite, *Acarapis woodi* (Rennie)), insect egg parasitoids, fungivores, facultative predators, and phytophages (Lindquist 1986; Lin and Zhang 2002). They are small (<0.3 mm long) and have a simplified active life cycle comprising only eggs, larvae, and adults (Lindquist 1986). Few genera and species are known from the Canadian Prairies Ecozone, despite their abundance in grassland soils and on plants (Walter 1987a; Behan-Pelletier and Kanashiro 2010). From the eight or nine presumed phytophagous genera of tarsonemids (Lindquist 1986), only one, *Steneotarsonemus*, has (at least two, possibly undescribed) species from an outdoor prairie habitat in Canada. *Steneotarsonemus* species are associated mainly with Poaceae, and because of their occurrence in grassland soils, sometimes as deep as 10 cm underground, some probably feed on the roots of grasses (Lindquist 1986; Walter 1987a). *Steneotarsonemus* can also feed on the leaf sheaths and inflorescences of native grasses, cereal crops (e.g., *S. spirifex* (Marchal)), and weeds (Jeppson *et al.* 1975; Lin and Zhang 2002). Some species show host specificity to a single plant species or genus (e.g., *S. spinki* Smiley on rice; Hummel *et al.* 2009). The bulb scale mite, *Steneotarsonemus laticeps* (Halbert), attacks the bulbs of Amaryllidaceae, and specimens at the CNC are recorded from greenhouse-grown daffodils in British Columbia.

Other tarsonemids might adversely or positively affect agriculture in the Prairies Ecozone. *Daidalotarsonemus* and *Dendroptus* species, both recorded in Canada outside the Prairies on various hosts, including *Prunus* and *Malus* spp., might feed directly on their hosts, at least facultatively (Lindquist 1986; Lofego *et al.* 2005). Species of *Dendroptus* can also prey on eriophyoids (Villanueva and Harmsen 1996) and possibly inside their galls, as can some *Tarsonemus* spp. (feeding on the maple spindle-gall mite; Patankar *et al.* 2012). Therefore, some tarsonemids may benefit agriculture by feeding on mite pests, but also by being an alternative food source for predatory mites themselves (e.g., phytoseiids) when pest species are scarce (McMurtry and Croft 1997). Tarsonemids feeding on epiphytic fungi might also help “sanitize” crops, as observed for tydeoids (English-Loeb *et al.* 1999). Other *Tarsonemus* species, notably *T. granarius*, are pests of stored grains that feed on, and perhaps spread, fungi that deteriorate stored grains (Lindquist 1972; Sinha and Wallace 1973). In warmer parts of the world, some non-parasitic tarsonemids (e.g., *Tarsonemus*, *Pseudacarapis* spp.) have obligatory or facultative associations with *Apis* or other bees and feed on fungi and pollen within the hive (Lindquist 1968; Eickwort 1994; Ochoa *et al.* 2003). Mites from bee nests are poorly studied in Canada.

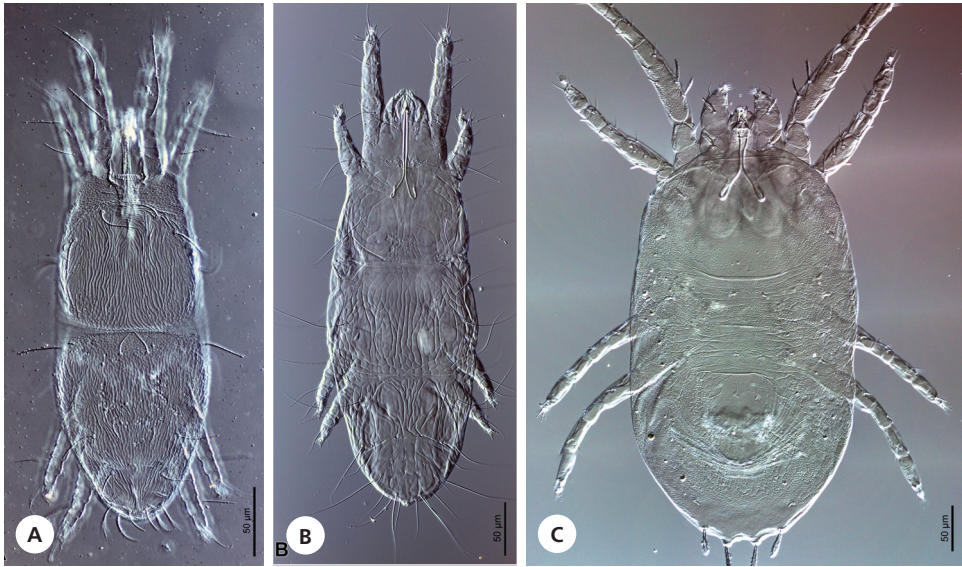
Two widespread greenhouse pests are predicted to show up occasionally in the Prairie Provinces. *Polyphagotarsonemus latus*, commonly known as the broad mite, is an important pest of ornamental plants and vegetables both in the tropics and also in temperate areas in greenhouses (Zhang 2003). As indicated by its Latin name, it is highly polyphagous and is sometimes nicknamed the two-spotted spider mite of tarsonemids (Lindquist 1986). *Phytonemus pallidus*, the cyclamen mite or strawberry mite, is an important pest of strawberries and watercress, as well as many ornamentals also attacked by *P. latus* (Gerson 1992; British Columbia Ministry of Agriculture 1999; Zhang 2003; Table 1). The cyclamen mite can overwinter outdoors in some parts of Canada, for example, within the leaf sheaths of strawberry plants (Parent 1963). Although not recorded in Canada, species in at least two other genera (*Hemitarsonemus* and suspected plant-feeding *Xenotarsonemus*) attack greenhouse ornamentals or field strawberries in the United States and elsewhere (De Leon 1962; Jeppson *et al.* 1975; Zhang 2003).

### ***Tetranychoida (Raphignathina)***

The tetranychoid superfamily comprises five families of strict phytophages, of which the two most speciose are also the most important economically: the spider mites (Tetranychidae) and the flat mites (Tenuipalpidae). Among the three remaining families, including the monogeneric Tuckerellidae and Allochaetophoridae, only Linotetranaeidae have been recorded in Canada. All members of the superfamily are instantly recognizable by their chelicerae, modified into long recurved J-shaped stylets (Fig. 4A–C), which are enclosed within a hemispherical capsule, the stylophore. These chelicerae are adapted for penetrating the epidermis and parenchymal tissues to release cell contents for ingestion.

### ***Tetranychidae***

Spider mites owe their name to the webs made by members of one of the two subfamilies (Tetranychinae) with silk secreted from their palps. This subfamily also contains most of the economically important species. The silk webs are built over leaf surface depressions or entire branches to help protect active life stages, but particularly spider mite eggs, against predators, desiccation, rainfall, and pesticide droplets. Silk threads are also used for “ballooning,” that is, enhanced wind dispersal, as well as for some aspects of mating behaviour (Helle and Sabelis 1985a; Hoy 2011). Spider mites are often brightly coloured and are variable in size (Fig. 2C



**Fig. 4.** Undescribed species of grass-associated tetranychoids photographed under compound light microscopy. A, *Dolichotetranychus* n. sp. A (Tenuipalpidae). B, *Linotetranus* nr *cylindricus* (Linotetranae). C, *Monoceronychus* n. sp. nr *aristoides* (Tetranychidae) collected from winter wheat.

and 4C). They include over 1,200 described species and some important crop pests (Helle and Sabelis 1985b; Migeon and Dorkeld 2013). Spider mites are particularly troublesome for agriculture because they can rapidly evolve resistance to pesticides and to host-plant defences (Hoy 2011). This adaptability is in part due to their short generation times, high fecundity, and haplo-diploid sex determination (arrhenotoky), but also to diverse gene complexes that allow detoxification of plant chemicals (Grbic *et al.* 2011). As a consequence, populations can differ broadly in pesticide resistance and host preference.

A total of 27 tetranychid species are presently known in the Canadian Prairies Ecozone (in addition, *Panonychus ulmi* is suspected to occur; Table 1). However, this value is certainly an underestimate due to the lack of survey in Canada; we predict that some 40 species occur in the ecozone on the basis of distributional and host plant records of spider mites in the United States (Baker and Tuttle 1994; Migeon and Dorkeld 2013).

Several tetranychid species are known or potential pests of plant species that occur in the Prairies Ecozone. Seven species are potential pests of berries (*Eotetranychus frosti*, *Tetranychus mcdanieli*, *T. schoenei*, *T. urticae*) or tree fruit crops (*Bryobia rubrioculus*, *P. ulmi*, *T. urticae*, *T. pacificus*) (Table 1). However, they are not commonly reported from the Prairies in the literature, and so are presumably only minor pests in the region; *E. frosti*, *P. ulmi*, and *T. schoenei* have never been mentioned as pests in the Prairie Provinces. *Tetranychus mcdanieli* is occasionally a pest of Saskatoon berries (*Amelanchier alnifolia*, Rosaceae) and other native bush fruit crops (K. Fry, pers. comm.). Seven species are pests of ornamental and urban trees, including conifers (*Oligonychus laricis*, *O. milleri*, *O. ununguis*) and deciduous trees (*E. populi*, *Schizotetranychus schizopus*, *Schizotetranychus* nr *schizopus*, and *T. schoenei*). Among these, the spruce spider mite, *O. ununguis*, may be the only one that has received any considerable attention because

of the serious damage it commonly inflicts on ornamental and wild conifers (Moody and Cerezke 1985; Ives and Wong 1988).

Other species in this group are important pests of field crops or ornamental plants. The two-spotted spider mite, *Tetranychus urticae*, occasionally attacks alfalfa and soybeans, as well as wheat and corn (J. Gavloski and J. Soroka, pers. comm.). However, four additional spider mites may damage cereal and pulse crops. The clover mite *Bryobia praetiosa* and other closely related species (Fig. 2C) damage pasture plants and lawns, as well as ornamental flowers. Mites in this species complex are also well-known for invading houses in large numbers through foundation cracks and window sills in spring or fall, when suitable hosts such as lawn grasses are near buildings (English and Snetsinger 1957; Anderson and Morgan 1958). Immature stages ready to moult, gravid females, or overwintering individuals seek natural elevated shelters (e.g., under bark scales of tree trunks) and will enter gaps and crevices in man-made structures if nearby. Severe infestations of a related but apparently undescribed *Bryobia* species (Fig. 2C) were observed damaging timothy grass fields in Alberta and Saskatchewan in 2006–2007 (J. Soroka and K. Merrifield, pers. comm.). *Oligonychus pratensis* was found to damage turfgrass in Alberta (specifically Kentucky bluegrass; K. Fry, pers. comm.), as well as winter wheat (Table 1). The brown wheat mite, *Petrobia latens*, was recorded from diverse herbaceous hosts in North America and overseas, attacking Poaceae such as barley, sorghum, and wheat, but also certain vegetables (Smith Meyer 1974; Jeppson *et al.* 1975). It is also known to damage winter wheat and alfalfa in the Canadian Prairies (S. Meers, pers. comm.). Although spider mites are generally not known as virus vectors (but see Jeppson *et al.* 1975 and Hoy 2011 for possible virus transmission by *T. urticae*), *Petrobia latens* was shown to transmit the barley streak mosaic virus in Montana (Robertson and Carroll 1988; Smidansky and Carroll 1996). *Tetranychus sinhai* has been reported as a pest of wheat, barley, and rye in the Prairie Provinces (Sinha and Wallace 1963; Gavloski and Meers 2011), but it is unknown whether it is still currently a pest. Considerable variation in susceptibility to *T. sinhai* was observed among wheat and barley varieties (Sinha and Wallace 1963; Wallace and Sinha 1965).

Eight other species are found on poaceaeous hosts in the Prairies Ecozone, including two on wheat (*Schizotetranychus elymus* and *Monoceronychus* n. sp. nr *aristoides*, Fig. 4C), giving a total of 14 associates of Poaceae (Table 1). Interestingly, Poaceae is the plant family with the most spider mite records worldwide. Nearly 300 species of spider mites have been reported from grasses, about two-thirds of which were reported only or mostly from these hosts (Migeon and Dorkeld 2013). Although some of the better known spider mites (major pests) are polyphagous, some have a narrower host range and show specificity to a particular plant family, such as the above-mentioned Poaceae. For instance, among species with five or more recorded hosts, 24 have at least 70% of their host range made up of poaceous hosts (Migeon and Dorkeld 2013). Three of these species (*T. sinhai*, *S. elymus*, *O. pratensis*) occur in Canada, and the last two of them belong to genera or species groups that include many or mostly grass-associated species. In addition, most species of the genus *Monoceronychus* are associated with grasses, indicating that it was probably associated ancestrally with Poaceae (Gutierrez and Helle 1985; Migeon and Dorkeld 2013).

### *Tenuipalpidae*

False spider mites or flat mites can be distinguished from most spider mites by their more or less flattened bodies, as well as short wrinkled legs, and often very short setae (Fig. 2D). Over 940 species are described worldwide (Beard *et al.* 2012a). Like spider mites, flat mites usually feed on the lower leaf surfaces, but can also feed on and damage fruits, and in some

cases they feed on bark or roots (Pritchard and Baker 1958; Gerson 2008). A few species are reported to induce galls on twigs or buds. They are generally smaller and slower moving than spider mites. They are particularly diverse in tropical–subtropical regions, and although 145 species have been reported from the United States (Baker and Suigong 1988), few are known from Canada, and these include 13 species from the Prairies (Table 1).

Tenuipalpids are an understudied group (Gerson 2008; Beard *et al.* 2012a), in part because they are easily overlooked, but also because the family includes relatively few major pests. Most pest species are members of the genus *Brevipalpus* (Fig. 2D), the most diverse and taxonomically confusing genus of the family (Welbourn *et al.* 2003; Beard *et al.* 2012a). A few members of the genus, such as the *B. phoenicis* species complex (Table 1), are reported worldwide, including in Canada, attacking greenhouse crops or indoor ornamentals (Zhang 2003; Gerson and Weintraub 2011). Outdoors in the Prairies, the only records of *Brevipalpus* are five morphospecies that we collected in 2012 from various forbs and shrubs (Table 1).

Most species of *Pentamerismus* and some *Aegyptobia* feed on cupressaceous (cypress family) conifers such as junipers and thujas (Mesa *et al.* 2009). This is reflected in the Prairies Ecozone, with at least one species of each genus occurring on juniper (Table 1). Some species of *Pentamerismus* can damage ornamental conifers.

At least three species of *Dolichotetranychus* occur in the Prairies Ecozone, all from grasses. Members of that genus are usually associated with Poaceae, or with other monocots (Baker and Pritchard 1956). Their elongate shape could be an adaptation for living under leaf sheaths or within inflorescences of their hosts (Fig. 4A). Some *Dolichotetranychus* species are reported to infest lawns in Australia and Japan (e.g., Ehara 2004; J. Beard, pers. comm.).

As with spider mites, the few flat mites receiving the most study (e.g., *Brevipalpus phoenicis* complex, *B. obovatus* Donnadieu) are highly polyphagous (Childers *et al.* 2003b). Although data are largely lacking, most of the other species are probably more host specific. For instance, we collected a possibly undescribed species of *Brevipalpus* (*cuneatus* group, sp. B; Table 1) in two sites 600 km apart from dotted blazingstar (*Liastris punctata*), a beautiful member of the Asteraceae and a food and medicinal plant used by Native American tribes. We have not yet identified this mite from any other plant.

### ***Linotetranychidae***

Linotetranychids, or cryptic false spider mites, are a small family of 11 described species representing four genera (Beard and Walter 2004). They are small, colourless, and slender, which may be an adaptation for living in the soil among roots of grasses and sedges, where they typically occur (Fig. 4B) (Baker 1953; Beard and Walter 2004). At least one species of *Linotetranychus*, possibly undescribed, occurs in the Prairies Ecozone (Behan-Pelletier and Kanashiro 2010; Table 1). Linotetranychids were found as deep as 60 cm underground in Colorado shortgrass steppe (Leetham and Milchunas 1985).

### ***Tuckerellidae***

Species of *Tuckerella*, the only known genus of the family, have an orange to red body that strikingly contrasts with the whitish fan-like dorsal setae and elongate, whip-like caudal setae. These setae gave the group their common names, ornate false spider mites or peacock mites. These uniquely shaped setae are used by the mite in self-defence, particularly the caudal ones, which are flicked at high speed back and forth to confuse approaching predators (see United States Department of Agriculture Systematic Entomology

Laboratory 2005 for a videotape of the behavior; Ochoa 1999). Species typically occur in warm regions, but one species was collected as far north as South Dakota from pasture soil cores (McDaniel and Bolen 1982; Table 1). It is therefore possible that uncollected tuckerellids are hidden in the rhizosphere (root zone) of Canadian grasslands. While some species presumably feed on the roots of grasses, others feed as pests on the bark of stems and twigs and on the fruits of tropical woody crops (e.g., mango, avocado, tea, coffee; Ochoa 1989; Beard *et al.* 2013).

### ***Tydeoidea (Eupodides)***

Some tydeoids are parasitic, but members of the non-parasitic groups (Tydeidae, Triophtydeidae, and Iolinidae) are numerous in soil, litter, and plant substrates, including grasslands (Walter 1987*a*, 2004; Behan-Pelletier and Kanashiro 2010). A few tydeoids have been reported as feeding on and damaging plant crops (e.g., *Tydeus* (= *Orthotydeus*) *californicus* (Banks), *Brachytydeus* (= *Lorryia*) *formosa* Cooreman), and if some species truly feed on plant tissue, they probably do so facultatively, within a more generally fungivorous or omnivorous diet (Krantz and Lindquist 1979; Walter *et al.* 2009). Indeed, the few studied species also feed on fungi, homopteran honeydew, pollen, algae, and arthropods such as eriophyoid mites and the eggs of spider mites and scale insects (Walter 1987*b*; Hessein and Perring 1988; Liguori *et al.* 2003). Tydeoids are therefore potentially beneficial mites, acting as sanitary agents by feeding on fungal pathogens (e.g., downy or powdery mildew) or preying on mite pests, and represent an alternate food source for other predatory biocontrol agents (Mendel and Gerson 1982; English-Loeb *et al.* 1999; Gerson *et al.* 2003). Pollen may also be included in the diet of plant-dwelling tydeoids, such as *Tydeus* (Tydeidae) and *Pronematus* (= *Homopronematus*; Iolinidae) spp. (Hessein and Perring 1988; Liguori *et al.* 2003), two genera that occur in the Canadian Prairies Ecozone, among several others. Tydeoids can also be relatively common in stored grains and oilseeds in the region, where at least eight species in several genera have been recorded (Sinha 1961; Momen and Sinha 1991). Other than being contaminants, they are not important pests of grains (Sinha 1963).

## **Acariformes: Order Sarcoptiformes**

The consumption of live plant tissue occurs sporadically in sarcoptiform mites, but this largely represents cases of facultative phytophagy. In contrast to nearly all parasitiform and most trombidiform mites, which are fluid feeders, sarcoptiform mites ingest solid particles such as animal and plant detritus, along with fungal hyphae and spores growing on this detritus. They scrape or cut off material with the aid of their robust, coarsely toothed chelicerae and rutella (Norton and Behan-Pelletier 2009).

### ***Oribatida (s.s.)***

Oribatid mites dominate soil arthropod faunas in terms of abundance and species richness, including those in the Canadian grasslands (Behan-Pelletier and Kanashiro 2010). They feed primarily on organic detritus and fungi. Many oribatids ingest wood and leaf tissue, but generally only after it has started to decay, and as such they are “saprophytophages”, also ingesting the microflora, that is, fungi, algae, and bacteria growing on the substrate (Norton and Behan-Pelletier 2009). Many oribatid genera and species are associated with vegetation, particularly arboreal habitats such as tree bark, but also foliage. These plant-dwelling oribatids are saprophages/microbivores, similar to soil oribatids, feeding on epiphytic fungi, algae, or lichen on the bark or foliage. There are a few observations of

oribatid species feeding directly on live vascular plant tissues and damaging the host (e.g., grass stems, roots of potatoes, strawberries, and tulips, Evans *et al.* 1961; rice shoots, Lan *et al.* 1986; leaves of an Asteraceae, Ramani and Haq 1987), and thus a few may be facultative phytophages of unclear economic importance (Zhang 2003; Norton and Behan-Pelletier 2009). Some of the species studied belong to genera found in the Prairies Ecozone (e.g., *Scheloriabates*, Behan-Pelletier and Kanashiro 2010). *Hydrozetes* species (Hydrozetidae) burrow into aquatic plants, notably duckweeds, especially those in the early stage of decomposition (Norton and Behan-Pelletier 2009; Walter *et al.* 2013). Some oribatid species might also feed directly on live moss tissues (Woodring 1963; Gerson 1969; Krantz and Lindquist 1979). Moreover, soil-dwelling oribatids opportunistically ingest wind-dispersed pollen grains (Behan-Pelletier and Hill 1983; Behan-Pelletier and Kanashiro 2010), and plant-dwelling oribatids may do the same (Wallwork 1983; V. Behan-Pelletier, pers. comm.).

### *Astigmatina (Astigmata)*

Unlike the Oribatida *s.s.* (i.e., which excludes Astigmata), only a few genera and species of free-living astigmatic mites occur in soils. Most species instead live in patchy, nutrient-rich organic habitats such as dead wood, tree wounds, carrion, cow dung, nests of vertebrates and insects, stored food, and house dust (OConnor 2009). But, like oribatids, most non-parasitic astigmatic mites are primarily fungivores or saprophages. However, tendencies toward phytophagy do occur in some genera of Acaridae, Glycyphagidae, and a few other related families, in which some species consume live, healthy tissues of foliage, bulbs, or grains, or plant tissue that was previously wounded or weakened by fungal pathogens. Free-living astigmatans are much paler, are less sclerotized, and reproduce usually much faster than their oribatid (*s.s.*) relatives (OConnor 1994).

Many astigmatan genera infest stored products and can feed directly on the food substrate (see below), but only two genera include species that are frequently reported to feed directly on live plants: *Rhizoglyphus* and *Tyrophagus* (Acaridae). Like most other free-living astigmatans, the usual diet of these mites is probably fungi (OConnor 1984), although they can feed opportunistically on other microorganisms such as algae and easily subdued animal prey (e.g., nematodes) (Walter 1987*b*). Information on the most studied species (or species complex) of these genera indicates that they can breed on a broad variety of substrates of plant and animal origin, particularly in decomposition (Diaz *et al.* 2000; Fan and Zhang 2007). They are occasional pests of greenhouse, field, and stored crops (Table 1). *Rhizoglyphus echinopus* and *R. robini*, often referred to as bulb mites, are commonly found on the bulbs and corms of ornamentals and root vegetables, especially Liliaceae and relatives such as tulips, daffodils, onions, and garlic (Gerson *et al.* 1985; Diaz *et al.* 2000; Fan and Zhang 2004). Although they can burrow in and feed on living tissues (OConnor 1994), their colonization and population growth is faster on bulbs that are infested by fungi (Okabe and Amano 1991). They infest cereal crops if the cereals are planted near infested hosts (Diaz *et al.* 2000) and can subsist in the soil, feeding on decaying organic matter until a richer food source comes along, for example, onions (Gerson *et al.* 1985). *Rhizoglyphus robini* is recorded from the Canadian Prairies Ecozone (Table 1).

This group also includes *Tyrophagus* species, which are found in mouldy environments and are known as “mould mites”, a name originally attributed to the ubiquitous and widespread *T. putrescentiae* (= *Tyrophagus communis* Fan and Zhang; see Klimov and OConnor 2009). At least three species occur in the Prairies Ecozone (Table 1). *Tyrophagus* species, including particularly *T. putrescentiae*, occur in stored food products; house dust;



mushroom and insect cultures; fruits; foliage and bulbs, especially when damaged; and other substrates, particularly those with a high-protein or high-fat content such as cheese (Fan and Zhang 2007). They are reported to damage greenhouse crops such as ornamentals, as well as cucumbers, tomatoes, and peppers, in Canada and elsewhere (Zhang 2003) and may also directly damage stored grains (Sinha 1979).

Among the 63 species of predatory, parasitic, and fungivorous mites (Mesostigmata, Prostigmata, Oribatida, Astigmata) recorded from stored products in the Prairie Provinces (Sinha 1963), most of the commonly encountered species are cosmopolitan, probably in large part due to extensive international commerce and movement of foods (White *et al.* 2011). Astigmatans are a major component of stored-product mite communities and include the main pests. They are primarily found in grains that have absorbed moisture (as are tarsonemids and tydeoids) and feed primarily on moulds, but can also feed directly on grains (see below). They contaminate the grain with their live and dead bodies, their feces, and the fungi that they help spread, thereby reducing its quality and palatability. However, mites are no longer considered a major problem in Canada, thanks to improved management of grain temperature and moisture content (White *et al.* 2011). Note, however, that food products, especially cereal-based, frequently contain a few mites—which we ingest, usually harmlessly (Thind and Clarke 2001). Many of these mites can disperse phoretically on insects associated with grains, but they may also enter storage areas on plant material transported from the field, or via vertebrate carriers such as synanthropic (associated with humans) rodents and birds, the nests of which are a common habitat for many stored-product astigmatic mite species (Krantz 1961; OConnor 1979). However, residues left in containers may be responsible for subsequent infestations of stored grains by mites (Sinha and Wallace 1966). Some astigmatans can cause allergic rhinitis and contact dermatitis in humans (e.g., Geary *et al.* 2000).

The most economically important stored-product astigmatic mites are *Acarus siro* (Acaridae), commonly called the grain mite or flour mite, and *Glycyphagus destructor* (Glycyphagidae). In Canada, they are usually abundant in stored wheat, oats, and barley (Sinha 1963, 1964b). Although these species are clearly fungal grazers that can breed on a fungal diet alone, they are able to directly damage cereal grains (Sinha 1964a, 1979; Griffiths 1970). *Acarus siro* can feed directly on the cereal germ, whereas *G. destructor* may only be able to feed on grain dust and broken kernels. At least three *Acarus* species occur in the Prairies Ecozone, and at least two of them, *A. siro* and *A. farris*, appear to be common in stored grains (Sinha and Wallace 1966; Table 1). Other widespread astigmatic mites that have been recorded infesting stored grains and other food products (e.g., hay, flour, cheese, mushroom cultures) in the Canadian Prairies Ecozone are listed in Table 1.

Several of these stored-product astigmatic mites also commonly invade the nests of social insects, including bees, where an accumulation of nutrient-rich food is typical (Eickwort 1994). They then scavenge on the fungi, organic detritus or pollen among the provisions, old honeycombs, or dead bee larvae. These facultative bee associates are typically the most abundant mites in honey bee hives, and *Acarus* spp., *Tyrolichus casei* (Acaridae), *Tyrophagus* spp., *Glycyphagus domesticus*, and *G. destructor* are particularly common (Eickwort 1988). *Sancassania* spp. (e.g., *S. berleseii*) (Acaridae) also scavenge on pollen, fungi, and dead bee larvae in the nests of various types of bees (Eickwort 1988; Table 1). *Carpoglyphus lactis* (Carpoglyphidae) occurs in products with high sugar content (e.g., dried fruits, potatoes, tree sap flows) that have begun to ferment (OConnor 2009). Because of this propensity for sugars, this mite also commonly occurs in honey bee hives, where it feeds on stored pollen and honey (Baker and Delfinado 1978) and fungi (Sinha

1966b). In contrast, *Kuzinia laevis* (Acaridae) is an obligate associate of bumble bees and is abundant in their nests, where it scavenges on pollen, honey, fungi, and organic remains (Klimov and OConnor 2004). Overall, these astigmatic mites may be mostly commensal, with little or no detriment to the bee colony (unless excessively abundant), although they could vector fungi and other potential pathogens. However, some species of *Tortonia* (Suidasiidae) are apparently detrimental to their hosts. One or two species in the Prairies are associated with megachilid bees and feed extensively on their provisions (Klimov and OConnor 2004; Table 1).

### Impact on Hosts, Dispersal, and Invasiveness

While the feeding activity of some mites appears to be negligible to their host plants, others have dramatic effects. Mites in all major phytophagous mite groups (eriophyoids, tetranychoids, tarsonemids) inject toxins with their saliva, which may cause necrosis, blistering, discoloration, abnormal growth, and defoliation, or transmit viral (e.g., WSMV by the wheat curl mite) or fungal pathogens (e.g., *Fusarium* by *Siteroptes* spp.) that can lead to plant sterility or death (Laemmlen and Hall 1973; Jeppson *et al.* 1975; Tomczyk and Kropczyńska 1985; Oldfield 1996; Childers *et al.* 2003a). Mite phytotoxicity and pathogen transmission to crops may be more pervasive than we know. Besides contributing to the spread of fungal pathogens (transported in sporothecae, or attaching to the body surface), plant-feeding mites interact synergistically with them by creating new points of entry in the host tissue for these pathogens via feeding punctures (Gray *et al.* 1975; Jeppson *et al.* 1975; Hummel *et al.* 2009). Additionally, mites may preferentially colonize hosts that are already attacked by fungi (Okabe and Amano 1991), consequently producing greater damage by co-infesting a host (Ochoa 1989). For instance, densities of the cereal rust mite (*A. hystrix*) were about five times higher on quackgrass and wheat when these hosts were infested by *Puccinia* rust. In another case study, the presence of the mango bud mite (*Aceria mangiferae* Sayed) enhanced the colonization of mango buds by *Fusarium* by a factor of 1.5–2 times, thereby increasing the severity of disease (Gamliel-Atinsky *et al.* 2010). Other mites may significantly reduce fruit or cereal crop yield, with or without the participation of pathogens or phytotoxins, and without any obvious symptoms.

The geographical distribution, host ranges, and impact on the hosts can change through time and space. Given some change in climatic conditions or agricultural practices, a population of mites benignly feeding on a crop may increase in abundance and become a serious pest (Arthur *et al.* 2011; Hill *et al.* 2012). Pests present in warmer regions may cross Canadian borders after range expansion from the United States following climate warming, or after accidental introduction of imported plant material. Mites can switch to new hosts when introduced into a new environment (e.g., newly developed or introduced plant crops) and have more impact than on their natural hosts or in their country of origin (Navia *et al.* 2010; Carrillo *et al.* 2012). Shifting to new host plants seemingly occurs in groups that are typically host specific (Smith *et al.* 2010).

Mites are small and have no wings, but are able to disperse long distances via phoresy and wind and as a result of human activities. Insects are common phoretic carriers for tarsonemids (e.g., the broad mite on whiteflies; Gerson and Weintraub 2011), astigmatans (e.g., bulb mites on beetles and flies; Diaz *et al.* 2000), and bee-associated mesostigmatans (Klimov and OConnor 2004). Phoresy on vertebrates is frequent for stored-product mites and other nest-dwelling mites (OConnor 1994). Therefore, the arrival of a foreign,

unwanted vertebrate or insect onto a crop or in a region may also indicate the introduction of mites of uncertain ecological significance. Windborne dispersal is a powerful strategy used by plant-associated mites, including eriophyoids and tetranychids, and probably also by tenuipalpids, tarsonemids, and siteroptids (O'Connor 1984; Helle and Sabelis 1985a; Lindquist 1986; Gerson 2008). For instance, about 700 species (including many undescribed) were collected over a one-year period in three pan traps installed on a single rooftop (Zhao and Amrine 1997). It is also possible that eriophyoids and certain *Steneotarsonemus* spp. disperse with plant seeds (Hummel *et al.* 2009; Navia *et al.* 2010). Last but not least, plant-associated mites may disperse by accidental, passive phoresy: on the clothing of people who wander under an infested tree (Gerson 2008); on tools and farm machinery that collect soil and plant debris where eggs and other life stages may reside (Umina *et al.* 2004); and particularly on commercial plant material that is transported inadvertently or for commercial purposes. Mites naturally hide along leaf veins, in bark cracks, in the calyx or surface depressions of fruits, and inside cavities created by insects (e.g., galls, galleries) and may easily be unnoticed during quarantine inspections (Beard *et al.* 2013). Possibly the highest risk of introduction is by perennial shrubs that are imported for horticultural and ornamental purposes. Imported live woody material offers many refugia for mites, and generally that host material will be planted in natural or semi-natural environments within a short time. Indeed, many species of tetranychids and eriophyoids introduced in Europe are associated with perennial shrubs or trees in parks and gardens (Navajas *et al.* 2010). And since most plant-feeding mites are arrhenotokous parthenogens, the mere dispersal of a single, virgin female onto a suitable host may be sufficient to establish a new colony in a new region, as the new, all-male progeny can mate back with the foundress.

Given the potential impact and dispersal described above, foreign plant-feeding mites—if occurring on hosts and climate similar to that in Canada—represent a threat to Canadian agriculture. Even if an intercepted mite species is already present in Canada, some form of “biorisk” may certainly still exist. Indeed, a foreign conspecific strain may have different host preferences, virulence, potential to transmit pathogens, and pesticide resistance from a native or naturalized strain. Alien viruses can also cross borders within a mite, or within a host plant imported for propagative purposes, regardless of the possible presence of conspecific mites or plants in Canada (Rodrigues and Childers 2013).

Some phytophagous mite species already occurring in Canada originate from elsewhere. Species associated with crops (often of Eurasian origin) or with other introduced plant species are likely to have been accidentally imported into North America along with the plant, especially if the mite is host specific or primarily associated with that host. This includes some greenhouse pests that are usually cosmopolitan (typically those that would not survive winters outdoors) and some pests of orchards and field crops, often widespread in temperate regions. The spider mites *Panonychus citri*, *P. ulmi*, and *Tetranychus urticae*; the tenuipalpid *Brevipalpus phoenicis* s.l.; and the tarsonemid *Polyphagotarsonemus latus* are probably introduced in North America (Navajas *et al.* 2010). Other adventive mites are those introduced along with honey bees, such as *Melittiphys alvearius*, as well as several of the stored-product mites. However, it is difficult to determine the origin of many of those cosmopolitan species because of the lack of biogeographical data and their extensive historical association with humans. The origin of some species is also masked by a confused taxonomy. For example, two or more names associated with different geographical regions may represent synonyms of a single species (e.g., *Eriophyes emarginatae* and the European *E. padi* Nalepa; Navajas

*et al.* 2010), or unresolved species complexes, including species associated with both introduced crops and native plants (e.g., *Aceria tosichella*, *Abacarus hystrix*).

### **An Unknown Diversity to Study, Protect, and Exploit**

Plant-feeding mites associated with crops of the Canadian Prairies Ecozone remain little known, and those on native or naturalized non-crop hosts even less so. At least 100 strict phytophages (Eriophyoidea, Tetranychoida, and at least three Tarsonemidae) are present in the Prairies Ecozone, and a similar diversity of mites feed facultatively on plant tissues, stored plant products, and pollen and nectar either on plants or in bee nests. This certainly represents a small portion of the actual fauna. If considering eriophyoids as the core of plant-feeding mite diversity, a few hundred species of strict phytophages can be expected in the ecozone, many of which may be unreported or undescribed. Adding to our lack of understanding, the geographical distribution and host associations of nearly all species also remain unresolved.

The limited knowledge of the Canadian acarofauna hampers decision making regarding the control and release of imported material inspected for pests at our borders, and it threatens our biodiversity and agriculture overall. Knowing whether or not intercepted mite species (and possibly also strains) already occur in Canada is a critical and necessary step for assessing pest risks. A more comprehensive knowledge of our mite pest fauna would permit more effective exploration and use of predatory mites for their control. Some plant-feeding mites, particularly eriophyoids, show potential to control noxious weeds; however, we are still learning which mites are currently associated with these plants. To be able to respond adequately to these agricultural and quarantine issues when they arise, and to seize opportunities for the biocontrol of pests and weeds, we must first better understand the identity, diversity, and host preferences of mites on crops, native plants, and weeds. To achieve this, we need to have close collaborations between extension officers, primary producers, biocontrol researchers, and taxonomists.

Given the diversity and host specificity of eriophyoid, tetranychoid, and tarsonemid mites associated with Poaceae, we hypothesize that grassland habitats were of great importance to the evolution and the maintenance of biodiversity of these groups of mites and others. The dearth of Canadian records from other plant groups common in the Prairies Ecozone, such as Fabaceae, Asteraceae, Cyperaceae, and Brassicaceae, may reflect a lack of collecting and knowledge, rather than an actual lack of mites associated with those plants. More research efforts targeting the taxonomy, distribution, and biology of plant-feeding mites in the Canadian Prairies are needed to better understand, protect, control, and exploit the plant-associated mites of this region.

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## Chapter 4

# Spiders (Arachnida: Araneae) of the Canadian Prairies

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**Abstract.** Spiders are the seventh most diverse order of arthropods globally and are prominent predators in all prairie habitats. In this chapter, a checklist for the spiders of the Prairie Provinces (767 recorded species and 44 possible species) is presented along with an overview of all 26 families that occur in the region. Eighteen of the species from the region are adventive. Linyphiidae is by far the dominant family, representing 39% of all species in the three provinces. Gnaphosidae and Lycosidae each represent 8% and three other families (Salticidae, Dictynidae, and Theridiidae) each account for 7%. A summary of biodiversity studies conducted in the Prairies Ecozone and from transition ecoregions is also provided. The Mixed Grassland Ecoregion has the most distinctive assemblage; *Schizocosa mccooki* and *Zelotes lasalanus* are common only in this ecoregion. Other ecoregions appear to harbour less distinctive assemblages, but most have been poorly studied. Lack of professional opportunities for spider systematists in Canada remains a major barrier to the advancement of the taxonomy and ecology of spiders.

**Résumé.** Les aranéides forment le septième ordre le plus diversifié d'arthropodes dans le monde; ce sont des prédateurs très présents dans tous les habitats des Prairies. Ce chapitre présente une liste des espèces d'araignées des provinces des Prairies (767 espèces connues et 44 prévues) ainsi qu'une vue d'ensemble des 26 familles présentes dans la région. Dix-huit des espèces de la région sont adventives. La famille des linyphiidés domine de très loin, représentant 39 % de toutes les espèces présentes dans les trois provinces. Deux autres familles (gnaphosidés et lycosidés) représentent chacune 8 % des espèces, et trois autres (salticidés, dictynidés et thériidiés) représentent chacune 7 % des espèces. Le chapitre présente également un résumé des études portant sur la biodiversité réalisées dans l'écozone des prairies et dans les écorégions de transition. L'écorégion de la prairie mixte présente l'assemblage le plus distinctif; *Schizocosa mccooki* et *Zelotes lasalanus* ne sont communs que dans cette écorégion. D'autres écorégions semblent abriter des assemblages moins distinctifs, mais la plupart restent mal connues. La pénurie de débouchés professionnels pour les systématiciens qui s'intéressent aux araignées au Canada continue de faire obstacle aux progrès de la taxonomie et de l'écologie de cette classe d'arthropodes.

### Introduction

Spiders are among the most ubiquitous predatory invertebrates in terrestrial ecosystems and have been able to colonize nearly all habitats on Earth, except for Antarctica (Turnbull 1973; Foelix 2011), including freshwater (Seymour and Hetz 2011), semi-aquatic (Graham

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*et al.* 2003), and marine intertidal (Roth 1967) habitats. In temperate terrestrial zones, spiders are among the most diverse and abundant groups of ground-dwelling predators (Gertsch 1979). Spiders are mainly generalist predators (Wise 1995) of invertebrates and, occasionally, of vertebrates (McCormick and Polis 1982), although a few species may also feed on pollen (Smith and Mommsen 1984; Ludy and Lang 2006). Spiders play an important functional role in ecosystems, affecting plant productivity through predation on herbivorous insects (Snyder and Wise 1999) and influencing litter decomposition by feeding on detritivores (Clarke and Grant 1968). In addition, spiders are important in the diet of various invertebrates and vertebrates (Wise 1995). Spiders are often useful as bioindicators in environmental studies because of their diversity, abundance, and ease of capture, as well as our ability to assign families effectively into functional guilds (e.g., Cárcamo 1997; Pinzón 2011). Despite the importance of spiders, their ecology remains poorly studied in the Prairies Ecozone. Many species, particularly in the Linyphiidae and Theridiidae, are undescribed, and we lack well-developed diagnostic keys for these and other families. Here we provide a short overview of spider phylogeny and taxonomic status in Canada, followed by a checklist of the spiders in the Prairie Provinces, a review of faunistic studies from the Prairies Ecozone and adjacent transition ecoregions, and an outline of areas for future research.

### Phylogenetic Placement

The order Araneae belongs to the class Arachnida, which includes a number of groups of eight-legged arthropods. Among other groups that are more common in warmer climates, common orders include Acari (mites and ticks), the most diverse of the class, and the scorpions (order Scorpiones), pseudoscorpions (order Pseudoscorpiones), and harvestmen or daddy-long-legs (order Opiliones). The tail-less whip scorpions (order Amblypygi), the whip scorpions (order Thelyphonida), and the short-tailed whip scorpions (order Schizomida) are the closest relatives to spiders (Shultz 1990; Coddington and Levi 1991; Shultz 2007; Penney and Selden 2011; Fig. 1).

Two monophyletic suborders are recognized within the order Araneae: Mesothelae and Opisthothelae (Fig. 2) (Platnick and Gertsch 1976; Penney and Selden 2011). These two suborders have existed since at least the Carboniferous period (ca. 350 million years before present (mbp)) (Shultz 1990, 2007). The Mesothelae is considered the most primitive and basal lineage and is represented mostly from Paleozoic fossils (>250 mbp) (Penney and Selden 2006; Selden and Penney 2010). It contains a single extant family, the Liphistiidae (three genera, 90 species), distributed only in China, Japan, Southeast Asia, and Sumatra (Platnick and Sedgwick 1984). The Opisthothelae is subdivided into the infraorders Mygalomorphae and Araneomorphae. The members of these two infraorders radiated at least during the Triassic (200–250 mbp). The Mygalomorphae (16 families, 328 genera, 2,775 species) includes the tarantulas and several other groups of primitive spiders, while the Araneomorphae (regarded as “true” spiders) is the most diversified and evolved lineage, with 95 families, 3,574 genera, and 41,167 species described to date (Platnick 2013; Platnick and Raven 2013). These two infraorders are distributed in all continents except for Antarctica.

Spiders are among the most diverse arthropod orders, ranking seventh after Coleoptera, Diptera, Hymenoptera, Lepidoptera, Hemiptera, and Acari in numbers of described species (Coddington and Levi 1991). Worldwide estimates of spider richness range from 76,000 (Platnick 1999) to 170,000 (Coddington and Levi 1991), although only 44,032 species have been described (Platnick 2013). Thus, only about 35% of the world’s species have

been described on the basis of a conservative estimate of diversity from the average of the two extremes (Agnarsson *et al.* 2013). Currently, mygalomorphs are represented in Canada by only four families and six species; five are reported only from British Columbia and one from Ontario (Paquin *et al.* 2010). The remaining 1,407 species and 39 families are included

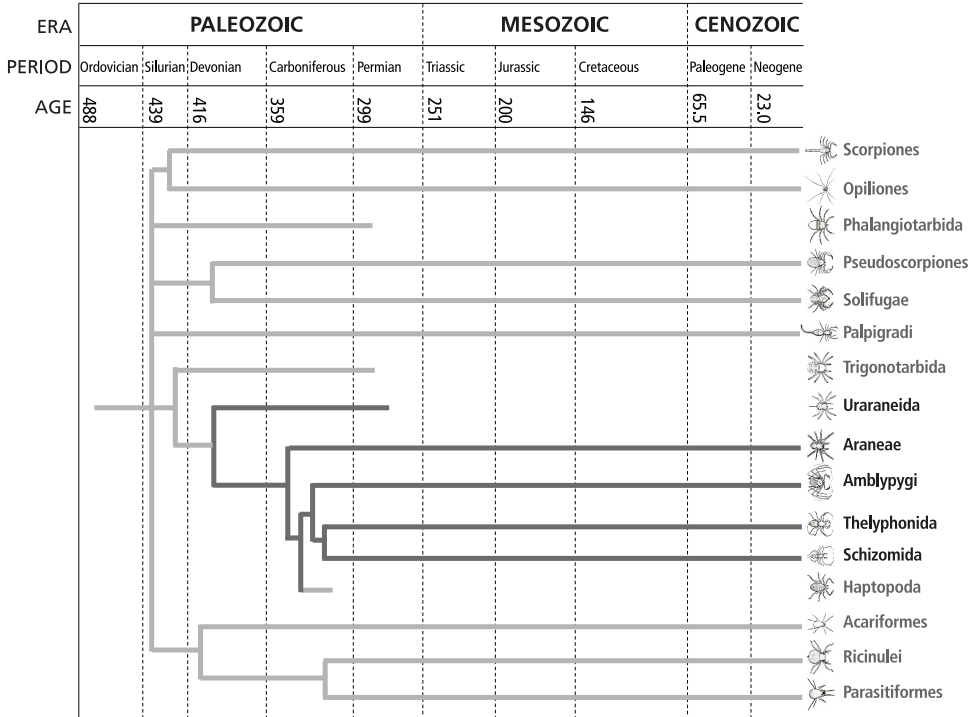


Fig. 1. Phylogeny of the class Arachnida with spiders and their closer relatives shown in bold (modified from Dunlop and Penney 2012).

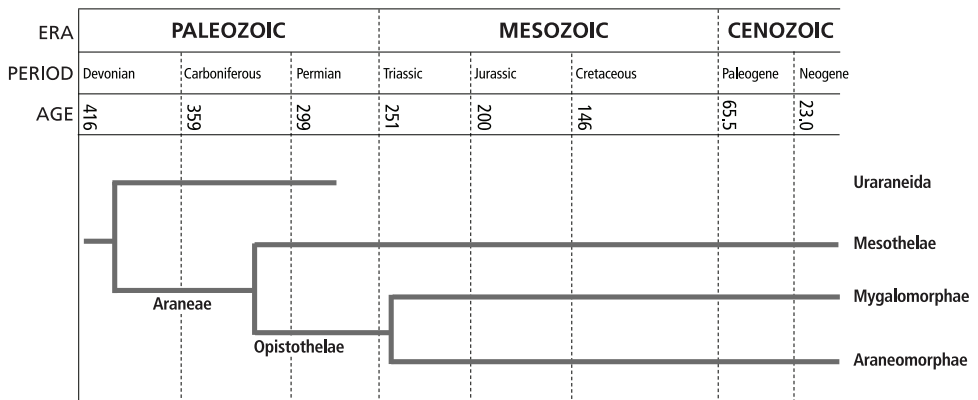


Fig. 2. Higher phylogeny of the order Araneae (modified from Dunlop and Penney 2012).

within the Araneomorphae and are widely distributed in the Nearctic region (Paquin *et al.* 2010), with many having Holarctic distributions. The Canadian fauna includes only about 3% of the world's species.

Significant progress has been made recently in understanding the evolution and phylogeny of spiders (Selden and Penney 2010; Penney and Selden 2011). Although the fossil record for spiders is not as extensive as that for insects, almost 1,200 valid species are known from fossils (Dunlop *et al.* 2013). Currently, 70 extant spider families are represented in the fossil record (Penney *et al.* 2012; Dunlop *et al.* 2013) and 27 families are recognized strictly from fossils (Penney and Selden 2006, 2011). The earliest known true spider fossil belongs to *Palaeothele montceauensis* Selden, 1996, from the late Carboniferous (295 mbp) (Selden 1996a, 1996b). This species is closely related to species in the Liphistiidae (Mesothelae), a family that is considered a living fossil. Ancestors to the spiders and their relatives were some of the first animals colonizing terrestrial habitats over 400 million years ago. The first spiders likely played an important role as predators. Penney (2004) has suggested that there is a relationship between the evolutionary radiations of spiders and their insect prey. It is possible that the use of silk to capture prey may have contributed to selection for the evolution of insect flight (Vollrath and Selden 2007).

### Taxonomy of Prairie Spiders

Considerable progress has been made in the taxonomy of spiders from the prairie region, but many gaps remain. Most of the common spider species, at least those often collected in pitfall traps, belong to one of the families for which keys to species are available (Tables 1 and 2). For example, almost half of the families that occur in the region are covered in *The Insects and Arachnids of Canada* series (Dondale and Redner 1978, 1982, 1990; Platnick and Dondale 1992; Dondale *et al.* 2003). Identification keys for species or descriptions are also available for Amaurobiidae (Leech 1972), Cybaeidae (Bennett 1991), and Agelenidae (Chamberlin and Ivie 1941; Bennett and Ubick 2005). However, there are no regional keys to identify species for some of the most speciose families, including the Linyphiidae (which accounts for about 40% of all the species in the Prairies; Table 1), Theridiidae, and Salticidae. Therefore, thorough biodiversity work is not possible without the help of an expert, which slows down collection and interpretation of data about spider assemblages. As with many other arthropod orders, several spider taxa require revision and numerous species remain to be described, particularly in the Linyphiidae and Theridiidae.

Although the Canadian spider fauna is relatively well-known (Paquin *et al.* 2010), no checklist for the Prairies has ever been published. Dondale (1979) reported 1,256 species from 33 families in Canada and estimated that another 144 species should occur. Bennett (1999) reported about 1,400 species in his later review of spider taxonomy and systematics in Canada and speculated that, once the leaf litter and tree canopy faunas were documented, the total number of species would reach around 1,500. The leaf litter will likely yield the most new species (Pinzón 2011). In the most recent checklist for Canada and Alaska, Paquin *et al.* (2010) recorded 1,413 species from 43 families; the Linyphiidae accounted for almost 40%. About a quarter of the Canadian total has been reported from the Mixed Grassland and Moist Mixed Grassland ecoregions of the Prairies Ecozone. Holmberg and Buckle (2002) noted that 356 species from 21 families are found in these ecoregions in Alberta and Saskatchewan, but did not list the species. Aitchison-Benell

and Dondale (1990) listed 483 species from 20 families from all ecoregions of Manitoba, and an additional 43 species were added when Wade and Roughley (2002) updated the Manitoba list. In a recent study in the boreal forest of northwestern Alberta, Pinzón (2011) found several undescribed species on the ground layer but none in the tree canopy (Pinzón 2011; Pinzón *et al.* 2011).

**Table 1.** Spider families listed in order of descending diversity of recorded species in the Prairie Provinces. References with keys to species are given. “Poss.” indicates species that occur in adjacent jurisdictions, but are not reported from the Prairie Provinces. “Adv.” indicates adventive species. Note that the Ubick *et al.* (2005) reference contains keys to genus for all families of North America (contributed by various experts).

Rank	Family	No. of Genera	No. of Spp.	%	Poss.	Adv.	Identification Keys
1	Linyphiidae	112	295	38.5	0	1	Ubick <i>et al.</i> 2005
2	Gnaphosidae	14	61	8.0	12	1	Dondale and Redner 1992
3	Lycosidae	9	59	7.7	3	0	Dondale and Redner 1990
4	Salticidae	22	56	7.3	0	2	Ubick <i>et al.</i> 2005
5	Dictynidae	11	53	6.9	1	0	Ubick <i>et al.</i> 2005; Chamberlin and Gertsch 1958
6	Theridiidae	23	51	6.6	0	2	Ubick <i>et al.</i> 2005; Levi 1957a,b
7	Thomisidae	7	38	5.0	5	0	Dondale and Redner 1978
8	Araneidae	16	37	4.8	7	4	Dondale <i>et al.</i> 2003; Levi 1971, 1973, 1974a,b
9	Philodromidae	4	29	3.8	1	1	Dondale and Redner 1978
10	Clubionidae	1	20	2.6	1	0	Dondale and Redner 1982
11	Tetragnathidae	2	13	1.7	3	1	Dondale <i>et al.</i> 2003
12	Hahniidae	5	10	1.3	5	0	Opell and Beatty 1976
13	Agelenidae	3	9	1.2	1	4	Chamberlin and Ivie 1941, 1942
14	Corinnidae	3	9	1.2	0	0	Dondale and Redner 1982
15	Amaurobiidae	4	8	1.0	5	0	Leech 1972
16	Pisauridae	1	4	0.5	0	0	Dondale and Redner 1990
17	Cybaeidae	2	2	0.3	0	0	Bennet 1991
18	Liocranidae	1	2	0.3	0	0	Ubick <i>et al.</i> 2005
19	Mimetidae	2	2	0.3	0	0	Ubick <i>et al.</i> 2005
20	Pholcidae	2	2	0.3	0	1	Ubick <i>et al.</i> 2005
21	Titanoecidae	1	2	0.3	0	0	Leech 1972
22	Amphinectidae	1	1	0.1	0	1	Ubick <i>et al.</i> 2005
23	Anypheidae	1	1	0.1	0	0	Dondale and Redner 1982
24	Miturgidae	1	1	0.1	0	0	Ubick <i>et al.</i> 2005
25	Oxyopidae	1	1	0.1	0	0	Dondale and Redner 1990
26	Uloboridae	1	1	0.1	0	0	Dondale <i>et al.</i> 2003
Totals		250	767		44	18	

**Table 2.** Common or abundant spider species (>5%) at the study sites reported from biodiversity studies using pitfall traps in the Prairies Ecozone and transition forest ecoregions. Numbers in parentheses correspond to the study numbers shown in Figs. 4 and 5 and Table 4 and to study references noted below the table.

Ecoregion or Habitat (Study Number) <sup>1</sup>	Species Assemblage
Mixed Grassland (2, 3, 4)	<i>Schizocosa mccooki</i> , <i>Zelotes lasalanus</i> , <i>Pardosa distincta</i>
Moist Mixed Grassland (1, 5)	<i>Pardosa dromaea</i> , <i>Pardosa</i> sp. nr. <i>tesquorum</i>
Tallgrass prairie - grass (7)	<i>Pardosa moesta</i> , <i>P. distincta</i> , <i>Alopecosa aculeata</i>
Tallgrass prairie - aspen (8)	<i>Pardosa moesta</i> , <i>Alopecosa aculeata</i> , <i>Agroeca ornata</i> , <i>Centromerus sylvaticus</i>
Aspen Parkland (prairie ponds, AB) (9)	<i>Pardosa fuscata</i> , <i>P. modica</i> , <i>Alopecosa aculeata</i>
Aspen Parkland (grassland reserve, MB) (6)	<i>Pardosa distincta</i> , <i>Alopecosa aculeata</i>
Boreal Transition (10, 11) (aspen mixwood forest)	<i>Allomengea dentisetis</i> , <i>Bathyphantes pallidus</i> , <i>Cybaeopsis euopla</i> , <i>Neoantistea magna</i> , <i>Ozyptila sincera canadensis</i> , <i>Pardosa fuscata</i> , <i>P. mackenziana</i> , <i>P. moesta</i> , <i>Pirata piraticus</i> , <i>Trochosa terricola</i> , <i>Xysticus luctuosus</i>
Foothills (12, 13)	<i>Allomengea dentisetis</i> , <i>Callioplus euoplus</i> , <i>Diplocentria bidentata</i>
Widespread <sup>2</sup>	<i>Hogna frondicola</i> , <i>Pardosa distincta</i> , <i>Pardosa modica</i> , <i>Alopecosa aculeata</i> , <i>Enoplognatha marmorata</i> , <i>Xysticus ferox</i>

<sup>1</sup> Study numbers correspond to those in Fig. 5 and Table 4: 1 = HC and RL (unpublished data); 2 = Finnamore and Buckle (1999); 3 = Pepper (1999); 4 = Finnamore *et al.* (2000); 5 = Doane and Dondale (1979); 6 = Stjernberg (2011); 7, 8 = Roughley *et al.* (2006); 9 = Graham (2002); 10 = Graham *et al.* (2003); 11 = JP and JS (unpublished data); 12, 13 = Cárcamo (1997).

<sup>2</sup> Widespread if frequent throughout the Prairies Ecozone and transition forest ecoregions.

Here we provide a current checklist of spiders of the Canadian Prairie Provinces (Table 3). The checklist was prepared by examining the publications cited earlier (particularly Paquin *et al.* (2010)) and selecting the species that occur in the three Prairie Provinces; consulting the *World Spider Catalogue*, version 14.0 (Platnick 2013), to update previously published checklists; and supplementing the list from our own biodiversity studies, recent published articles and theses, or unpublished surveys in the region. Furthermore, we list as possible occurrences species known in adjacent provinces or areas of the United States, which may be discovered with more intensive sampling. The taxonomy and nomenclature from the *World Spider Catalogue*, version 14.0 (Platnick 2013), were adopted for this review. Determinations were performed by the authors listed in Table 4 for their respective studies. Undescribed species of Linyphiidae are kept in the personal collection of D.J. Buckle, who was involved with all studies within the ecozone. Voucher specimens from the canola study at Lethbridge and from the southwestern foothills forests by HC were placed with the arthropod and plant collections housed at the Lethbridge Research Centre of Agriculture and Agri-Food Canada; for others, the reader is referred to sources listed in Table 4.

**Table 3.** Checklist of spider species in the Canadian Prairie Provinces. Species in bold were not reported in the checklist by Paquin *et al.* (2010). **Key:** \*adventive species; <sup>p</sup>species that occurs in adjacent jurisdictions and may occur in the Prairies; <sup>1</sup>formerly *Steatoda medialis* (Levi 1957a; Gertsch 1960), a new record for Canada. **Provincial abbreviations:** **AB:** Alberta, **SK:** Saskatchewan, **MB:** Manitoba. *Species checklist available at:* <http://dx.doi.org/10.5886/qwco8c3a>

Family, Genus, and Species	AB	SK	MB
<b>AGELENIDAE</b>			
<i>Agelenopsis actuosa</i> (Gertsch and Ivie, 1936)	AB	SK	MB
<i>Agelenopsis oklahoma</i> (Gertsch, 1936)	AB	SK	-
<i>Agelenopsis oregonensis</i> (Chamberlin and Ivie, 1935)	AB <sup>p</sup>	-	-
<i>Agelenopsis potteri</i> (Blackwall, 1846)	AB	SK	MB
<i>Agelenopsis utahana</i> (Chamberlin and Ivie, 1933)	AB	SK	MB
<i>Novalena intermedia</i> (Chamberlin and Gertsch, 1930)	AB	-	-
<i>Tegenaria agrestis</i> (Walckenaer, 1802)*	AB	-	-
<i>Tegenaria atrica</i> C.L. Koch, 1843*	-	SK	-
<i>Tegenaria domestica</i> (Clerck, 1757)*	AB	SK	MB
<i>Tegenaria duellica</i> Simon, 1875*	AB	SK	-
<b>AMAUROBIIDAE</b>			
<i>Amaurobius borealis</i> Emerton, 1909	AB	-	MB
<i>Arctobius agelenoides</i> (Emerton, 1919)	AB	SK	MB
<i>Callobius bennetti</i> (Blackwall, 1846)	-	SK <sup>p</sup>	MB
<i>Callobius canada</i> (Chamberlin and Ivie, 1947)	AB <sup>p</sup>	-	-
<i>Callobius enus</i> (Chamberlin and Ivie, 1947)	AB <sup>p</sup>	SK <sup>p</sup>	-
<i>Callobius nevadensis</i> (Simon, 1884)	AB <sup>p</sup>	SK <sup>p</sup>	-
<i>Callobius nomeus</i> (Chamberlin, 1919)	AB	SK	MB
<i>Callobius severus</i> (Simon, 1884)	AB	-	-
<i>Cybaeopsis euopla</i> (Bishop and Crosby, 1935)	AB	SK	MB
<i>Cybaeopsis tibialis</i> (Emerton, 1890)	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Cybaeopsis wabritaska</i> (Leech, 1972)	AB	SK <sup>p</sup>	-
<i>Zanomys aquilonia</i> Leech, 1972	AB <sup>p</sup>	-	-
<i>Zanomys kaiba</i> Chamberlin, 1948	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<b>AMPHINECTIDAE</b>			
<i>Metaltella simoni</i> (Keyserling, 1878)*	AB	-	-
<b>ANYPHAENIDAE</b>			
<i>Anyphaena pacifica</i> (Banks, 1896)	AB	SK	-
<b>ARANEIDAE</b>			
<i>Acanthepeira stellata</i> (Walckenaer, 1805)	-	-	MB
<i>Aculepeira carbonarioides</i> (Keyserling, 1892)	AB	-	-
<i>Aculepeira packardi</i> (Thorell, 1875)	AB	SK	MB
<i>Araneus corticarius</i> (Emerton, 1885)	AB	SK	MB
<i>Araneus diadematus</i> (Clerck, 1757)*	AB	SK <sup>p</sup>	-
<i>Araneus gemma</i> (McCook, 1888)	AB <sup>p</sup>	SK <sup>p</sup>	-
<i>Araneus gemmoides</i> Chamberlin and Ivie, 1935	AB	SK	MB
<i>Araneus groenlandicola</i> (Strand, 1906)	AB	SK <sup>p</sup>	MB
<i>Araneus iviei</i> (Archer, 1951)	AB	SK	MB
<i>Araneus marmoreus</i> Clerck, 1757	AB	SK	MB
<i>Araneus nordmanni</i> (Thorell, 1870)	AB	SK	MB
<i>Araneus pratensis</i> Emerton, 1884	-	-	MB
<i>Araneus saevus</i> (L. Koch, 1872)	AB	SK	MB



<i>Araneus thaddeus</i> (Hentz, 1847)	-	-	MB
<i>Araneus trifolium</i> (Hentz, 1847)	AB	SK	MB
<i>Araneus washingtoni</i> Levi, 1971	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Araniella displicata</i> (Hentz, 1847)	AB	SK	MB
<i>Araniella proxima</i> (Kulczynski, 1885)	AB	SK	MB <sup>p</sup>
<i>Argiope aurantia</i> (Lucas, 1833)	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Argiope trifasciata</i> (Forskaal, 1775)	AB	SK	MB
<i>Cercidia prominens</i> (Westring, 1861)*	AB	SK <sup>p</sup>	MB
<i>Cyclosa conica</i> (Pallas, 1772)	AB	SK	MB
<i>Eustala anastera</i> (Walckenaer, 1841)	AB	SK	MB
<i>Hypsosinga alberta</i> Levi, 1972	AB	SK	MB <sup>p</sup>
<i>Hypsosinga funebris</i> (Keyserling, 1892)	AB	SK	MB
<i>Hypsosinga groenlandica</i> Simon, 1889	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Hypsosinga pygmaea</i> (Sundevall, 1832)	AB	SK	MB
<i>Hypsosinga rubens</i> (Hentz, 1847)	AB	SK	MB
<i>Larinia borealis</i> Banks, 1894	AB	SK	MB
<i>Larinioides cornutus</i> (Clerck, 1757)	AB	SK	MB
<i>Larinioides patagiatus</i> (Clerck, 1757)	AB	SK	MB
<i>Larinioides scolopetarius</i> (Clerck, 1757)*	AB	SK <sup>p</sup>	MB
<i>Mangora maculata</i> (Keyserling, 1865)	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Mangora placida</i> (Hentz, 1847)	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Metepeira foxi</i> Gertsch and Ivie, 1936	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Metepeira grandiosa</i> Gertsch and Ivie, 1941	AB	SK	MB <sup>p</sup>
<i>Metepeira palustris</i> Gertsch and Ivie, 1942	AB	SK	MB
<i>Neoscona arabesca</i> (Walckenaer, 1847)	AB	SK	MB
<i>Neoscona pratensis</i> (Hentz, 1847)	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Parazygiella dispar</i> (Keyserling, 1885)	AB <sup>p</sup>	SK <sup>p</sup>	-
<i>Singa keyserlingi</i> McCook, 1894	AB	SK	MB
<i>Zygiella atrica</i> (C.L. Koch, 1845)	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Zygiella nearctica</i> Gertsch, 1964	AB	SK	MB
<i>Zygiella x-notata</i> (Clerck, 1757)*	AB <sup>p</sup>	SK <sup>p</sup>	-

## CLUBIONIDAE

<i>Clubiona abboti</i> L. Koch, 1866	AB	SK	MB
<i>Clubiona bryantae</i> Emerton, 1924	AB	SK	MB
<i>Clubiona canadensis</i> Emerton, 1890	AB	SK	MB
<i>Clubiona chippewa</i> Gertsch, 1941	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Clubiona furcata</i> Emerton, 1919	AB	SK	MB
<i>Clubiona johnsoni</i> Gertsch, 1941	AB <sup>p</sup>	SK	MB
<i>Clubiona kastoni</i> Gertsch, 1941	AB	SK	MB
<i>Clubiona kiowa</i> Gertsch, 1941	-	-	MB
<i>Clubiona kulczynskii</i> Lessert, 1905	AB	SK	MB
<i>Clubiona maritima</i> L. Koch, 1867	-	SK <sup>p</sup>	MB
<i>Clubiona mixta</i> Emerton, 1890	AB <sup>p</sup>	SK	MB
<i>Clubiona moesta</i> Banks, 1890	AB	SK	MB
<i>Clubiona mutata</i> Gertsch, 1941	AB	SK	MB
<i>Clubiona norveica</i> Strand, 1900	AB	SK	MB
<i>Clubiona obesa</i> (Hentz, 1847)	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Clubiona opeongo</i> Edwards, 1958	AB	SK	MB
<i>Clubiona pacifica</i> Banks, 1896	AB	-	-
<i>Clubiona pallidula</i> (Clerck, 1757)	AB <sup>p</sup>	-	-

<i>Clubiona praematura</i> Emerton, 1909	AB	SK <sup>P</sup>	MB
<i>Clubiona riparia</i> L. Koch, 1866	AB	SK	MB
<i>Clubiona trivialis</i> C.L. Koch, 1843	AB	SK	MB
CORINNIDAE			
<i>Castianeira alteranda</i> Gertsch, 1942	AB	SK	MB <sup>P</sup>
<i>Castianeira cingulata</i> (C.L. Koch, 1841)	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Castianeira descripta</i> (Hentz, 1847)	AB	SK	MB
<i>Castianeira longipalpa</i> (Hentz, 1847)	AB	SK	MB
<i>Phrurotimpus borealis</i> (Emerton, 1911)	AB	SK	MB
<i>Phrurotimpus certus</i> Gertsch, 1941	AB	SK	MB
<i>Scotinella madisonia</i> Levi, 1951	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Scotinella manitou</i> Levi, 1951	-	-	MB
<i>Scotinella pugnata</i> (Emerton, 1890)	AB	SK	MB
CYBAEIDAE			
<i>Cybaeota calcarata</i> (Emerton, 1911)	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Cybaeus sinuosus</i> Fox, 1937	AB	SK <sup>P</sup>	-
DICTYNIDAE			
<i>Argenna obesa</i> Emerton, 1911	AB	SK <sup>P</sup>	MB
<i>Argenna yakima</i> Chamberlin and Gertsch, 1958	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Brommella monticola</i> (Gertsch and Mulaik, 1936)	AB	-	-
<i>Cicurina arcuata</i> Keyserling, 1887	-	SK	MB
<i>Cicurina brevis</i> (Emerton, 1890)	-	SK <sup>P</sup>	MB
<i>Cicurina intermedia</i> Chamberlin and Ivie, 1933	AB	SK <sup>P</sup>	-
<i>Cicurina placida</i> Banks, 1892	-	SK <sup>P</sup>	MB
<i>Cicurina robusta</i> Simon, 1886	AB	SK	MB
<i>Cicurina simplex</i> Simon, 1886	AB	-	-
<i>Cicurina varians</i> Gertsch and Mulaik, 1940	AB	-	-
<i>Dictyna alaskae</i> Chamberlin and Ivie, 1947	AB	SK	MB
<i>Dictyna arundinacea</i> (Linnaeus, 1757)	AB	SK	MB
<i>Dictyna bostoniensis</i> Emerton, 1888	AB	SK	MB <sup>P</sup>
<i>Dictyna brevitarsa</i> Emerton, 1915	AB	SK	MB <sup>P</sup>
<i>Dictyna calcarata</i> Banks, 1904	AB <sup>P</sup>	SK <sup>P</sup>	MB <sup>P</sup>
<i>Dictyna coloradensis</i> Chamberlin, 1919	AB	SK	MB
<i>Dictyna foliacea</i> Hentz, 1850	AB	SK	MB
<i>Dictyna major</i> Menge, 1869	AB	SK	MB
<i>Dictyna minuta</i> Emerton, 1888	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Dictyna personata</i> Gertsch and Mulaik, 1936	AB	SK	MB <sup>P</sup>
<i>Dictyna quadrispinosa</i> Emerton, 1919	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Dictyna sancta</i> Gertsch, 1946	AB	SK	MB
<i>Dictyna subpinicola</i> Ivie, 1947	AB	SK	MB <sup>P</sup>
<i>Dictyna terrestris</i> Emerton, 1911	AB	SK	MB
<i>Dictyna volucripes</i> Keyserling, 1881	AB	SK	MB
<i>Emblyna annulipes</i> (Blackwall, 1846)	AB	SK	MB
<i>Emblyna borealis cavernosa</i> (Jones, 1947)	AB	SK <sup>P</sup>	-
<i>Emblyna chitina</i> (Chamberlin and Gertsch, 1958)	AB	SK <sup>P</sup>	-
<i>Emblyna completoides</i> (Ivie, 1947)	AB	SK	MB
<i>Emblyna consulta</i> (Gertsch and Ivie, 1936)	AB	SK	MB <sup>P</sup>
<i>Emblyna cornupeta</i> (Bishop and Ruderman, 1946)	AB	-	-
<i>Emblyna hentzi</i> Kaston, 1945	-	-	MB

<i>Emblyna horta</i> (Gertsch and Ivie, 1936)	AB	SK	MB <sup>p</sup>
<i>Emblyna jonesae</i> (Roewer, 1955)	AB	SK	MB <sup>p</sup>
<i>Emblyna littoricolens</i> (Chamberlin and Ivie, 1935)	-	SK	-
<i>Emblyna manitoba</i> (Ivie, 1947)	AB	SK	MB
<i>Emblyna mariae</i> Chamberlin, 1947	AB	-	-
<i>Emblyna maxima</i> (Banks, 1892)	AB	SK	MB
<i>Emblyna peragrata</i> (Bishop and Ruderman, 1946)	AB	-	-
<i>Emblyna phylax</i> (Gertsch and Ivie, 1936)	AB	SK	MB
<i>Emblyna reticulata</i> (Gertsch and Ivie, 1936)	AB	-	-
<i>Emblyna sublata</i> (Hentz, 1850)	AB	SK	MB
<i>Hackmania lorna</i> Chamberlin and Gertsch, 1958	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Hackmania prominula</i> (Tullgren, 1948)	AB	SK	MB
<i>Hackmania saphes</i> (Chamberlin, 1948)	AB	-	-
<i>Iviella reclusa</i> (Gertsch and Ivie, 1936)	-	SK	-
<i>Lathys alberta</i> Gertsch, 1946	AB	SK <sup>p</sup>	MB
<i>Lathys pallida</i> (Marx, 1891)	AB	SK	MB
<i>Mallos niveus</i> O. P.-Cambridge, 1902	AB	SK	-
<i>Mallos pallidus</i> Banks, 1904	AB	SK	MB
<i>Mexitlia trivittata</i> Banks, 1901	AB	-	-
<i>Phantyna bicornis</i> Emerton, 1915	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Phantyna terranea</i> Ivie, 1947	AB	SK	-
<i>Tricholathys spiralis</i> Chamberlin and Ivie, 1935	AB	SK	MB
GNAPHOSIDAE			
<i>Callilepis ermella</i> Chamberlin, 1928	AB <sup>p</sup>	-	-
<i>Callilepis pluto</i> Banks, 1896	AB	SK	MB
<i>Cesonia bilineata</i> (Hentz, 1847)	-	SK <sup>p</sup>	MB
<i>Drassodes gosiutus</i> Chamberlin, 1919	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Drassodes mirus</i> Platnick and Shadab, 1976	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Drassodes neglectus</i> (Keyserling, 1887)	AB	SK	MB
<i>Drassodes saccatus</i> (Emerton, 1890)	AB	SK	MB <sup>p</sup>
<i>Drassyllus depressus</i> (Emerton, 1890)	AB	SK	MB
<i>Drassyllus dromeus</i> Chamberlin, 1922	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Drassyllus insularis</i> (Banks, 1900)	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Drassyllus lamprus</i> (Chamberlin, 1920)	AB	SK	MB <sup>p</sup>
<i>Drassyllus nannellus</i> Chamberlin and Gertsch, 1940	AB	SK	MB <sup>p</sup>
<i>Drassyllus niger</i> (Banks, 1896)	AB	SK	MB
<i>Drassyllus saphes</i> Chamberlin, 1936	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Gnaphosa borea</i> Kulczynski, 1908	AB	SK	MB
<i>Gnaphosa brumalis</i> Thorell, 1875	AB	SK	MB
<i>Gnaphosa clara</i> (Keyserling, 1887)	AB	SK	MB <sup>p</sup>
<i>Gnaphosa microps</i> Holm, 1939	AB	SK	MB
<i>Gnaphosa muscorum</i> (L. Koch, 1866)	AB	SK	MB
<i>Gnaphosa orites</i> Chamberlin, 1922	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Gnaphosa parvula</i> Banks, 1896	AB	SK	MB
<i>Haplodrassus bicornis</i> (Emerton, 1909)	AB	SK	MB
<i>Haplodrassus chamberlini</i> Platnick and Shadab, 1975	AB	SK	MB
<i>Haplodrassus eunis</i> Chamberlin, 1922	AB	SK	MB <sup>p</sup>
<i>Haplodrassus hiemalis</i> (Emerton, 1909)	AB	SK	MB
<i>Haplodrassus signifer</i> (C.L. Koch, 1839)	AB	SK	MB
<i>Herpyllus ecclesiasticus</i> Hentz, 1832	AB	SK	MB

<i>Herpyllus hesperolus</i> Chamberlin, 1928	AB	SK	MB <sup>p</sup>
<i>Herpyllus propinquus</i> (Keyserling, 1887)	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Micaria aenea</i> Thorell, 1877	AB	SK	MB
<i>Micaria alpina</i> L. Koch, 1872	-	-	MB
<i>Micaria coloradensis</i> Banks, 1896	AB	SK	MB <sup>p</sup>
<i>Micaria constricta</i> Emerton, 1894	AB	SK <sup>p</sup>	MB
<i>Micaria emertoni</i> Gertsch, 1935	AB	SK	-
<i>Micaria foxi</i> Gertsch, 1933	AB	SK	-
<i>Micaria gertschi</i> Barrows and Ivie, 1942	AB	SK	MB
<i>Micaria idana</i> Platnick and Shadab, 1988	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Micaria laticeps</i> Emerton, 1909	AB	SK	MB <sup>p</sup>
<i>Micaria longipes</i> Emerton, 1890	AB	SK	MB <sup>p</sup>
<i>Micaria longispina</i> Emerton, 1911	AB	SK	MB <sup>p</sup>
<i>Micaria medica</i> Platnick and Shadab, 1988	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Micaria mormon</i> Gertsch, 1935	AB	SK	MB <sup>p</sup>
<i>Micaria porta</i> Platnick and Shadab, 1988	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Micaria pulicaria</i> (Sundevall, 1831)	AB	SK	MB
<i>Micaria riggsi</i> Gertsch, 1942	AB	SK	-
<i>Micaria rossica</i> Thorell, 1875	AB	SK	MB
<i>Micaria tripunctata</i> Holm, 1978	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Micaria utahna</i> Gertsch, 1933	AB <sup>p</sup>	-	-
<i>Nodocion eclecticus</i> Chamberlin, 1924	AB <sup>p</sup>	-	-
<b><i>Nodocion mateonus</i></b> Chamberlin, 1922	-	-	MB
<i>Nodocion rufithoracicus</i> Worley, 1928	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Nodocion voluntarius</i> (Chamberlin, 1919)	AB	SK <sup>p</sup>	-
<i>Orodassus canadensis</i> Platnick and Shadab, 1975	AB	SK	MB
<i>Orodassus coloradensis</i> (Emerton, 1877)	AB	SK	MB
<i>Sergiolus angustus</i> (Banks, 1904)	AB	SK	-
<i>Sergiolus bicolor</i> Banks, 1900	-	-	MB
<i>Sergiolus capulatus</i> (Walckenaer, 1837)			MB
<i>Sergiolus columbianus</i> (Emerton, 1917)	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Sergiolus decoratus</i> Kaston, 1945	AB <sup>p</sup>	SK	MB
<i>Sergiolus iviei</i> Platnick and Shadab, 1981	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Sergiolus montanus</i> (Emerton, 1890)	AB	SK	MB
<i>Sergiolus ocellatus</i> (Walckenaer, 1837)	AB	SK	MB <sup>p</sup>
<i>Sosticus loricatus</i> (L. Koch, 1866)*	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Urozelotes rusticus</i> (L. Koch, 1872)	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Zelotes exiguoides</i> Platnick and Shadab, 1983	-	-	MB
<i>Zelotes fratris</i> Chamberlin, 1920	AB	SK	MB <sup>p</sup>
<i>Zelotes hentzi</i> Barrows, 1945	-	-	MB <sup>p</sup>
<i>Zelotes laccus</i> (Barrows, 1919)	-	SK	MB <sup>p</sup>
<i>Zelotes lasalanus</i> Chamberlin, 1928	AB	SK	MB
<i>Zelotes puritanus</i> Chamberlin, 1922	AB	SK	MB
<i>Zelotes sula</i> Lowrie and Gertsch, 1955	AB	SK	MB <sup>p</sup>
<b>HAHNIIDAE</b>			
<i>Antistea brunnea</i> (Emerton, 1909)	AB	SK	MB
<i>Cryphoea exlineae</i> Roth, 1988	AB	-	-
<i>Cryphoea montana</i> Emerton, 1909	-	SK	-
<i>Ethobuella tuonops</i> Chamberlin and Ivie, 1937	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Hahnina cinerea</i> Emerton, 1890	AB	SK	MB

<i>Hahnia glacialis</i> Sørensen, 1898	AB	SK <sup>p</sup>	MB
<i>Hahnia ononidum</i> Simon, 1875	AB	SK	MB
<i>Neoantistea agilis</i> (Keyserling, 1887)	AB	SK	MB
<i>Neoantistea gosiuta</i> Gertsch, 1934	AB <sup>p</sup>	SK	MB
<i>Neoantistea magna</i> (Keyserling, 1887)	AB	SK	MB
LINYPHIIDAE			
<i>Agnyphantes arboreus</i> (Emerton, 1915)	AB	-	-
<i>Agyneta allosubtilis</i> Loksa, 1965	AB	SK	MB
<i>Agyneta amersaxatilis</i> Saaristo and Koponen, 1998	AB	SK	MB
<b><i>Agyneta danielbelangeri</i> Dupérré, 2013</b>	AB	-	-
<i>Agyneta fabra</i> (Keyserling, 1886)	AB	SK	MB
<b><i>Agyneta girardi</i> Dupérré, 2013</b>	AB <sup>p</sup>	SK	MB
<i>Agyneta lophophor</i> (Chamberlin and Ivie, 1933)	AB	SK	MB <sup>p</sup>
<i>Agyneta olivacea</i> (Emerton, 1882)	AB	SK	MB
<i>Agyneta ordinaria</i> (Chamberlin and Ivie, 1947)	AB	-	-
<b><i>Agyneta perspicua</i> Dupérré, 2013</b>	AB	-	-
<i>Agyneta protrudens</i> (Chamberlin and Ivie, 1933)	AB	SK	MB <sup>p</sup>
<i>Agyneta simplex</i> (Emerton, 1926)	AB	SK	MB
<i>Agyneta unimaculata</i> (Banks, 1892)	AB	SK <sup>p</sup>	MB
<b><i>Agyneta watertoni</i> Dupérré, 2013</b>	AB	-	-
<i>Allomengea dentisetis</i> (Grube, 1861)	AB	SK	MB
<i>Allomengea scopigera</i> (Grube, 1859)	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Allomengea vidua</i> (L. Koch, 1879)	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Aphileta microtarsa</i> (Emerton, 1882)	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Aphileta misera</i> (O. P.-Cambridge, 1882)	AB	SK	MB
<i>Arcuphantes fragilis</i> Chamberlin and Ivie, 1943	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Baryphyma gowerense</i> (Locket, 1965)	AB	SK	MB
<i>Baryphyma trifrons affine</i> (Schenkel, 1930)	AB	SK	MB
<i>Bathyphantes alascensis</i> (Banks, 1900)	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Bathyphantes brevipes</i> (Emerton, 1917)	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Bathyphantes brevis</i> (Emerton, 1911)	AB	SK	MB
<i>Bathyphantes canadensis</i> (Emerton, 1882)	AB	SK	MB
<i>Bathyphantes eumenis</i> (L. Koch, 1879)	AB	SK <sup>p</sup>	MB
<i>Bathyphantes gracilis</i> (Blackwall, 1841)	AB	SK	MB
<i>Bathyphantes pallidus</i> (Banks, 1892)	AB	SK	MB
<i>Bathyphantes pogonias</i> Kulczynski, 1885	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Bathyphantes reprobis</i> Kulczynski, 1916	AB	SK <sup>p</sup>	MB
<i>Caviphantes saxetorum</i> (Hull, 1916)	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Centromerus longibulbus</i> (Emerton, 1882)	AB	SK	MB
<i>Centromerus persolutus</i> (O. P.-Cambridge, 1875)	AB <sup>p</sup>	SK	MB
<i>Centromerus sylvaticus</i> (Blackwall, 1841)	AB	SK	MB
<i>Ceraticelus alticeps</i> (Fox, 1891)	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Ceraticelus atriceps</i> (O. P.-Cambridge, 1874)	AB	SK	MB
<i>Ceraticelus bulbosus</i> (Emerton, 1882)	AB	SK	MB
<i>Ceraticelus crassiceps</i> Chamberlin and Ivie, 1939	AB	SK	MB
<i>Ceraticelus fissiceps</i> (O. P.-Cambridge, 1874)	AB	SK	MB
<i>Ceraticelus laetabilis</i> (O. P.-Cambridge, 1874)	AB	SK	MB
<i>Ceraticelus laetus</i> (O. P.-Cambridge, 1874)	AB <sup>p</sup>	SK	MB
<i>Ceraticelus laticeps</i> (Emerton, 1894)	AB	SK <sup>p</sup>	MB
<i>Ceraticelus limnologicus</i> Bishop and Crosby, 1925	AB <sup>p</sup>	SK <sup>p</sup>	MB

<i>Ceraticelus minutus</i> (Emerton, 1882)	-	-	MB
<i>Ceraticelus rowensis</i> Levi and Levi, 1955	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Ceraticelus similis</i> (Banks, 1892)	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Ceratinella alaskae</i> Chamberlin and Ivie, 1947	AB	SK	MB
<i>Ceratinella brunnea</i> Emerton, 1882	AB	SK	MB
<i>Ceratinella ornatula alaskana</i> Chamberlin, 1949	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Ceratinella parvula</i> (Fox, 1891)	AB	SK	MB
<i>Ceratinops annulipes</i> (Banks, 1892)	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Ceratinops crenatus</i> (Emerton, 1882)	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Ceratinops inflatus</i> (Emerton, 1923)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Ceratinops latus</i> (Emerton, 1882)	AB <sup>P</sup>	SK	MB
<i>Ceratinops littoralis</i> (Emerton, 1913)	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Ceratinops sylvaticus</i> (Emerton, 1913)	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Ceratinopsis interpres</i> (O. P.-Cambridge 1974)	-	-	MB
<i>Ceratinopsis labradorensis</i> Emerton, 1925	AB	SK	MB
<i>Ceratinopsis nigriceps</i> Emerton 1882	-	-	MB
<i>Cheniseo sphagnicultor</i> Bishop and Crosby, 1935	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Cnephlocotes obscurus</i> (Blackwall, 1834)	AB	SK	MB
<i>Collinsia ksenia</i> (Crosby and Bishop, 1928)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Collinsia perplexa</i> (Keyserling, 1886)	AB	-	-
<i>Collinsia plumosa</i> (Emerton, 1882)	AB	SK	MB
<i>Coloncus siou</i> Chamberlin, 1949	AB	SK	MB <sup>P</sup>
<i>Dicymbium elongatum</i> (Emerton, 1882)	AB	SK <sup>P</sup>	MB
<i>Diplocentria bidentata</i> (Emerton, 1882)	AB	SK	MB
<i>Diplocentria perplexa</i> (Chamberlin and Ivie, 1939)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Diplocentria rectangulata</i> (Emerton, 1915)	AB	SK	MB
<i>Diplocephalus subrostratus</i> (O. P.-Cambridge, 1873)	AB	SK	MB
<i>Diplocephalus cristatus</i> (Blackwall, 1833)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Diplostyla concolor</i> (Wider, 1834)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Disembolus hyalinus</i> Millidge, 1981	AB	-	-
<i>Disembolus implicatus</i> Millidge, 1981	AB	-	-
<i>Disembolus phanus</i> (Chamberlin, 1949)	AB	-	-
<i>Dismodicus alticeps</i> Chamberlin and Ivie, 1947	AB	SK	MB
<i>Dismodicus decemoculatus</i> (Emerton, 1882)	AB	SK	MB
<i>Drapetisca alteranda</i> Chamberlin, 1909	AB	SK	MB
<i>Entelecara sombra</i> (Chamberlin and Ivie, 1947)	AB	SK	MB
<i>Eridantes erigonoides</i> (Emerton, 1882)	-	SK <sup>P</sup>	MB
<i>Eridantes utibilis</i> Crosby and Bishop, 1933	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Erigone alettris</i> Crosby and Bishop, 1928	AB	SK	MB <sup>P</sup>
<i>Erigone alsaida</i> Crosby and Bishop, 1928	AB	SK	MB
<i>Erigone atra</i> Blackwall, 1833	AB	SK	MB
<i>Erigone autumnalis</i> Emerton, 1882	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Erigone blaesa</i> Crosby and Bishop, 1928	AB	SK	MB
<i>Erigone cristatopalpus</i> Simon, 1884	AB	SK	MB
<i>Erigone dentigera</i> O. P.-Cambridge, 1874	AB	SK	MB
<i>Erigone dentosa</i> O. P.-Cambridge, 1894	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Erigone psychrophila</i> Thorell, 1871	-	-	MB
<i>Erigone whymeri</i> O. P.-Cambridge, 1877	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Estrandia grandaeva</i> (Keyserling, 1886)	AB	SK	MB
<i>Eulaira arctoa</i> Holm, 1970	AB	SK <sup>P</sup>	MB <sup>P</sup>

<i>Eulaira chelata</i> Chamberlin and Ivie, 1939	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Floricomus rostratus</i> (Emerton, 1882)	AB	SK <sup>P</sup>	MB
<i>Frederickus wilburi</i> (Levi and Levi, 1955)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Frontinella communis</i> (Walckenaer, 1841)	AB	SK	MB
<i>Glyphesis idahoanus</i> (Chamberlin, 1949)	AB <sup>P</sup>	SK	MB
<i>Glyphesis scopulifer</i> (Emerton, 1882)	AB	SK	MB
<i>Gnathonarium suppositum</i> (Kulczynski, 1885)	AB	SK	MB
<i>Gnathonaroides pedalis</i> (Emerton, 1923)	AB	SK	MB
<i>Gonatium crassipalpum</i> Bryant, 1933	AB	SK	MB
<i>Grammonota angusta</i> Dondale, 1959	AB	SK	MB
<i>Grammonota capitata</i> Emerton, 1924	-	-	MB
<i>Grammonota gentilis</i> Banks, 1898	AB	SK	MB
<i>Grammonota gigas</i> (Banks, 1896)	AB	SK	MB
<i>Grammonota inornata</i> Emerton, 1882	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Grammonota maritima</i> Emerton, 1925	AB	SK	MB <sup>P</sup>
<i>Grammonota pictilis</i> (O.P.-Cambridge, 1875)	AB <sup>P</sup>	SK	MB
<i>Grammonota vittata</i> Barrows, 1919	AB	SK	MB
<i>Helophora insignis</i> (Blackwall, 1841)	AB	SK	MB
<i>Helophora tunagyna</i> Chamberlin and Ivie, 1943	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Hilaira canaliculata</i> (Emerton, 1915)	AB	SK	MB
<i>Hilaira herniosa</i> (Thorell, 1875)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Horcotes quadricristatus</i> (Emerton, 1882)	AB	SK <sup>P</sup>	MB
<i>Hybauchenidium cymbadentatum</i> (Crosby and Bishop, 1935)	AB	SK	MB
<i>Hybauchenidium gibbosum</i> (Sørensen, 1898)	AB	SK	MB
<i>Hypomma marxi</i> (Keyserling, 1886)	AB	SK	MB
<i>Hypselistes florens</i> (O. P.-Cambridge, 1873)	AB	SK	MB
<i>Hypselistes jacksoni</i> (O. P.-Cambridge, 1902)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Idionella anomala</i> Gertsch and Ivie, 1936	AB <sup>P</sup>	SK	MB <sup>P</sup>
<i>Idionella formosa</i> (Banks, 1892)	AB <sup>P</sup>	SK	MB
<i>Idionella rugosa</i> (Crosby, 1905)	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Improphantes complicatus</i> (Emerton, 1882)	AB	SK	MB
<i>Incestophantes duplicatus</i> (Emerton, 1913)	AB	SK	MB
<i>Incestophantes lamprus</i> Chamberlin, 1920	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Incestophantes mercedes</i> Chamberlin and Ivie, 1943	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Islandiana flaveola</i> (Banks, 1892)	AB	SK	MB
<i>Islandiana longisetosa</i> (Emerton, 1882)	AB	SK <sup>P</sup>	MB
<i>Islandiana princeps</i> Braendegaard, 1932	AB	SK	MB
<i>Kaestneria pullata</i> (O. P.-Cambridge, 1863)	AB	SK	MB
<i>Kaestneria rufula</i> (Hackman, 1954)	AB	SK	MB
<i>Lepthyphantes aldersoni</i> Levi and Levi, 1955	AB	-	-
<i>Lepthyphantes alpinus</i> (Emerton, 1882)	AB	SK	MB
<i>Lepthyphantes chamberlini</i> Schenkel, 1950	AB	-	-
<i>Lepthyphantes intricatus</i> (Emerton, 1911)	AB	SK	MB
<i>Lepthyphantes leprosus</i> (Ohlert, 1865)*	AB	SK	MB <sup>P</sup>
<i>Lepthyphantes rainieri</i> Emerton, 1926	AB	-	-
<i>Lepthyphantes turbatrix</i> (O. P.-Cambridge, 1877)	AB	SK	MB
<i>Lepthyphantes washingtoni</i> Zorsch, 1937	AB	SK	MB
<i>Lophomma depressum</i> (Emerton, 1882)	-	-	MB
<i>Lophomma vaccinii</i> (Emerton, 1926)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Macrargus multesimus</i> (O. P.-Cambridge, 1875)	AB	SK	MB

<i>Maro amplus</i> Dondale and Buckle, 2001	AB	SK	MB
<i>Maso sundevalli</i> (Westring, 1851)	AB	SK	MB
<i>Masoncus dux</i> Chamberlin, 1949	-	-	MB
<i>Mecynargus paetulus</i> (O. P.-Cambridge, 1875)	AB	SK <sup>P</sup>	MB
<i>Megalephyphantes nebulosus</i> (Sundevall, 1830)	AB	SK	MB
<i>Mermessus denticulatus</i> (Emerton, 1909)	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Mermessus mediocris</i> (Millidge, 1987)	-	-	MB
<i>Mermessus tridentatus</i> (Emerton, 1882)	-	-	MB
<i>Mermessus trilobatus</i> (Emerton, 1882)	AB	SK	MB
<i>Mermessus undulatus</i> (Emerton, 1914)	AB	SK	MB
<i>Metapobactrus pacificus</i> (Emerton, 1923)	AB	-	-
<i>Metapobactrus prominulus</i> (O. P.-Cambridge, 1872)	AB	SK	MB <sup>P</sup>
<i>Micrargus longitarsus</i> (Emerton, 1882)	AB	-	-
<i>Microlinyphia impigra</i> (O. P.-Cambridge, 1871)	AB	SK	MB
<i>Microlinyphia mandibulata mandibulata</i> (Emerton, 1882)	AB	SK	MB
<i>Microlinyphia pusilla</i> (Sundevall, 1829)	AB	SK	MB
<i>Microneta viaria</i> (Blackwall, 1841)	AB	SK	MB
<i>Montilaira uta</i> (Chamberlin, 1919)	AB	-	-
<i>Mythoplastoides erectus</i> (Emerton, 1915)	AB	-	-
<i>Neodietrichia hesperia</i> (Crosby and Bishop, 1933)	AB <sup>P</sup>	SK	MB
<i>Neriene clathrata</i> (Sundevall, 1829)	AB	SK	MB
<i>Neriene radiata</i> (Walckenaer, 1841)	AB	SK	MB
<i>Oedothorax alascensis</i> (Banks, 1900)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Oedothorax trilobatus</i> (Banks, 1896)	AB	SK <sup>P</sup>	MB
<i>Oreoneta banffkluane</i> Saaristo and Marusik, 2004	AB	-	-
<i>Oreonetides filicatus</i> (Crosby, 1937)	AB	-	-
<i>Oreonetides flavus</i> (Emerton, 1915)	AB	-	-
<i>Oreonetides rectangulatus</i> (Emerton, 1913)	AB	SK	MB
<i>Oreonetides vaginatus</i> (Thorell, 1872)	AB	SK	MB
<i>Oreophantes recurvatus</i> (Emerton, 1913)	AB	SK	MB
<i>Oryphantes aliquantulus</i> Dupérré and Paquin, 2007	AB	SK	MB
<i>Pelecopsis bishopi</i> Kaston, 1945	AB	SK <sup>P</sup>	MB
<i>Pelecopsis mengei</i> (Simon, 1884)	AB	SK	MB
<i>Pelecopsis moesta</i> (Banks, 1892)	AB	SK	MB
<i>Pelecopsis sculpta</i> (Emerton, 1917)	AB	-	-
<i>Perregrinus deformis</i> (Tanasevitch, 1982)	-	SK	-
<i>Phlattothrata flagellata</i> (Emerton, 1911)	AB	SK	MB <sup>P</sup>
<i>Phlattothrata parva</i> (Kulczynski, 1926)	AB	SK	MB
<i>Pityohyphantes alticeps</i> Chamberlin and Ivie, 1943	AB	-	-
<i>Pityohyphantes costatus</i> (Hentz, 1850)	AB	SK	MB
<i>Pityohyphantes cristatus</i> Chamberlin and Ivie, 1942	AB	SK	-
<i>Pityohyphantes limitaneus</i> (Emerton, 1915)	AB	SK	MB
<i>Pityohyphantes subarcticus</i> Chamberlin and Ivie, 1943	AB	SK	MB
<i>Pocadicnemis americana</i> Millidge, 1976	AB	SK	MB
<i>Pocadicnemis pumila</i> (Blackwall, 1841)	AB	-	-
<i>Poeciloneta aggressa</i> (Chamberlin and Ivie, 1943)	AB	-	-
<i>Poeciloneta calcaratus</i> (Emerton, 1909)	AB	SK	MB
<i>Poeciloneta fructuosa</i> (Keyserling, 1886)	AB	-	-
<i>Poeciloneta lyricus</i> (Zorsch, 1937)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Poeciloneta theridiformis</i> (Emerton, 1911)	-	SK	-



<i>Poecilonea variegata</i> (Blackwall, 1841)	AB	SK	-
<i>Porrhomma terrestre</i> (Emerton, 1882)	AB	SK	MB
<i>Praestigia kulczynskii</i> Eskov, 1979	AB	SK	MB
<i>Saaristoa sammamish</i> (Levi and Levi, 1955)	AB	-	-
<i>Satilatlas carens</i> Millidge, 1981	-	SK	-
<i>Satilatlas gertschi</i> Millidge, 1881	AB <sup>P</sup>	SK	MB
<i>Satilatlas marxi</i> Keyserling, 1886	AB <sup>P</sup>	SK	MB
<i>Sciastes dubius</i> (Hackman, 1954)	-	-	MB
<i>Sciastes hastatus</i> Millidge, 1984	-	-	MB
<i>Sciastes mentasta</i> (Chamberlin and Ivie, 1947)	AB	SK <sup>P</sup>	MB
<i>Sciastes truncatus</i> (Emerton, 1882)	AB	SK	MB
<i>Scirites pectinatus</i> (Emerton, 1911)	AB	SK	MB
<i>Scironis tarsalis</i> (Emerton, 1911)	AB	SK	MB
<i>Scotinotylus alienus</i> (Kulczynski, 1885)	AB	-	-
<i>Scotinotylus alpinus</i> (Banks, 1896)	AB	SK <sup>P</sup>	MB
<i>Scotinotylus boreus</i> Millidge, 1981	AB	SK	MB
<i>Scotinotylus exsectoides</i> Millidge, 1981	AB	SK	MB
<i>Scotinotylus pallidus</i> (Emerton, 1882)	AB	SK	MB
<i>Scotinotylus sacer</i> (Crosby, 1929)	AB	SK	MB
<i>Scotinotylus sacratus</i> Millidge, 1981	AB	-	-
<i>Scotinotylus sanctus</i> (Crosby, 1929)	AB	-	-
<i>Scotinotylus sinatulus</i> Millidge, 1981	-	SK	-
<i>Scotinotylus vernalis</i> (Emerton, 1882)	AB <sup>P</sup>	SK	MB
<i>Scyletria inflata</i> Bishop and Crosby, 1938	AB	SK	MB
<i>Semljicola obtusus</i> (Emerton, 1915)	AB	-	-
<i>Silometopoides pingrensis</i> (Crosby and Bishop, 1933)	AB	-	-
<i>Sisicottus crossoclavis</i> Miller, 1999	AB	-	-
<i>Sisicottus montanus</i> (Emerton, 1882)	AB	SK	MB
<i>Sisicottus nesides</i> (Chamberlin, 1921)	AB	-	-
<i>Sisicottus orites</i> (Chamberlin, 1919)	AB	-	-
<i>Sisicottus panopeus</i> Miller, 1999	AB	-	-
<i>Sisicus apertus</i> (Holm, 1939)	AB	SK	MB
<i>Sisicus penifusifer</i> Bishop and Crosby, 1938	AB	SK	MB
<i>Sisicus volutasilex</i> Dupérré and Paquin, 2007	AB	-	-
<i>Sisis rotundus</i> (Emerton, 1925)	AB	SK	MB
<i>Smodix reticulata</i> (Emerton, 1915)	AB	-	-
<i>Soucron arenarium</i> (Emerton, 1925)	AB	SK	MB
<i>Sougambus bostoniensis</i> (Emerton, 1882)	AB <sup>P</sup>	SK	MB
<i>Spirembolus monticolens</i> (Chamberlin, 1919)	AB	-	-
<i>Spirembolus prominens</i> Millidge, 1980	AB	-	-
<i>Spirembolus spirotubus</i> (Banks, 1895)	AB	SK	MB <sup>P</sup>
<i>Stemonyphantes blauveltae</i> Gertsch, 1951	AB	SK	MB
<i>Styloctetor stativus</i> (Simon, 1881)	AB	SK	MB
<i>Subbekasha flabellifera</i> Millidge, 1984	AB <sup>P</sup>	SK	MB
<i>Symmigma minimum</i> (Emerton, 1923)	AB	-	-
<i>Tachygyna haydeni</i> Chamberlin and Ivie, 1939	AB	-	-
<i>Tachygyna pallida</i> Chamberlin and Ivie, 1939	AB	-	-
<i>Tachygyna ursina</i> (Bishop and Crosby, 1938)	AB	-	-
<i>Tapinocyba bicarinata</i> (Emerton, 1913)	AB	SK <sup>P</sup>	MB

<i>Tapinocyba cameroni</i> Dupérré and Paquin, 2007	AB	SK <sup>P</sup>	MB
<i>Tapinocyba dietrichi</i> Crosby and Bishop, 1933	AB	-	-
<i>Tapinocyba minuta</i> (Emerton, 1909)	AB	SK	MB
<i>Tapinocyba prima</i> Dupérré and Paquin, 2005	AB	SK <sup>P</sup>	MB
<i>Tapinocyba simplex</i> (Emerton, 1882)	AB	SK	MB
<i>Tapinopa bilineata</i> Banks, 1893	-	-	MB
<i>Tennesseellum formicum</i> (Emerton, 1882)	AB	SK	MB
<i>Tenuiphantes sabulosus</i> (Keyserling, 1886)	AB	SK <sup>P</sup>	MB
<i>Tenuiphantes zebra</i> (Emerton, 1882)	AB	SK	MB
<i>Tenuiphantes zelatus</i> Zorsch, 1937	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Tmeticus affinis</i> (Blackwall, 1855)	AB	-	-
<i>Tmeticus ornatus</i> (Emerton, 1914)	AB	SK	MB
<i>Tunagyna debilis</i> (Banks, 1892)	AB	SK	MB
<i>Tusukuru hartlandianus</i> (Emerton, 1913)	-	-	MB
<i>Vermontia thoracica</i> (Emerton, 1913)	AB	SK	MB
<i>Wabasso cacuminatus</i> Millidge, 1984	AB	SK <sup>P</sup>	MB
<i>Wabasso quaestio</i> (Chamberlin, 1949)	-	-	MB
<i>Walckenaeria arctica</i> Millidge, 1983	AB	SK	MB
<i>Walckenaeria atrotibialis</i> (O. P.-Cambridge, 1878)	AB	SK	MB
<i>Walckenaeria auranticeps</i> (Emerton, 1882)	AB	SK	MB
<i>Walckenaeria brevifaria</i> (Crosby and Bishop, 1931)	-	-	MB
<i>Walckenaeria castanea</i> (Emerton, 1882)	AB	SK	MB
<i>Walckenaeria communis</i> (Emerton, 1882)	AB	SK	MB
<i>Walckenaeria cornuella</i> (Chamberlin and Ivie, 1939)	AB	-	-
<i>Walckenaeria cuspidata brevicula</i> (Crosby and Bishop, 1931)	AB	SK	MB <sup>P</sup>
<i>Walckenaeria digitata</i> (Emerton, 1913)	AB	SK	MB
<i>Walckenaeria directa</i> (O. P.-Cambridge, 1874)	AB	SK	MB
<i>Walckenaeria dondalei</i> Millidge, 1983	AB	SK	MB <sup>P</sup>
<i>Walckenaeria exigua</i> Millidge, 1983	AB	SK	MB
<i>Walckenaeria fallax</i> Millidge, 1983	AB	-	-
<i>Walckenaeria helenae</i> Millidge, 1983	AB	-	-
<i>Walckenaeria karpinskii</i> (O. P.-Cambridge, 1873)	AB	-	-
<i>Walckenaeria kochi</i> (O. P.-Cambridge, 1872)	AB	SK	MB
<i>Walckenaeria lepida</i> (Kulczynski, 1885)	AB	SK	MB
<i>Walckenaeria pallida</i> (Emerton, 1882)	-	-	MB
<i>Walckenaeria pinocchio</i> (Kaston, 1945)	AB <sup>P</sup>	SK	MB
<i>Walckenaeria prominens</i> Millidge, 1983	AB	SK	MB
<i>Walckenaeria pullata</i> Millidge, 1983	AB	-	-
<i>Walckenaeria redneri</i> Millidge, 1983	AB <sup>P</sup>	SK	MB
<i>Walckenaeria spiralis</i> (Emerton, 1882)	AB <sup>P</sup>	SK	MB
<i>Walckenaeria subdirecta</i> Millidge, 1983	-	-	MB
<i>Walckenaeria subspiralis</i> Millidge, 1983	AB	SK	MB
<i>Walckenaeria tibialis</i> (Emerton, 1882)	-	-	MB
<i>Walckenaeria tricornis</i> (Emerton, 1882)	AB	SK	MB <sup>P</sup>
<i>Walckenaerianus aimakensis</i> Wunderlich, 1995	AB	-	-
<i>Wubana atypica</i> (Chamberlin and Ivie, 1936)	AB	-	-
<i>Zornella armata</i> (Banks, 1906)	AB	SK	MB
<i>Zornella cryptodon</i> (Chamberlin, 1920)	AB	-	-

## LIOCRANIDAE

<i>Agroeca ornata</i> Banks, 1892	AB	SK	MB
<i>Agroeca pratensis</i> Emerton, 1890	AB	SK	MB

## LYCOSIDAE

<i>Acantholycosa solituda</i> Levi and Levi, 1951	AB	-	-
<i>Alopecosa aculeata</i> (Clerck, 1757)	AB	SK	MB
<i>Alopecosa hirtipes</i> (Kulczynski, 1907)	-	-	MB
<i>Alopecosa kochi</i> (Keyserling, 1877)	AB	SK	MB <sup>p</sup>
<i>Arctosa alpigena</i> (Doleschall, 1852)	AB	SK	MB
<i>Arctosa emertoni</i> Gertsch, 1934	AB	SK	MB
<i>Arctosa insignita</i> (Thorell, 1872)	-	-	MB
<i>Arctosa littoralis</i> (Hentz, 1844)	AB <sup>p</sup>	SK	MB
<i>Arctosa raptor</i> (Kulczynski, 1885)	AB	SK	MB
<i>Arctosa rubicunda</i> (Keyserling, 1877)	AB	SK	MB
<i>Geolycosa missouriensis</i> (Banks, 1895)	AB	SK	MB
<i>Geolycosa wrighti</i> (Emerton, 1912)	-	-	MB
<i>Hogna frondicola</i> (Emerton, 1885)	AB	SK	MB
<i>Pardosa altamontis</i> Chamberlin and Ivie, 1946	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Pardosa anomala</i> Gertsch, 1933	AB	-	-
<i>Pardosa bucklei</i> Kronestedt, 1975	AB	SK	-
<i>Pardosa concinna</i> (Thorell, 1877)	AB	SK	MB
<i>Pardosa distincta</i> (Blackwall, 1846)	AB	SK	MB
<i>Pardosa dorsalis</i> Banks, 1894	AB	-	-
<i>Pardosa dorsuncata</i> Lowrie and Dondale, 1981	AB	SK <sup>p</sup>	-
<i>Pardosa dromaea</i> (Thorell, 1878)	AB	SK	MB
<i>Pardosa furcifera</i> (Thorell, 1875)	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Pardosa fuscula</i> (Thorell, 1875)	AB	SK	MB
<i>Pardosa glacialis</i> (Thorell, 1872)	-	-	MB
<i>Pardosa groenlandica</i> (Thorell, 1872)	AB	SK	MB
<i>Pardosa hyperborea</i> (Thorell, 1872)	AB	SK	MB
<i>Pardosa lapponica</i> (Thorell, 1872)	-	SK	MB
<i>Pardosa mackenziana</i> (Thorell, 1877)	AB	SK	MB
<i>Pardosa metlakatla</i> Emerton, 1917	AB	-	-
<i>Pardosa modica</i> (Blackwall, 1846)	AB	SK	MB
<i>Pardosa moesta</i> Banks, 1892	AB	SK	MB
<i>Pardosa mulaiki</i> Gertsch, 1934	AB	SK	MB
<i>Pardosa ontariensis</i> Gertsch, 1933	AB	SK	MB
<i>Pardosa palustris</i> (Linnaeus, 1758)	AB <sup>p</sup>	-	-
<i>Pardosa pedia</i> Dondale, 2007	-	SK	-
<i>Pardosa podhorskii</i> (Kulczynski, 1907)	-	-	MB
<i>Pardosa sinistra</i> (Thorell, 1877)	AB	-	-
<i>Pardosa sternalis</i> (Thorell, 1877)	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Pardosa steva</i> Lowrie and Gertsch, 1955	AB	-	-
<i>Pardosa tesquorum</i> (Odenwall, 1901)	AB	SK	MB
<i>Pardosa tetonensis</i> Gertsch, 1933	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Pardosa uintana</i> Gertsch, 1933	AB	SK	MB
<i>Pardosa wyuta</i> Gertsch, 1934	AB <sup>p</sup>	SK <sup>p</sup>	-
<i>Pardosa xerampelina</i> (Keyserling, 1877)	AB	SK	MB
<i>Pirata aspirans</i> Chamberlin, 1904	-	-	MB

<i>Pirata bryantae</i> Kurata, 1944	AB	SK	MB
<i>Pirata montanus</i> Emerton, 1885	-	-	MB
<i>Pirata piraticus</i> (Clerck, 1757)	AB	SK	MB
<i>Pirata praedo</i> Kulczynski, 1885	AB <sup>p</sup>	SK	MB
<i>Pirata sedentarius</i> Montgomery, 1904	AB	SK	-
<i>Piratula canadensis</i> (Dondale and Redner, 1980)	AB	SK <sup>p</sup>	MB
<i>Piratula cantralli</i> (Wallace and Exline, 1978)	AB	SK <sup>p</sup>	MB
<i>Piratula insularis</i> (Emerton, 1885)	AB	SK	MB
<i>Piratula minuta</i> (Emerton, 1885)	-	SK	MB
<i>Schizocosa avida</i> (Walckenaer, 1837)	-	-	MB
<i>Schizocosa bilineata</i> (Emerton, 1985)	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Schizocosa cespitum</i> Dondale and Redner, 1978	AB <sup>p</sup>	SK	MB <sup>p</sup>
<i>Schizocosa crassipalata</i> Roewer, 1951	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Schizocosa mccooki</i> Montgomery, 1904	AB	SK	MB <sup>p</sup>
<i>Schizocosa mimula</i> (Gertsch, 1934)	AB	SK	MB
<i>Schizocosa minnesotensis</i> Gertsch, 1934	AB	SK	-
<i>Schizocosa retrorsa</i> (Banks, 1911)	AB	SK <sup>p</sup>	MB
<i>Trochosa terricola</i> Thorell, 1856	AB	SK	MB
MIMETIDAE			
<i>Ero canionis</i> Chamberlin and Ivie, 1935	AB	SK	MB
<i>Mimetus epeiroides</i> Emerton, 1882	AB	SK	MB
MITURGIDAE			
<i>Cheiracanthium inclusum</i> (Hentz, 1847)	AB	SK	MB <sup>p</sup>
OXYOPIDAE			
<i>Oxyopes scalaris</i> Hentz, 1845	AB <sup>p</sup>	SK <sup>p</sup>	MB
PHILODROMIDAE			
<i>Apollophanes margareta</i> Lowrie and Gertsch, 1955	AB <sup>p</sup>	-	-
<i>Ebo bucklei</i> Platnick, 1972	AB	SK	MB
<i>Ebo dondalei</i> (Sauer, 1968)	AB	SK	MB <sup>p</sup>
<i>Ebo iviei</i> Sauer and Platnick, 1972	AB	SK	MB
<i>Ebo latithorax</i> Keyserling, 1884	AB	SK	MB <sup>p</sup>
<i>Ebo parabolis</i> (Schick, 1965)	AB	-	-
<i>Ebo pepinensis</i> Gertsch, 1933	AB	SK	MB
<i>Philodromus alascensis</i> Keyserling, 1884	AB	SK	MB
<i>Philodromus cespitum</i> (Walckenaer, 1802)	AB	SK	MB
<i>Philodromus histrio</i> (Latreille, 1819)	AB	SK	MB
<i>Philodromus imbecillus</i> Keyserling, 1880	AB	SK	MB
<i>Philodromus infuscatus infuscatus</i> Dondale and Redner, 1969	AB <sup>p</sup>	SK <sup>p</sup>	MB <sup>p</sup>
<i>Philodromus mysticus</i> Dondale and Redner, 1975	AB	SK	MB
<i>Philodromus oneida</i> Levi, 1951	AB	SK	MB
<i>Philodromus peninsulanus</i> Gertsch, 1934	-	-	MB
<i>Philodromus pernix</i> Blackwall, 1846	AB	SK	MB
<i>Philodromus placidus</i> Banks, 1892	AB	SK	MB
<i>Philodromus praelustris</i> Keyserling, 1880	AB	SK	MB
<i>Philodromus rufus quartus</i> Dondale and Redner, 1968	AB	SK	MB
<i>Philodromus rufus vibrans</i> Dondale, 1964	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Philodromus spectabilis</i> Keyserling, 1880	AB	SK	MB
<i>Philodromus vulgaris</i> (Hentz, 1847)	AB	SK	MB
<i>Thanatus altimontis</i> Gertsch, 1934	AB <sup>p</sup>	SK	MB <sup>p</sup>

<i>Thanatus bungei</i> (Kulczynski, 1908)	AB <sup>P</sup>	SK <sup>P</sup>	MB <sup>P</sup>
<i>Thanatus coloradensis</i> Keyserling, 1880	AB	SK	MB
<i>Thanatus formicinus</i> (Clerck, 1757)	AB	SK	MB
<i>Thanatus rubicellus</i> Mello-Leitão, 1929	AB	SK	MB
<i>Thanatus striatus</i> C.L. Koch, 1845	AB	SK	MB
<i>Thanatus vulgaris</i> Simon, 1870*	AB <sup>P</sup>	SK <sup>P</sup>	MB <sup>P</sup>
<i>Tibellus asiaticus</i> Kulczynski, 1908	AB	SK	MB
<i>Tibellus duttoni</i> (Hentz, 1847)	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Tibellus maritimus</i> (Menge, 1875)	AB	SK	MB
<i>Tibellus oblongus</i> (Walckenaer, 1802)	AB	SK	MB
PHOLCIDAE			
<i>Pholcophora americana</i> Banks, 1896	AB	-	-
<i>Pholcus phalangioides</i> (Fuesslin, 1775)*	AB	SK	-
PISAURIDAE			
<i>Dolomedes scriptus</i> Hentz, 1845	-	-	MB
<i>Dolomedes striatus</i> Giebel, 1869	AB	SK	MB
<i>Dolomedes tenebrosus</i> Hentz, 1844	-	-	MB
<i>Dolomedes triton</i> (Walckenaer, 1837)	AB	SK	MB
SALTICIDAE			
<i>Admestina wheeleri</i> Peckham and Peckham, 1888	-	SK <sup>P</sup>	MB
<i>Chalcoscirtus alpicola</i> (L. Koch, 1876)	AB	SK	MB <sup>P</sup>
<i>Chalcoscirtus carbonarius</i> Emerton, 1917	AB	-	-
<i>Eris militaris</i> (Hentz, 1845)	AB	SK	MB
<i>Euophrys monadnock</i> Emerton, 1891	AB	SK	MB
<i>Evarcha proszynskii</i> Marusik and Logunov, 1998	AB	SK	MB
<i>Habronattus altanus</i> (Gertsch, 1934)	AB	SK	MB
<i>Habronattus americanus</i> (Keyserling, 1885)	AB	SK	MB
<i>Habronattus amicus</i> (Peckham and Peckham, 1909)	AB	SK	MB <sup>P</sup>
<i>Habronattus borealis</i> (Banks, 1895)	-	SK <sup>P</sup>	MB
<i>Habronattus captiosus</i> (Gertsch, 1934)	AB	SK <sup>P</sup>	MB
<i>Habronattus cognatus</i> (Peckham and Peckham, 1901)	AB	SK	MB
<i>Habronattus cuspidatus</i> Griswold, 1987	AB	SK	MB <sup>P</sup>
<i>Habronattus decorus</i> (Blackwall, 1846)	AB	SK	MB
<i>Habronattus oregonensis</i> (Peckham and Peckham, 1888)	AB	SK <sup>P</sup>	-
<i>Habronattus sansoni</i> (Emerton, 1915)	AB	SK <sup>P</sup>	-
<i>Habronattus texanus</i> (Chamberlin, 1924)	AB <sup>P</sup>	SK	MB
<i>Hentzia palmarum</i> (Hentz, 1832)	-	SK <sup>P</sup>	MB
<i>Maevia inclemens</i> (Walckenaer, 1837)	-	SK <sup>P</sup>	MB
<i>Naphrys pulex</i> (Hentz, 1846)	-	SK <sup>P</sup>	MB
<i>Neon ellamae</i> Gertsch and Ivie, 1955	-	-	MB
<i>Neon nelli</i> Peckham and Peckham, 1888	AB	SK	MB
<i>Peckhamia picata</i> (Hentz, 1846)	AB <sup>P</sup>	SK	MB
<i>Pelegrina proterva</i> (Walckenaer, 1837)	AB	SK	MB
<i>Pelegrina aeneola</i> (Curtis, 1893)	AB	SK <sup>P</sup>	-
<i>Pelegrina arizonensis</i> (Peckham and Peckham, 1901)	AB	SK	MB <sup>P</sup>
<i>Pelegrina clemata</i> (Levi and Levi, 1951)	AB	SK	MB <sup>P</sup>
<i>Pelegrina flavipes</i> (Peckham and Peckham, 1888)	AB	SK	MB
<i>Pelegrina insignis</i> (Banks, 1892)	AB	SK	MB
<i>Pelegrina montana</i> (Emerton, 1891)	AB	SK	MB

<i>Pellenes ignifrons</i> (Grube, 1861)	AB	SK <sup>P</sup>	-
<i>Pellenes lapponicus</i> (Sundevall, 1833)	AB	SK	MB <sup>P</sup>
<i>Pellenes wrighti</i> Lowrie and Gertsch, 1955	AB <sup>P</sup>	SK	MB
<i>Phidippus audax</i> (Hentz, 1843)	AB <sup>P</sup>	SK	MB <sup>P</sup>
<i>Phidippus borealis</i> Banks, 1895	AB	SK	MB
<i>Phidippus clarus</i> Keyserling, 1885	-	SK	MB <sup>P</sup>
<i>Phidippus comatus</i> Peckham and Peckham, 1901	-	SK	-
<i>Phidippus cryptus</i> Edwards, 2004	AB	SK	MB
<i>Phidippus johnsoni</i> (Peckham and Peckham, 1883)	AB	SK	MB <sup>P</sup>
<i>Phidippus princeps</i> (Peckham and Peckham, 1883)	AB <sup>P</sup>	SK	MB
<i>Phidippus purpuratus</i> Keyserling, 1885	AB	SK	MB
<i>Phidippus whitmani</i> Peckham and Peckham, 1909	-	SK <sup>P</sup>	MB
<i>Platycryptus undatus</i> (De Geer, 1778)	-	SK <sup>P</sup>	MB
<i>Salticus scenicus</i> (Clerck, 1757)*	AB	SK	MB
<i>Sassacus vitis</i> (Cockerell, 1894)	AB	SK <sup>P</sup>	-
<i>Sibianor aemulus</i> (Gertsch, 1934)	AB	SK	MB
<i>Sitticus cutleri</i> Proszynski, 1980	AB	SK	MB <sup>P</sup>
<i>Sitticus fasciger</i> (Simon, 1880)*	AB <sup>P</sup>	SK <sup>P</sup>	MB
<i>Sitticus finschi</i> (L. Koch, 1879)	AB	SK	MB
<i>Sitticus floricola palustris</i> (Peckham and Peckham, 1883)	AB	SK	MB
<i>Sitticus ranieri</i> Peckham and Peckham, 1909	AB	SK	MB
<i>Sitticus striatus</i> Emerton, 1911	AB	SK	MB
<i>Synageles occidentalis</i> Cutler, 1988	AB	SK	MB
<i>Talavera minuta</i> (Banks, 1894)	AB	SK	MB
<i>Tutelina harti</i> (Peckham, 1891)	-	SK <sup>P</sup>	MB
<i>Tutelina similis</i> (Banks, 1895)	AB	SK	MB
<b>TETRAGNATHIDAE</b>			
<i>Metellina curtisi</i> (McCook, 1894)	AB <sup>P</sup>	SK <sup>P</sup>	MB <sup>P</sup>
<i>Metellina mimetoides</i> Chamberlin and Ivie, 1941	AB <sup>P</sup>	SK <sup>P</sup>	MB <sup>P</sup>
<i>Metellina segmentata</i> (Clerck, 1757)*	AB <sup>P</sup>	SK <sup>P</sup>	MB <sup>P</sup>
<i>Pachygnatha clercki</i> Sundevall, 1823	AB	SK	MB
<i>Pachygnatha dorothea</i> McCook, 1894	AB	SK	MB
<i>Pachygnatha tristriata</i> C.L. Koch, 1845	AB	SK <sup>P</sup>	MB
<i>Pachygnatha xanthostoma</i> C.L. Koch, 1845	AB	SK	MB
<i>Tetragnatha caudata</i> Emerton, 1884	AB	SK	MB
<i>Tetragnatha dearmata</i> Thorell, 1873	AB	SK	MB
<i>Tetragnatha elongata</i> Walckenaer, 1841	AB	SK	MB
<i>Tetragnatha extensa</i> (Linnaeus, 1758)	AB	SK	MB
<i>Tetragnatha laboriosa</i> Hentz, 1850	AB	SK	MB
<i>Tetragnatha pallescens</i> F.O.P.-Cambridge, 1903	AB	SK	MB
<i>Tetragnatha shoshone</i> Levi, 1981	AB	SK	MB
<i>Tetragnatha straminea</i> Emerton, 1885	AB	SK	MB
<i>Tetragnatha versicolor</i> Walckenaer, 1841	AB	SK	MB
<b>THERIDIIDAE</b>			
<i>Achaearenea globosus</i> (Hentz, 1850)	-	-	MB
<i>Asagena americana</i> Emerton, 1882	AB	SK	MB
<i>Asagena fulva</i> (Keyserling, 1884)	AB	SK <sup>P</sup>	MB <sup>P</sup>
<b><i>Asagena medialis</i> (Banks, 1898)<sup>-1</sup></b>	AB	SK <sup>P</sup>	-
<i>Canalidion montanum</i> Emerton, 1882	AB	SK	MB

<i>Chryso albomaculata</i> O. P.-Cambridge, 1882	-	-	MB
<i>Chryso nordica</i> (Chamberlin and Ivie, 1947)	-	SK	-
<b><i>Chryso pelyx</i> (Levi, 1957)</b>	-	-	MB
<i>Crustulina sticta</i> (O. P.-Cambridge, 1861)	AB	SK	MB
<i>Dipoena nigra</i> (Emerton, 1882)	-	SK	MB
<i>Enoplognatha caricis</i> (Fickert, 1876)	AB	SK	MB
<i>Enoplognatha intrepida</i> (Sørensen, 1898)	AB	SK	MB
<i>Enoplognatha joshua</i> Chamberlin and Ivie, 1942	AB	SK	-
<i>Enoplognatha marmorata</i> (Hentz, 1850)	AB	SK	MB
<i>Euryopsis argentea</i> Emerton, 1882	AB	SK	MB
<i>Euryopsis funebris</i> (Hentz, 1850)	-	SK <sup>p</sup>	MB
<i>Euryopsis gertschi</i> Levi, 1951	AB <sup>p</sup>	SK	MB
<i>Euryopsis pepini</i> Levi, 1954			
<i>Euryopsis saukea</i> Levi, 1951	AB	SK	MB
<i>Euryopsis scriptipes</i> Banks, 1908	AB	SK	MB <sup>p</sup>
<i>Lasaeola prona</i> Menge, 1868	AB <sup>p</sup>	SK	MB <sup>p</sup>
<i>Latrodectus hesperus</i> Chamberlin and Ivie, 1935	AB	SK	-
<i>Neottiura bimaculata</i> (Linnaeus, 1767)*	AB	SK <sup>p</sup>	MB <sup>p</sup>
<i>Ohlertidion ohlerti</i> Thorell, 1870	AB	SK	MB
<i>Parasteatoda tepidariorum</i> (C.L. Koch, 1841)	AB	SK	MB
<i>Phylloneta impressa</i> L. Koch, 1881	AB	SK	MB <sup>p</sup>
<i>Rhomphaea fictilium</i> (Hentz, 1850)	AB <sup>p</sup>	SK <sup>p</sup>	MB
<i>Robertus arcticus</i> Chamberlin and Ivie, 1947	AB	SK	MB
<i>Robertus banksi</i> (Kaston, 1946)	AB	SK	MB
<i>Robertus borealis</i> (Kaston, 1946)	AB	SK	MB <sup>p</sup>
<i>Robertus crosbyi</i> (Kaston, 1946)	AB	SK <sup>p</sup>	MB
<i>Robertus fuscus</i> (Emerton, 1894)	AB	SK	MB
<i>Robertus riparius</i> (Keyserling, 1886)	AB	SK <sup>p</sup>	MB
<i>Robertus vigerens</i> (Chamberlin and Ivie, 1933)	AB	SK <sup>p</sup>	-
<i>Rugathodes aurantius</i> (Emerton, 1915)	AB	SK	MB
<i>Rugathodes sexpunctatus</i> (Emerton, 1882)	AB	SK	MB
<i>Steatoda albomaculata</i> (De Geer, 1778)	AB	SK	MB
<i>Steatoda borealis</i> (Hentz, 1850)	AB	SK	MB
<i>Steatoda castanea</i> (Clerck, 1757)*	AB	-	MB
<i>Theonoe stridula</i> Crosby, 1906	AB <sup>p</sup>	SK	MB
<i>Theridion differens</i> Emerton, 1882	AB	SK	MB
<i>Theridion frondeum</i> Hentz, 1850	AB	SK	MB
<i>Theridion glaucescens</i> Becker, 1879	-	SK <sup>p</sup>	MB
<i>Theridion hemerobium</i> Simon, 1914	-	SK <sup>p</sup>	MB
<i>Theridion murarium</i> Emerton, 1881	AB	SK	MB
<i>Theridion petraeum</i> L. Koch, 1872	AB	SK	MB
<i>Theridion pictum</i> (Walckenaer, 1802)	AB	SK	MB
<i>Theridion rabuni</i> Chamberlin and Ivie, 1944	-	SK	-
<i>Theridula emertoni</i> Levi, 1954	AB	SK	MB
<i>Thymoites minnesota</i> Levi, 1964	AB	SK	MB
<i>Thymoites unimaculatus</i> (Emerton, 1882)	AB <sup>p</sup>	SK	MB
<b>THOMISIDAE</b>			
<i>Bassaniana utahensis</i> (Gertsch, 1932)	AB	SK	MB
<i>Coriarachne brunneipes</i> Banks, 1893	AB	-	MB

<i>Mecaphesa asperata</i> (Hentz, 1847)	AB	SK	MB
<i>Mecaphesa celer</i> (Henz, 1847)	AB	-	-
<i>Mecaphesa sierrensis</i> Schick, 1965	AB <sup>P</sup>	-	-
<i>Misumena vatia</i> (Clerck, 1757)	AB	SK	MB
<i>Misumenoides formosipes</i> (Walckenaer, 1837)	AB	-	-
<i>Ozyptila beaufortensis</i> Strand, 1916	AB	-	-
<i>Ozyptila conspurcata</i> Thorell, 1877	AB	-	MB
<i>Ozyptila curvata</i> Dondale and Redner, 1975	-	-	MB
<i>Ozyptila gertschi</i> Kurata, 1944	AB	SK	MB
<i>Ozyptila pacifica</i> Banks, 1985	AB <sup>P</sup>	-	-
<i>Ozyptila sincera canadensis</i> Dondale and Redner, 1975	AB	SK	MB
<i>Xysticus acquiescens</i> Emerton, 1919	AB	SK	MB
<i>Xysticus alboniger</i> Turnbull, Dondale and Redner, 1965	AB <sup>P</sup>	SK <sup>P</sup>	MB <sup>P</sup>
<i>Xysticus ampullatus</i> Turnbull, Dondale and Redner, 1965	-	-	MB
<i>Xysticus auctifucus</i> Keyserling, 1880	-	SK	-
<i>Xysticus banksi</i> Bryant, 1930	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Xysticus benefactor</i> Thorell, 1880	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Xysticus bicuspis</i> Keyserling, 1887	-	SK <sup>P</sup>	MB <sup>P</sup>
<i>Xysticus britcheri</i> Gertsch, 1934	AB	SK	MB
<i>Xysticus canadensis</i> Gertsch, 1953	AB	SK	MB
<i>Xysticus chippewa</i> Gertsch, 1953	AB	SK	MB <sup>P</sup>
<i>Xysticus cunctator</i> Thorell, 1877	AB	SK	MB <sup>P</sup>
<i>Xysticus discursans</i> Keyserling, 1880	AB	SK	MB
<i>Xysticus elegans</i> Keyserling, 1880	AB	SK	MB
<i>Xysticus ellipticus</i> Turnbull, Dondale and Redner, 1965	AB	SK	MB
<i>Xysticus emertoni</i> Keyserling, 1880	AB	SK	MB
<i>Xysticus ferox</i> (Hentz, 1847)	AB	SK	MB
<i>Xysticus fervidus</i> Gertsch, 1953	AB <sup>P</sup>	SK	-
<i>Xysticus gertschi</i> Schick, 1965	AB	SK <sup>P</sup>	MB <sup>P</sup>
<i>Xysticus gosiutus</i> Gertsch, 1933	AB <sup>P</sup>	-	-
<i>Xysticus gulosus</i> Keyserling, 1880	AB	SK	MB
<i>Xysticus locuples</i> Keyserling, 1880	AB <sup>P</sup>	-	-
<i>Xysticus luctans</i> (C.L. Koch, 1845)	AB	SK	MB
<i>Xysticus luctuosus</i> (Blackwall, 1836)	AB	SK	MB
<i>Xysticus montanensis</i> Keyserling, 1887	AB	SK	MB
<i>Xysticus nigromaculatus</i> Keyserling, 1884	AB	SK	MB
<i>Xysticus obscurus</i> Collett, 1877	AB	SK	MB
<i>Xysticus pellax</i> O. P.-Cambridge, 1894	AB <sup>P</sup>	SK	MB <sup>P</sup>
<i>Xysticus posti</i> Sauer, 1968	AB <sup>P</sup>	-	-
<i>Xysticus punctatus</i> Keyserling, 1880	AB	SK	MB
<i>Xysticus triguttatus</i> Keyserling, 1880	AB	SK	MB
<i>Xysticus triangulosus</i> Emerton 1894	-	-	MB
<i>Xysticus winnipegensis</i> Turnbull, Dondale and Redner, 1965	-	-	MB
TITANOECIDAE			
<i>Titanoeca nigrella</i> (Chamberlin, 1919)	AB	-	MB
<i>Titanoeca nivalis</i> Simon, 1874	AB	SK	MB
ULOBORIDAE			
<i>Hyptiotes gertschi</i> Chamberlin and Ivie, 1935	AB <sup>P</sup>	SK	MB



## Spiders of the Prairies

In this section, we provide a short overview of all the families found in the Prairie Provinces and highlight some of the species most commonly reported in biodiversity studies in the ecozone (summarized in Table 4). Families are listed alphabetically, but for each family, we indicate its rank in parentheses, on the basis of the number of species recorded in the Prairie Provinces, and provide the number of genera (from Table 1). We use the term “Prairies” to refer to the three Prairie Provinces and the term “shortgrass prairie” for the Mixed Grasslands Ecoregion within the Prairies Ecozone. Throughout the rest of this chapter (and in Table 4), we refer to the relative abundances of species by using the standardized proportionate ACFOR designation that has been proposed as an international standard for a common framework in discussions of species conservation (Holliday *et al.*, see Chapter 1, Volume 4). The standard is reproduced below and available in numerical form at <http://www.glaucus.org.uk/watch3.htm#STANDARD%20ACFOR>:

*ACFOR standard categories used in Table 4 and throughout the text.*

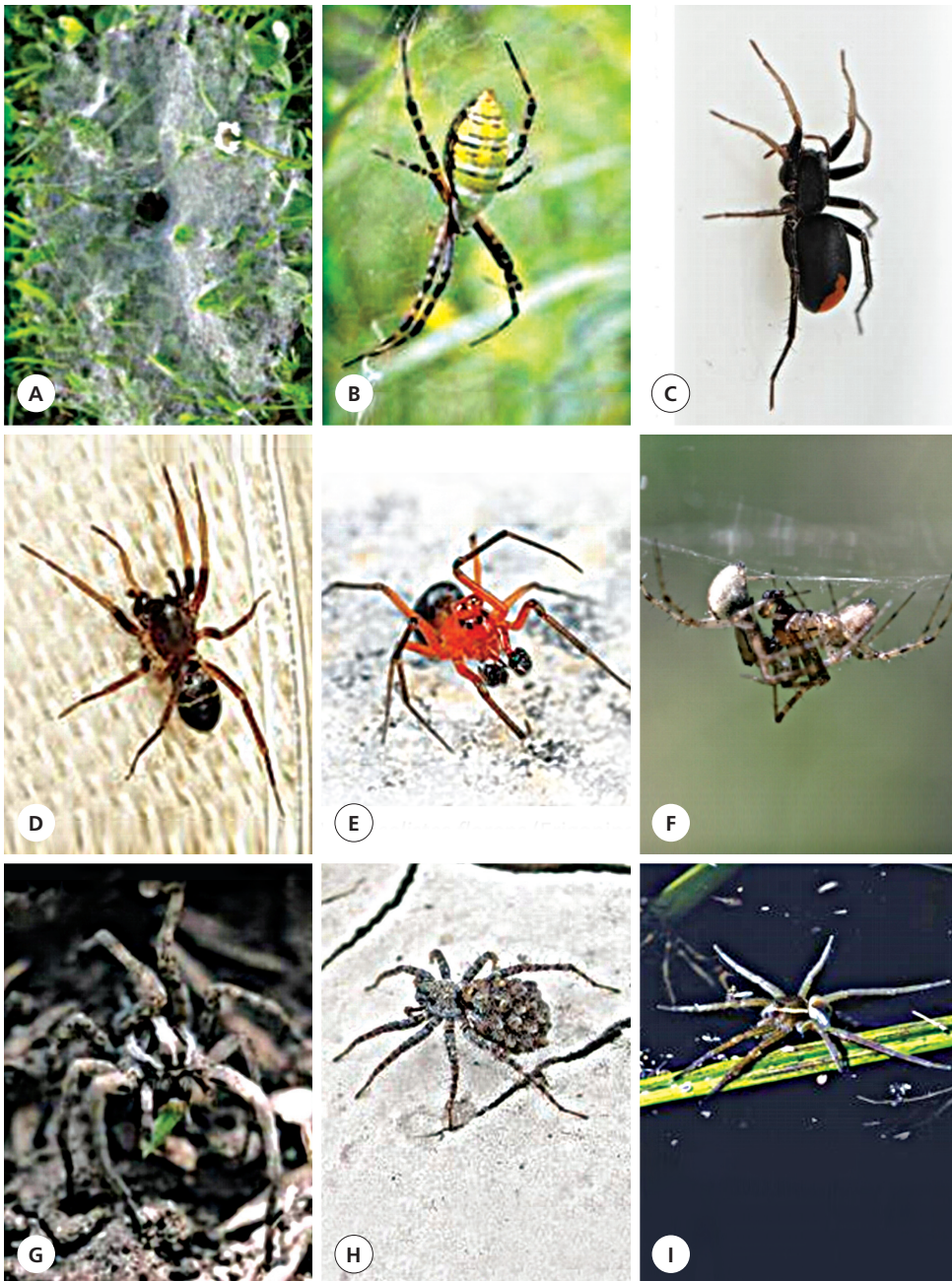
Designation	Abbreviation	Proportion of Total Collection (%)
Abundant	A	≥50
Common	C	≥5 and <50
Frequent	F	≥0.5 and <5
Occasional	O	≥0.05 and <0.5
Rare	R	<0.05

### *Agelenidae, Funnel Web Spiders (13<sup>th</sup>, 3 genera: 9 species; Fig. 3A)*

The funnel web spiders are common ground dwellers in both grasslands and forests of the region. *Agelenopsis*, with four species, is the only native genus present in the region. *Agelenopsis oklahoma* occurs in shortgrass prairie, whereas *A. actuosa* occurs in more moist grasslands and Aspen Parkland. *Agelenopsis utahana* is a boreal species that has been collected mainly in forested transition ecoregions (Table 4). Four adventive species from the genus *Tegenaria* have been collected in some urban centres. This genus includes some of the most “feared” spiders (Vetter and Antonelli 2002) such as the hobo spider (*T. agrestis*); despite common folklore, numerous scientific tests have failed to show that this species is a necrotic lesion biter (Bennett and Vetter 2004). *Tegenaria domestica* is widespread, whereas the giant house spider *T. duellica* (formerly *T. gigantea*—a true giant with a 100 mm leg span and one of the largest spiders in Canada) is spreading east from British Columbia and has now been recorded in Saskatchewan (Buckle and Randell 1995). *Tegenaria agrestis* has been reported from cities in Alberta (Edmonton and Grande Cache (RL, unpublished data) and Lethbridge (HC, unpublished data)), whereas another species, *T. atrica*, is known only from Saskatchewan (Paquin *et al.* 2010; D. Buckle, pers. comm. to HC).

### *Amaurobiidae, Tangle Nest Spiders (15<sup>th</sup>, 4 genera: 8 species)*

The tangle nest spiders are represented by five genera and 10 species in the Prairie Provinces, but none have been reported from grassland ecoregions within the ecozone. *Amaurobius borealis* and *Cybaeopsis euopla* are common spiders in litter of southern boreal aspen



**Fig. 3.** A–I, Examples of spiders found in the Prairie Provinces. A, Characteristic funnel web of family Agelenidae (Photo: D. Giberson). B, Garden spider, *Argiope trifasciata* (Araneidae) (Photo: H. Goulet). C, *Castianeira* sp., a grassland ant mimic (probably *C. descripta*) (Photo: J. Acorn). D, *Micaria pulicaria*, a widespread gnaphosid ant mimic (Photo: M. Howe, [www.Spiders.us](http://www.Spiders.us)). E, *Hypselistes florens* (Erigoninae), a male dwarf sheet spider (Photo: T. Murray). F, *Pityohyphantes subarcticus* (Linyphiinae), mating pair on web (Photo: J. Pinzón). G, Wolf spider (*Schizocosa* sp., Lycosidae) eating a green grass bug in a wheat field in southern Alberta (Photo: D. Pittman). H, *Pardosa* female wolf spider (Lycosidae) carrying spiderlings on her back (Photo: H. Goulet). I, *Dolomedes triton*, a fishing spider (Pisauridae) common on prairie ponds (Photo: J. Pinzón).

forests (Buddle *et al.* 2000), in the foothills (Cárcamo 1997), in boreal forests (Pinzón *et al.* 2012), in the Boreal Transition Ecoregion (JP and JS, unpublished data), and in the Aspen Parkland Ecoregion (Graham 2002).

***Araneidae, Orb Weavers (8<sup>th</sup>, 16 genera: 37 species; Fig. 3B)***

The orb-weaving spider family is a relatively large family, but only few species with low relative abundances have been collected in prairie habitats. This is likely, at least in part, a methodological artifact associated with pitfall or pan trapping, since most species build their webs in layers above the ground level. For example, *Neoscona arabesca* was common in canola foliage sampled by sweeping in southern Alberta, but absent from pitfall catches in similar sites (HC, unpublished data). *Araneus* is the most speciose genus in the family, but is more common in forested transition zones than in grassland habitats, where only juveniles have been collected (Table 4). *Araneus marmoreus* and *Cyclosa conica* were among the most common orb weaver species in the understory of the Boreal Transition Ecoregion (JP and JS, unpublished data). *Hypsosinga funebris* is frequently collected in shortgrass reserves in both Alberta and Saskatchewan, but other araneid species seem to be only occasional residents of these habitats.

***Clubionidae, Sac Spiders (10<sup>th</sup>, 1 genus: 20 species)***

The clubionid sac spiders are represented in the region by the genus *Clubiona*; the only other North American genus, *Elaver*, has not yet been recorded in the Prairies. Four species have been reported from biodiversity studies in the grassland ecoregions and three from transition forested zones (Table 4). *Clubiona mutata* is a common element of shortgrass prairie habitats, and *Clubiona canadensis* is frequent in foothills and aspen forests. The latter species has been commonly collected from ground, bark, and foliage habitats in the boreal forest (Pinzón and Spence 2010).

***Corinnidae, Corinnid Sac Spiders (14<sup>th</sup>, 3 genera: 9 species; Fig. 3C)***

The Corinnidae were formerly included in the Clubionidae and are now the largest family of sac spiders worldwide. The corinnid sac spiders are poorly represented in the Prairies Ecozone in terms of diversity, but the genus *Castianeira*, with species that mimic ants, occurs in the region. *Castianeira descripta* is the only species frequently recorded from grassland habitats (Table 4). *Castianeira longipalpa* inhabits tallgrass prairie in southern Manitoba, but is more common in aspen habitats (Roughley *et al.* 2006). Three other species also have been reported in faunistic studies, but only in transition forests adjacent to the Prairies Ecozone.

***Dictynidae, Mesh Web Weavers or Meshweavers (5<sup>th</sup>, 11 genera: 53 species)***

These spiders build irregular webs in various places, including buildings and vegetation in tree canopies, in understories, and at the ground level (Pinzón *et al.* 2011). The genus *Dictyna* is the most speciose of the family, with 25 species recorded in the three provinces. The genus is well represented in the Prairies Ecozone, both in diversity (15 spp.) and relative abundance (Tables 3 and 4). *Dictyna major*, for example, was the dominant species in canola foliage in 2010 in a canola study near Lethbridge (HC and RL, unpublished data). *Dictyna terrestris* was common in grassland reserves in southern Alberta and Saskatchewan (Finnamore and Buckle 1999; Finnamore *et al.* 2000) (Table 4), and *D. brevitarisa* was frequently collected from the understory vegetation in the Boreal Transition Ecoregion (JP and JS, unpublished data). *Emblyna completoides*, *E.*

*cornupeta*, and *E. horta* are also frequent in the Mixed Grassland Ecoregion. *Tricholathys dakota* appears to be more common in the Moist Mixed Grassland Ecoregion than in the drier shortgrass prairies (Table 4).

***Gnaphosidae, Ground Spiders (2<sup>nd</sup>, 14 genera: 61 species; Fig. 3D)***

With notable exceptions, the ground spiders are nocturnal wandering predators that do not build webs, but spin silk retreats where they spend the day. Of the 61 species recorded in the three provinces, 35 have been collected in biodiversity studies in the Prairies Ecozone and 13 of them at relatively high frequencies (>1%) (Table 4). *Zelotes lasalanus* represented 13% of the entire spider catch at Grasslands National Park in southern Saskatchewan (Finnamore *et al.* 2000). *Micaria*, the most speciose genus (17 spp.), appears to be predominantly a grassland genus. Fifteen species were collected from the Prairies Ecozone (Table 4): 12 only from the Mixed Grassland Ecoregion, one only from the Moist Mixed Grassland (*Micaria* sp.), one only from aspen habitats (*M. aenea*), and one widespread (*M. pulicaria*, Fig. 3D). Many *Micaria* species are active diurnally and are also ant mimics (Pekar and Jarab 2011).

***Hahniidae, Dwarf Sheet Spiders (12<sup>th</sup>, 5 genera: 10 species)***

The dwarf sheet spiders build webs close to the ground in the leaf litter in small depressions, or on low vegetation (Opell and Beatty 1976). Hahniids are usually small- to medium-sized spiders (2–5 mm) and can be recognized easily by the transverse arrangement of their spinnerets. They are seldom collected in arid prairie habitats of the Mixed Grassland Ecoregion (Table 4). Pepper (1999) reported *Neoantistea gosiuta* and *N. magna* as rare components of grazed rangeland in southwestern Saskatchewan, but *N. magna* was a frequent species farther north in the Moist Mixed Grassland near Clavet (Doane and Dondale 1979). *Hahnina cinerea* is a frequent spider in tallgrass prairie in southern Manitoba (Roughley *et al.* 2006) and was collected, albeit rarely, in the Boreal Transition Ecoregion (JP and JS, unpublished data).

***Linyphiidae, Linyphiids (1<sup>st</sup>, 112 genera: 295 species; Fig. 3E and F)***

This is by far the largest family in Canada and in the Prairie Provinces and is the second most diverse spider family worldwide after the Salticidae (jumping spiders). In fact, linyphiids accounted for 39% of all spider species recorded in the three provinces (Table 1). Depending on the sampling method or habitat, they can also dominate spider assemblages in terms of frequency of captures, as shown by Dondale (1970) for a meadow in southern Ontario. The subfamily Erigoninae (dwarf spiders) contains the bulk of the diversity (Table 3). Erigonines are small, generally less than 3 mm, and inhabit the leaf litter, where they feed on microarthropods such as collembolans (Aitchison 1984). Males of some genera have ornate head protuberances (Fig. 3E) and highly complex emboli (genitalia), whereas females are frequently undifferentiated and are difficult to identify by using morphological traits. Most genera require revision, and comprehensive keys are currently available to identify males only (Draney and Buckle 2005). Intensive collecting and sorting by experts is expected to generate new species in most areas, as shown in the biodiversity studies summarized in Table 4. For example, Dupérré (2013) described four new species of the 13 *Agyneta* species (Linyphiidae) in the Prairies Ecozone, demonstrating the high number of new species to be described in this family. All 295 species from the 112 genera reported in Table 3 have been collected in at least one of the Prairie Provinces. Around 65 species from 36 genera were reported in the eight biodiversity studies from the

Prairies Ecozone reviewed here, including several individuals that could not be identified to species (Table 4). *Ceraticelus* and *Walckenaeria* were the most diverse in the Prairies Ecozone, with eight and nine described species, respectively (at least three *Walckenaeria* noted were undescribed; Don Buckle, pers. comm.). Most species have been collected infrequently, which is probably an artifact of pitfall trapping. Erigonines can balloon as immatures and adults, and many either do not fall onto traps or can escape from them by using their draglines (RL, field obs.). Furthermore, because of their small size and somewhat fragile nature, careful sorting is required to retrieve them from samples. The most frequently collected species at any of the grassland sites within the Prairies Ecozone (Table 4) was *Erigone alettris*, which was collected by sweeping canola (HC and RL, unpublished data) near Lethbridge, where it reached 4% frequency. It was collected at lower frequencies in pitfall traps at other grassland sites and in the Boreal Transition Ecoregion under aspen forest at George Lake (Table 4). *Islandiana holmi*, *Tennesseellum formicum*, and *Coloncus siou* have also been frequently reported in some dry grassland sites. *Centromerus sylvaticus* was frequent (7%) in the more humid tallgrass grassland and the adjacent aspen habitat studied by Roughley *et al.* (2006); *Goneatara nasutus* and *Pelecopsis mengei* were also frequent in these habitats. In transition aspen forests in the foothills and at George Lake, *Allomengea dentisetis* (38%) and *Bathyphantes pallidus* (14%) were far more common (Table 4). However, *Helophora insignis*, *Dismodicus alticeps*, and *Pityohyphantes subarcticus* were also common components of the understory foliage fauna at George Lake. *Pityohyphantes* (Fig. 3F) has not been reported in any of the Prairies Ecozone biodiversity studies reviewed here.

#### ***Liocranidae, Liocranid Sac Spiders (18<sup>th</sup>, 1 genus: 2 species)***

Two species in the genus *Agroeca* (formerly under Clubionidae) occur in the Prairie Provinces, and both have been reported from the Prairies Ecozone. *Agroeca ornata* is a common species in tallgrass prairie and in aspen forests, but it was not reported from any of the drier grassland sites (Table 4). *Agroeca pratensis* was frequent in some of the same humid habitats and an occasional species at the site within the Moist Mixed Grassland Ecoregion of Saskatchewan studied by Doane and Dondale (1979).

#### ***Lycosidae, Wolf Spiders (3<sup>rd</sup>, 9 genera: 59 species; Fig. 3G and H)***

This is the third largest family in the region in terms of number of reported species, although its diversity is close to that of the Dictynidae and Gnaphosidae. However, wolf spiders are generally the most common spiders collected in pitfall traps in grassland prairie habitats because of their ground-dwelling habits. At 28 species, the genus *Pardosa* is also the most speciose of any spider family within the Prairie Provinces. However, it will likely be surpassed in the Prairie Provinces by the linyphiid genus *Walckenaeria* (Erigoninae), currently at 27 species, and which probably harbours more undescribed species than *Pardosa*. Lycosidae represented 13–72% of the spider catches in the studies reported in Table 4. Several *Pardosa* species are common and widespread across various prairie ecoregions. In particular, *Schizocosa mccooki* is common in the more arid regions of the southern prairies of Alberta and Saskatchewan and the grassland reserves within the Aspen Parkland Ecoregion of southern Manitoba (Table 4). Part of the dominance of *S. mccooki* may be a sampling artifact related to its active wandering lifestyle that makes individuals prone to falling in pitfall traps. Aspects of the life history of the more common *Pardosa* species have been discussed by Dondale (1977), Doane and Dondale (1979), and Buddle (2000, 2002).

***Mimetidae, Pirate Spiders (19<sup>th</sup>, 2 genera: 2 species)***

Only two mimetid species occur in the Prairie Provinces and both have been reported from the Prairies Ecozone. *Ero canionis* has been collected in tallgrass and aspen habitats in the ecozone and forest transition ecoregions. *Mimetus epeiroides* has been recorded from grassland habitats of southern Alberta and Saskatchewan (Table 4).

***Philodromidae, Running Crab Spiders (9<sup>th</sup>, 4 genera: 29 species)***

Philodromidae share the common name of crab spiders with Thomisidae because of their laterigrade legs and gait resembling that of crabs. Four of the five Canadian genera are represented in the ecozone, but only 13 of the 28 species known from the three Prairie Provinces were collected in the faunistic studies within the ecozone reviewed here (Table 4). All 13 species appear to be mainly grassland inhabitants, as they were not reported from forested sites. *Thanatus coloradensis* was one of the more common species in the Mixed Grassland Ecoregion, but it was not reported in the more humid tallgrass or aspen sites. The grassland members of this family appear to be reasonably diverse in the west, as only one of the five species reported from southern Ontario (Dondale 1970) was not found in the Prairies.

***Pisauridae, Fishing or Nursery Web Spiders (16<sup>th</sup>, 1 genus: 4 species; Fig. 3I)***

The fishing or nursery web spiders are widespread semi-aquatic inhabitants of ponds and lakes, where they prey on small vertebrates (tadpoles, minnows, sticklebacks) and many species of invertebrates (Zimmermann and Spence 1989). They do not wander far from standing water (Graham *et al.* 2003) and therefore are rarely collected in faunistic studies in terrestrial habitats. *Dolomedes* is the only genus in the Prairie Provinces, and four species are known to occur here. Four species occur in Manitoba but only *D. triton* (Fig. 3I) and *D. striatus* have been reported in Alberta and Saskatchewan. *Dolomedes triton* is one of the few spider species in the Prairie Provinces whose population dynamics, life cycle, and sexual behaviour have been studied thoroughly (Zimmermann and Spence 1989, 1992, 1998; Spence *et al.* 1996).

***Salticidae, Jumping Spiders (4<sup>th</sup>, 22 genera: 56 species; Fig. 4A)***

The jumping spiders can be considered as the “charismatic” taxon (the group with the most public appeal) among the spiders, and several workers (e.g., Bennett 1999; Buddle and Shorthouse 2000) have commented on their public appeal. This is the largest family worldwide, but ranks only fourth in terms of number of described species in the Prairie Provinces. Despite their public appeal, lack of taxonomic resources hinders their identification to species; only keys to genus are available (e.g., Richmand *et al.* 2005). Three species in the genus *Habronattus* (*H. altanus*, *H. americanus*, *H. cuspidatus*) and two undescribed *Pellenes* species were frequently represented in the faunistic studies of the Mixed Grassland Ecoregion in Alberta and Saskatchewan, but not reported from the other more humid sites of the Prairies Ecozone (Table 4). Seven of the 22 putative species reported from the ecozone in Table 4 were undetermined because of taxonomic challenges.

***Tetragnathidae, Long-Jawed Orb-Weavers (11<sup>th</sup>, 2 genera: 13 species; Fig. 4B)***

The long-jawed orb-weavers are represented by the genera *Tetragnatha* and *Pachygnatha* in the Prairies Ecozone (Table 4). The genus *Metellina* occurs in British Columbia and Montana and likely occurs in the Prairies as well. *Pachygnatha tristriata* and *P.*

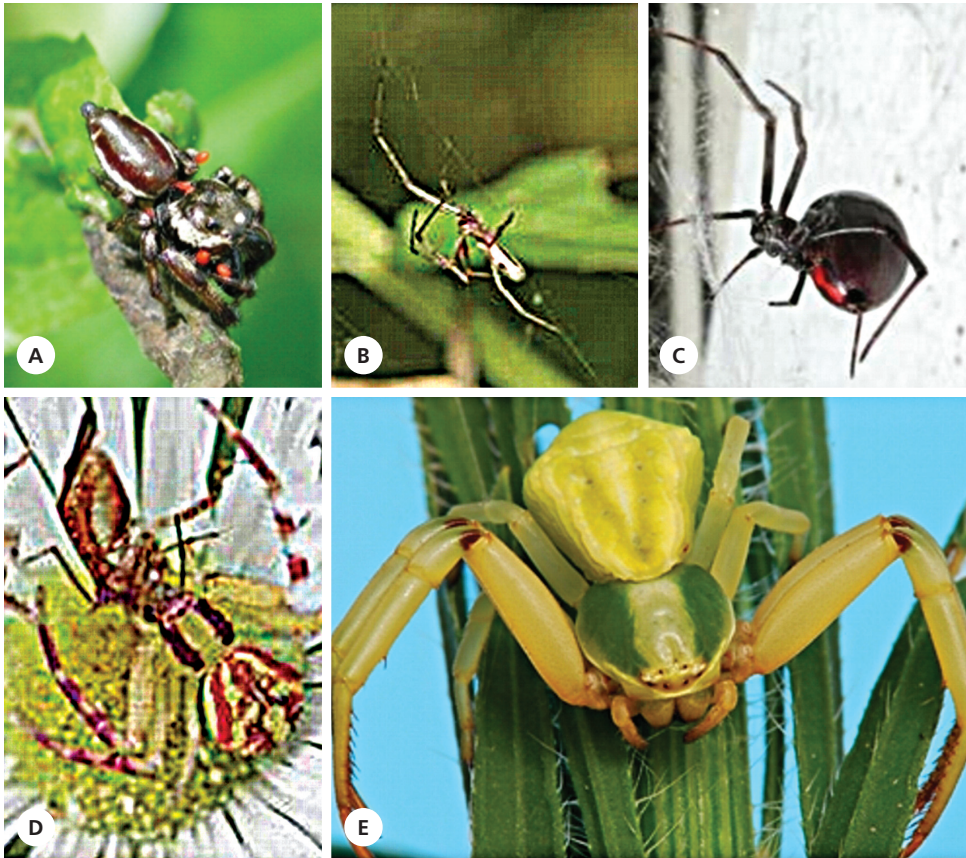


Fig. 4. A–E, Additional examples of spiders found in the Prairie Provinces. A, *Phidippus* sp., a jumping spider, with mites on body (Photo: H. Goulet). B, *Tetragnatha* sp., an orb-weaving spider common in grasslands (Photo: H. Goulet). C, Black widow (*Latrodectus hesperus*) (Theridiidae), female with characteristic red arrow marking (Photo: H. Goulet). D, Flower spider (*Misumena vatia*, Thomisidae), male about to eat a lygus bug (Photo: H. Goulet). E, *Misumenooides formosipes* (Thomisidae), close-up of immature female (Photo: M. Keeling, [www.Spiders.us](http://www.Spiders.us)); newly recorded outside Ontario in a canola field near Lethbridge.

*xanthostoma* were collected occasionally in the more humid habitats of the tallgrass and aspen sites within the ecozone, but not in the more arid or mesic grassland sites. In contrast, *Tetragnatha laboriosa*, a known grassland species, was the most common species (37%) in canola foliage and was also present in all three Mixed Grassland studies summarized here (Table 4). *Tetragnatha versicolor* was collected at Grasslands National Park in a river riparian zone (Finnamore *et al.* 2000) and, together with *Tetragnatha straminea*, was also commonly collected from the foliage of the understory at George Lake in the Boreal Transition Ecoregion (JP and JS, unpublished data). *Tetragnatha versicolor* is widespread and frequent in humid habitats that support shrubs or trees.

***Theridiidae, Comb-Footed Spiders (6<sup>th</sup>, 23 genera: 51 species; Fig. 4C)***

The comb-footed spiders build small webs of various irregular shapes and are also called tangle-web or cobweb spiders (Levi 1957a). Only 16 of the 51 species that occur in the

three provinces were reported in the faunistic studies within the Prairies Ecozone, and two species of *Euryopis* and one of *Theridion* were undetermined (Table 4). Most species were collected infrequently (<0.5%), except for *Enoplognatha marmorata*, which accounted for 2% of the collection in a site within the Moist Mixed Grassland Ecoregion. This species was reported from most sites within and outside the ecozone, including the meadow site in southern Ontario (Table 4). Collecting Theridiidae by beating or vacuuming did not result in an increase in relative abundance of comb-footed spiders. For example, only three of 13 species in an aspen site at George Lake had sampled frequencies between 0.5 and 5% (JP and JS, unpublished data). Similar results were obtained by Dondale (1970), who found only two frequent species, but nine others that were rare or occasional at the Heasman's meadow site in southern Ontario.

***Thomisidae, Crab Spiders (7<sup>th</sup>, 7 genera: 38 species; Fig. 4D and E)***

Crab spiders (both in Thomisidae and Philodromidae) are ambush predators that are well camouflaged in flowers or in leaf litter (Dondale and Redner 1978). Twenty-five of the 36 thomisid species (and all genera other than *Coriarachne*) recorded from the Prairie Provinces have been collected in the Prairies Ecozone (Table 4). *Misumenoides formosipes* was collected from canola foliage near Lethbridge, constituting a new record for a locality outside Ontario. The genus *Xysticus* ranks third in species richness (26 species) among all spider genera after *Pardosa* (28) and *Walckenaeria* (27) for the three Prairie Provinces (Table 3), but the genus *Xysticus* is the most speciose within the Prairies Ecozone, with 17 species reported (Table 4). *Xysticus acquiescens*, and to a lesser extent *X. cunctator*, were common species in all grassland sites in Alberta and Saskatchewan, including the site under canola cultivation. *Xysticus ferox* was more widespread than the former two species, as it was also collected in various grassland and aspen habitats in Manitoba (Roughley *et al.* 2006; Stjernberg 2011) and in the Aspen Parkland Ecoregion of Alberta (Graham 2002). *Ozyptila sincera canadensis* (8.6%), *X. obscurus* (4.9%), *X. luctuosus* (4.7%), and *X. canadensis* (2.7%) were frequently collected from the ground at George Lake in the Boreal Transition Ecoregion (JP and JS, unpublished data).

***Titanoecidae, No Common Name (21<sup>st</sup>, 1 genus: 2 species)***

This small family, formerly considered part of the Amaurobiidae (Leech 1972), is represented by the genus *Titanoeca* with two species. *Titanoeca nigrella* is common in grassland sites of southern Saskatchewan and frequent in grassland sites of southern Alberta. *Titanoeca nivalis*, however, has been collected only as an occasional species from the tallgrass reserve in Manitoba (Table 4).

***Other Families (22<sup>nd</sup> to 26<sup>th</sup>, 1 or 2 genera: 1 or 2 species)***

The remaining small families each have one or two species in the Prairie Provinces, but were not reported in the biodiversity studies within the Prairies Ecozone reviewed here. The fauna of the Prairies Ecozone includes two genera of Cybaeidae and Pholcidae and one genus each of the Anyphaenidae, Miturgidae, Oxyopidae, and Uloboridae (Table 3). The family Oxyopidae, represented by *Oxyopes scalaris*, has been collected in Manitoba, Montana, Idaho, and British Columbia; therefore, it should occur in the rest of the Prairie Provinces. *Metaltella simoni* (Amphinectidae) is an adventive from southern South America reported from urban habitats in Alberta (Leech and Steiner 1992).











Family	Pr1	Pr2	Pr3	Pr4	Pr5	Pr6	Pr7	Pr8	Pr9	FT10	FT11	FT12	FT13	FT14
Species	MMG	MG	MG	MG	MMG	AP	TGG	TGA	AP	BT	BT	WAU	WAU	MEF
<i>Haplodrassus chamberlini</i>	-	1.54	0.26	-	-	-	-	-	-	-	-	-	-	-
<i>Haplodrassus eunis</i>	-	-	-	-	-	0.000	-	-	-	-	0.04	-	-	-
<i>Haplodrassus hiemalis</i>	-	-	-	-	-	0.032	0.66	0.54	0.03	0.23	0.49	-	0.06	0.04
<i>Haplodrassus signifer</i>	-	1.72	0.64	0.16	0.93	0.668	-	-	0.09	-	-	-	-	0.04
<i>Haplodrassus immat.</i>	-	-	-	-	-	-	0.23	-	-	-	-	-	-	-
<i>Micaria aenea</i>	-	-	-	-	-	-	-	-	-	-	0.31, R	-	0.06	-
<i>Micaria coloradensis</i>	-	0.71	0.65	-	-	-	-	-	-	-	-	-	-	-
<i>Micaria emertoni</i>	-	2.54	-	-	-	-	-	-	-	-	-	-	-	-
<i>Micaria foxi</i>	-	-	-	0.03	-	-	-	-	-	-	-	-	-	-
<i>Micaria gertschi</i>	-	0.12	0.81	0.59	-	0.004	-	-	-	-	-	-	-	0.04
<i>Micaria laticeps</i>	-	-	-	-	-	0.935	-	-	-	-	-	-	-	-
<i>Micaria longipes</i>	-	0.06	0.13	-	-	0.008	-	-	-	-	-	-	-	-
<i>Micaria longispina</i>	-	0.06	-	0.47	-	-	-	-	-	-	-	-	-	-
<i>Micaria medica</i>	-	0.12	-	-	-	-	-	-	-	-	-	-	-	-
<i>Micaria mormon</i>	-	0.77	-	0.66	-	-	-	-	-	-	-	-	-	-
<i>Micaria porta</i>	-	1.3	-	-	-	-	-	-	-	-	-	-	-	-
<i>Micaria pulicaria</i>	-	-	0.65	-	-	0.004	0.7	0.09	-	0.27	0.31	-	-	0.04
<i>Micaria riggsi</i>	-	0.06	2.55	0.61	-	-	-	-	-	-	-	-	-	-
<i>Micaria rossica</i>	-	-	1.16	-	-	-	-	0.05	-	-	-	-	-	-
<i>Micaria sp.</i>	-	-	-	-	0.95	-	-	-	-	-	-	-	-	-
<i>Micaria sp. 1</i>	-	-	0.13	1.05	-	-	-	-	-	-	-	-	-	-
<i>Nodocion mateonus</i>	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-
<i>Nodocion rufithoracicus</i>	-	0.41	0.1	0.54	-	-	-	-	-	-	-	-	-	-
<i>Orodorassus canadensis</i>	-	-	-	-	-	-	-	-	-	-	0.04	-	0.19	-
<i>Sergiolus capulatus</i>	-	-	-	-	-	0.024	-	-	-	-	-	-	-	0.04
<i>Sergiolus decoratus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Sergiolus montanus</i>	-	-	-	-	-	-	-	-	-	-	0.04	-	0.06	-
<i>Sergiolus ocellatus</i>	-	-	-	-	-	-	-	0.05	-	-	-	-	-	-
<i>Zelotes exiguioides</i>	-	-	-	-	-	0.061	-	-	-	-	-	-	-	-
<i>Zelotes fratris</i>	-	-	0.06	-	0.23	0.061	1.79	3.3	0.12	1.18	1.46	-	0.26	0.04









Family	Pr1	Pr2	Pr3	Pr4	Pr5	Pr6	Pr7	Pr8	Pr9	FT10	FT11	FT12	FT13	FT14
Species	MMG	MG	MG	MG	MMG	AP	TGG	TGA	AP	BT	BT	WAU	WAU	MEF
<i>Idionella anomala</i>	-	-	0.03	0.35	-	-	-	-	-	-	-	-	-	-
<i>Idionella rugosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Impropyphantes complicatus</i>	-	-	-	-	-	-	-	-	-	-	0.22, O	-	1.48	-
<i>Incestophantes duplicatus</i>	-	-	-	-	-	-	-	-	-	-	R	-	-	-
<i>Islandiana flaveola</i>	-	0.59	0.13	2.21	-	-	1.01	0.41	-	-	-	-	-	0.04
<i>Islandiana holmi</i>	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Islandiana longisetosa</i>	-	-	-	-	-	0.077	-	-	-	-	-	-	-	-
<i>Islandiana princeps</i>	-	1.24	0.03	0.02	-	0.000	-	-	-	R	-	-	-	-
<i>Kaestneria pullata</i>	-	-	-	-	-	0.004	-	-	0.06	R	-	-	-	-
<i>Leptyphantes alpinus</i>	-	-	-	-	-	1.207	-	-	-	-	1.02, R	0.14	3.67	-
<i>Leptyphantes intricatus</i>	-	-	-	-	-	-	-	-	-	-	0.8	0.28	0.39	-
<i>Leptyphantes nr. washingtoni</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.06	-
<i>Leptyphantes sp. (undet.)</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.06	-
<i>Leptyphantes sp. 10</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.52	-
<i>Leptyphantes sp. 5</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.13	-
<i>Leptyphantes turbarix</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Linyphiidae sp. 1</i>	-	-	-	-	-	-	-	-	-	-	0.04, O	-	-	-
<i>Linyphiidae sp. 2</i>	-	-	-	-	-	-	-	-	-	-	0.04, R	-	-	-
<i>Linyphiidae sp. 3</i>	-	-	-	-	-	-	-	-	-	-	0.04, R	-	-	-
<i>Linyphiinae sp. 1</i>	-	-	0.03	-	-	-	-	-	-	-	0.04	-	-	-
<i>Lophomma vaccinii</i>	-	-	-	-	-	-	-	-	-	-	0.04	-	-	-
<i>Maso sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Maso sundevallii</i>	-	-	-	-	-	0.040	-	-	-	-	R	-	-	-
<i>Meioneta C. sp.A</i>	-	-	-	-	-	0.008	-	-	0.01	-	-	-	-	-
<i>Mermessus tridentatus</i>	-	-	-	-	-	0.077	0.09	0.36	-	0.04	-	-	-	5.74
<i>Mermessus trilobatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Metopobacterus prominulus</i>	-	-	-	0.07	-	-	-	-	-	-	0.04	-	-	-
<i>Micrargus longitarsus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Microlinyphia mandibulata</i>	-	0.06	-	-	-	0.008, R	-	-	-	-	0.27, R	-	-	-
<i>Microlinyphia pusilla</i>	-	-	0.03	-	-	-	-	-	-	0.27	-	-	-	-

<i>Microneta viaria</i>	-	-	-	-	-	0.15	0.13	0.42	0.32	-
<i>Nerene clathrata</i>	-	-	-	0.04	0.04	-	0.22, R	-	-	0.04
<i>Nerene radiata</i>	-	-	-	-	-	0.04	0.04, F	-	-	-
<i>Oreonetides</i> sp. A	-	-	-	-	-	-	-	-	0.32	-
<i>Oreonetides vaginatus</i>	-	-	-	-	-	-	1.2	-	0.45	-
<i>Oreophantes recurvatus</i>	-	-	-	-	-	-	0.04	-	-	-
<i>Oryphantes aliquantulus</i>	-	-	-	-	-	-	0.04	-	-	-
<i>Pelecopsis mingei</i>	-	-	-	0.01	0.01	-	-	-	-	-
<i>Pelecopsis</i> sp. A	-	-	-	O	-	-	-	-	-	-
<i>Pityohyphantes costatus</i>	-	-	-	-	-	0.04	-	-	-	-
<i>Pityohyphantes subarcticus</i>	-	-	-	-	-	-	0.62, C	-	0.13	-
<i>Pocadicnemis americana</i>	-	0.03	0.01	-	0.09	0.04	0.09	-	1.22	-
<i>Pocadicnemis pumila</i>	-	-	-	-	-	-	-	-	-	0.04
<i>Poeciloneta</i> sp. A	-	-	-	-	-	-	-	-	0.06	-
<i>Porrhomma terrestre</i>	-	-	-	-	-	-	0.09	-	-	0.04
<i>Sciastes truncatus</i>	-	-	-	-	-	-	0.53	0.42	2.51	-
<i>Scotinotylus alpinus</i>	-	-	-	-	-	0.008	-	-	-	-
<i>Scotinotylus exsectoides</i>	-	-	-	-	-	-	-	-	-	-
<i>Scotinotylus pallidus</i>	-	-	-	-	0.101	-	-	-	0.13	-
<i>Scylaceus pallidus</i>	-	-	-	-	-	-	-	-	-	0.04
<i>Scyletria inflata</i>	-	-	-	-	-	-	-	-	-	-
<i>Sisicottus montanus</i>	-	-	-	-	-	-	0.31	0.14	1.35	-
<i>Sisicottus nesides</i>	-	-	-	-	-	-	-	-	0.32	-
<i>Sisicus apertus</i>	-	-	-	-	-	-	-	-	0.13	-
<i>Sisus rotundus</i>	-	-	-	-	-	-	-	-	0.13	-
<i>Soucron arenarium</i>	-	-	-	-	-	0, R	-	-	-	-
<i>Souessa spinifera</i>	-	-	-	-	-	-	-	-	-	0.04
<i>Spirembolus spirotubus</i>	0.91	-	-	-	-	-	-	-	-	-
<i>Stemonyphantes blauveltae</i>	-	0.13	-	-	-	-	-	-	-	-
<i>Syloctetor stativus</i>	-	-	-	-	-	-	0.09	-	-	-
<i>Tapinocyba cameroni</i>	-	-	-	-	-	-	0.18	-	-	-
<i>Tapinocyba minuta</i>	-	-	-	-	-	-	-	-	-	-
<i>Tapinocyba simplex</i>	-	-	-	-	0.04	-	-	-	-	0.04

Family	Pr1	Pr2	Pr3	Pr4	Pr5	Pr6	Pr7	Pr8	Pr9	FT10	FT11	FT12	FT13	FT14
Species	MMG	MG	MG	MG	MMG	AP	TGG	TGA	AP	BT	BT	WAU	WAU	MEF
<i>Tapinocyba</i> sp. 1	-	-	1.49	1.11	-	-	-	-	-	-	-	-	-	-
<i>Tapinocyba</i> sp. 2	-	-	0.39	-	-	-	-	-	-	-	-	-	-	-
<i>Tapinocyba</i> sp. A	-	-	-	-	-	-	-	-	0.01	-	-	-	0.19	-
<i>Tapinopa bilineata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Tenneseellum formicum</i>	-	1.66	0.87	2.57	-	0.020	-	-	-	-	-	-	-	-
<i>Walckenaeria arctica</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.39	-
<i>Walckenaeria atroibialis</i>	-	-	-	-	-	-	-	-	-	0.11	0.58	-	0.64	-
<i>Walckenaeria auranticeps</i>	-	-	-	-	-	-	-	-	-	-	0.04	-	-	-
<i>Walckenaeria castanea</i>	-	-	-	-	-	0.012, R	-	-	-	-	0.22	0.28	1.67	-
<i>Walckenaeria communis</i>	-	-	0.03	-	-	0.202	-	-	-	1.29	0.13	-	0.06	-
<i>Walckenaeria digitata</i>	-	-	-	-	-	0.028	-	-	-	-	-	-	-	-
<i>Walckenaeria directa</i>	-	-	0.1	-	-	0.008	0.04	0.09	-	-	0.18	0.14	0.64	0.04
<i>Walckenaeria exigua</i>	-	-	-	-	-	-	0.04	-	-	-	-	-	-	-
<i>Walckenaeria fusciceps</i>	-	-	-	-	-	-	-	-	0.06	0.04	-	-	-	-
<i>Walckenaeria indirecta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Walckenaeria karpinski</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.06	-
<i>Walckenaeria leptida</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.06	-
<i>Walckenaeria pallida</i>	-	-	-	-	-	0.012	-	-	-	-	-	-	-	-
<i>Walckenaeria palustris</i>	-	-	-	-	-	-	0.04	0.09	-	-	-	-	0.13	-
<i>Walckenaeria</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Walckenaeria</i> sp. 1	-	-	0.03	0.09	-	-	-	-	-	-	-	-	-	-
<i>Walckenaeria</i> sp. 2	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-
<i>Walckenaeria</i> sp. 3	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-
<i>Walckenaeria</i> sp. C	-	-	-	-	-	-	-	-	-	-	-	-	0.52	-
<i>Walckenaeria spiralis</i>	-	-	-	-	-	0.040	0.31	0.09	O	0.04	-	-	0.13	-
<i>Walckenaeria tricornis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Walckenaeria vigilax</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.83
<i>Wubana atypica</i>	-	-	-	-	-	-	-	-	-	-	-	0.14	-	-
<i>Zornella armata</i>	-	-	-	-	-	-	-	-	-	0.04	1.15	-	1.55	-

<b>LJOCRANIDAE</b>														
<i>Agroeca ornata</i>	-	-	-	-	-	0.004	10.19	3.25	0.01	0.04	6.33	0.28	5.73	-
<i>Agroeca pratensis</i>	-	-	-	0.25	-	0.121	0.48	2.71	0.16	0.61	-	-	-	-
<i>Agroeca</i> immat.	-	-	-	-	-	-	0.05	-	-	-	-	-	-	-
<b>LYCOSIDAE</b>														
<i>Atopocosa aculeata</i>	-	0.12	4.11	0.07	0.8	9.492	3.59	7.64	5.95	0.87	1.59	1.11	1.16	-
<i>Atopocosa kochi</i>	-	-	-	0.04	-	-	-	-	-	-	-	-	-	-
<i>Arctosa alpigena</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.19	-
<i>Arctosa emertoni</i>	-	0.24	-	-	20.4	-	-	-	0.07	0.42	-	-	-	0.34
<i>Arctosa rubicunda</i>	-	-	-	0.03	-	0.616	0.13	2.12	-	-	0.62	-	-	-
<i>Geolycosa missouriensis</i>	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-
<i>Hogna frondicola</i>	-	0.41	0.49	-	7.1	1.020	-	1.27	-	-	-	-	-	0.34
<i>Hogna heluo</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Pardosa coloradensis</i>	-	-	-	-	2.53	-	-	-	-	-	-	-	-	-
<i>Pardosa concinna</i>	?	-	7.05	0.03	0.05	-	-	-	-	-	-	-	-	-
<i>Pardosa distincta</i>	F	6.33	27.04	5.31	2.88	60.12, F	0.09	17.17	0.04	0.11	-	-	-	0.34
<i>Pardosa dromaea</i>	C	0.06	0.03	-	21.1	-	-	-	-	-	-	-	-	-
<i>Pardosa fuscata</i>	-	-	0.03	-	1.08	0.012	0.31	-	53.97, F	5.86	0.04	-	-	-
<i>Pardosa groenlandica</i>	-	-	-	-	-	-	-	-	4.63, O	-	-	-	-	-
<i>Pardosa hyperborea</i>	-	-	-	-	-	-	-	-	-	-	0.04	-	0.77	-
<i>Pardosa mackenziana</i>	-	-	-	-	-	0.012	0.17	-	-	0.19	5.05, R	23.92	16.81	-
<i>Pardosa milvina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Pardosa modica</i>	R	4.26	0.55	0.02	0.75	0.000	0.04	0.36	15.43	-	-	-	-	0.04
<i>Pardosa moesta</i>	-	0.06	-	-	0.1	0.903	54.02	33.03	4.09, O	41.67	1.02	1.81	1.03	0.34
<i>Pardosa mulaiiki</i>	F	0.18	0.26	0.06	-	-	-	-	0.12	-	-	-	-	-
<i>Pardosa</i> nr. <i>tesquorum</i>	-	-	-	-	6.93	-	-	-	-	-	-	-	-	-
<i>Pardosa ontariensis</i>	-	0.83	12.06	0.29	-	0.004	-	-	-	-	-	-	-	-
<i>Pardosa pedata</i>	-	-	-	0.04	-	-	-	-	-	-	-	-	-	-
<i>Pardosa saxatilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	2.26
<i>Pardosa sternalis</i>	F	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pardosa</i> spp. (undet. juveniles)	-	-	-	0.03	-	-	3.4	-	-	-	-	-	-	-
<i>Pardosa tesquorum</i>	F	-	-	0.08	-	-	-	-	0.14	-	-	-	-	-
<i>Pardosa uintana</i>	-	-	-	-	-	-	-	-	-	-	0.04	-	0.64	-

Family	Pr1	Pr2	Pr3	Pr4	Pr5	Pr6	Pr7	Pr8	Pr9	FT10	FT11	FT12	FT13	FT14
Species	MMG	MG	MG	MG	MMG	AP	TGG	TGA	AP	BT	BT	WU	WU	MEF
<i>Pardosa xerampelina</i>	-	-	-	-	-	-	-	0.05	0.01	1.1	1.06	0.14	0.13	-
<i>Pirata aspirans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Pirata bryantae</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.39	-
<i>Pirata canadensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pirata insularis</i>	-	-	-	-	-	-	0.52	0.18	-	0.19	0.09	-	-	0.04
<i>Pirata minutus</i>	-	-	-	-	-	0.008	0.09	0.5	-	-	-	-	-	6.79
<i>Pirata montanus</i>	-	-	-	-	-	-	0.04	0.05	-	-	-	-	-	-
<i>Pirata piraticus</i>	-	-	-	-	4.18	-	0.7	0.27	2.49, A	16.84	-	-	-	0.04
<i>Schizocosa avida</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1.15
<i>Schizocosa cespium</i>	-	-	2.88	0.5	0.88	-	-	0.05	-	-	-	-	-	-
<i>Schizocosa communis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.34
<i>Schizocosa crassipalpata</i>	-	-	-	-	-	-	-	0.36	-	-	-	-	-	0.95
<i>Schizocosa mecooki</i>	C	17.87	0.36	7.09	-	2.357	-	-	-	-	-	-	-	-
<i>Schizocosa minnesotensis</i>	-	0.53	0.19	0.13	0.18	0.008	-	-	-	-	-	-	-	-
<i>Schizocosa saltatrix</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Schizocosa</i> sp.	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-
<i>Trebacosa marxi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Trochosa terricola</i>	?	-	-	-	0.08	0.134	2.27	2.62	1.74	3.73	5.36	4.17	8.76	0.04
<b>MIMETIDAE</b>														
<i>Ero cantonis</i>	-	-	-	-	-	0.004	0.31	0.09	-	0.04	0.31, O	-	0.06	-
<i>Mimetus epeiroides</i>	-	0.41	-	0.27	-	0.004	-	-	-	-	-	-	-	-
<b>PHILODROMIDAE</b>														
<i>Ebo bucklei</i>	-	0.41	0.81	0.11	0.1	-	-	-	-	-	-	-	-	-
<i>Titanebo dondalei</i>	-	0.06	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ebo iviei</i>	-	-	-	0.06	-	-	-	0.05	-	-	-	-	-	-
<i>Ebo pepinensis</i>	-	0.06	-	-	-	-	-	-	-	-	-	-	-	-
<i>Philodromus cespitum</i>	0.61	1.54	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Philodromus exilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Philodromus histrio</i>	-	0.06	0.13	0.06	-	0.016, F	-	0.09	-	-	-	-	-	-



Family	Pr1	Pr2	Pr3	Pr4	Pr5	Pr6	Pr7	Pr8	Pr9	FT10	FT11	FT12	FT13	FT14
Species	MMG	MG	MG	MG	MMG	AP	TGG	TGA	AP	BT	BT	WAW	WAW	MEF
<i>Ictus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Maevia inclemens</i>	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-
<i>Neon nelli</i>	-	-	-	-	-	-	-	-	-	-	0.04	-	-	-
<i>Peckhamia picata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Pelegrina flavipes</i>	-	-	-	-	-	-	-	-	-	-	0.09, O	-	-	-
<i>Pelegrina galathea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Pelegrina insignis</i>	-	0.06	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pelegrina proterva</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Pellenes</i> sp.	-	-	0.16	-	0.2	-	-	-	-	-	-	-	-	-
<i>Pellenes</i> sp. 1	-	0.24	2.26	0.06	-	-	-	-	-	-	-	-	-	-
<i>Pellenes</i> sp. 2	-	-	2.81	1.93	-	-	-	-	-	-	-	-	-	-
<i>Pellenes wrighti</i>	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-
<i>Phidippus borealis</i>	-	-	-	-	0.109	-	-	-	-	-	-	-	-	-
<i>Phidippus clarus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.34
<i>Phidippus johsonii</i>	0.3	-	-	-	1.053	-	-	-	-	-	-	-	-	-
<i>Phidippus princeps</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.34
<i>Phidippus purpuratus</i>	-	0.12	0.1	0.43	-	0.15, R	-	-	-	-	0.04	-	-	-
<i>Phidippus</i> sp.	-	-	-	-	0.08	-	-	-	-	-	-	-	-	-
<i>Phidippus</i> sp. 1	-	-	0.16	0.01	-	-	-	-	-	-	-	-	-	-
<i>Phidippus whitmani</i>	-	-	-	-	0.036	-	-	0.14	-	-	-	-	-	-
<i>Salticidae</i> sp.	-	-	0.1	-	-	-	-	-	-	-	-	-	0.26	-
<i>Salticus scenicus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Sitticus floricola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
<i>Synageles occidentalis</i>	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-
<i>Talavera minuta</i>	-	-	-	0.21	-	-	-	0.09	-	-	-	-	-	2.5
<i>Tutelina similis</i>	-	0.12	-	-	0.024, R	-	-	0.05	-	-	-	-	-	-
<i>Tutelina</i> sp. 1	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-
<b>TETRAGNATHIDAE</b>														
<i>Pachygnatha clercki</i>	-	-	-	-	-	-	-	-	1.17, C	0.04	-	-	-	-
<i>Pachygnatha dorothea</i>	-	-	-	-	-	-	-	-	0.03, C	-	-	-	-	0.04









## Overview of Biodiversity Studies

In this section, we summarize the biodiversity studies conducted in the Prairies Ecozone, together with a few studies from bordering transition ecoregions that may share some of the spider species (Fig. 5). A meadow site from southern Ontario is included as an example of a comprehensive biodiversity study that uses a method other than pitfall trapping; it also demonstrates the difference in species composition of eastern and western spider assemblages. All of the studies discussed are summarized in Table 4, where the relative abundances (%) or the ACFOR designations are provided.

There have been several faunistic surveys of spiders in the boreal forests of Alberta, but few published studies from the Prairies Ecozone portion of the province. One study that is close (<20 km; Fig. 5) to the Aspen Parkland Ecoregion of the ecozone (Graham *et al.* 2003) reported on habitat affinities of a spider assemblage in a Boreal Transition Ecoregion meadow. Graham *et al.* (2003) demonstrated high spider species richness along a transect

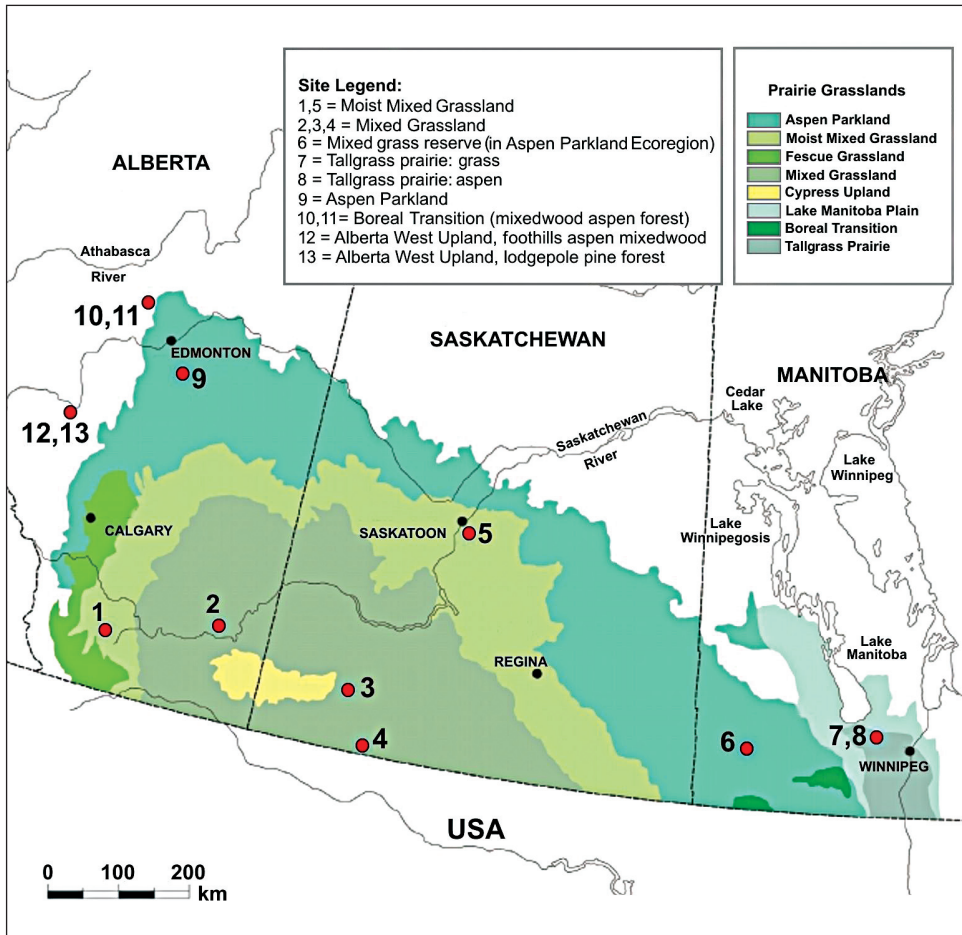


Fig. 5. Locations (red circles) of all the study sites summarized in Table 4 where spiders have been studied in the Prairies Ecozone (1–9) and adjacent transition ecoregions (10–13). Map modified from Shorthouse (2010).

from a freshwater pond into riparian grassland at George Lake (about 85 km northwest of Edmonton). In a relatively short period (21 May to 6 September 1998), they collected 60 species in 14 families from only 3,141 specimens collected with pitfall traps. The study demonstrated clear habitat associations for a number of spider species along the pond-to-grassy habitat transect. For example, the lycosid *Pirata piraticus* was positively associated with high moisture levels, whereas *Pardosa moesta* and the linyphiid *Bathyphantes pallidus* were more abundant in the drier habitats.

Additional spider collections have been made at the George Lake field study site of the University of Alberta during the frost-free seasons between 2011 and 2013 (JP and JRS, unpublished data). The study focused on spiders from the ground and low understory forest layers, which were collected by using pitfall traps (20 m apart in a grid pattern in 1 ha of mixedwood forest) and by beating understory vegetation onto a canvas sheet, respectively. The 140 species collected included 104 species (from 2,259 individuals) at the ground and 75 species (from 11,434 individuals) at the foliage layers; 40 species were collected both at the ground and foliage layers. Twenty-two species were frequent and eight common (on the ACFOR scale) in pitfall traps, accounting for 27.9% and 62.2% of the total number of individuals collected, respectively. The eight common species were *Bathyphantes pallidus*, *Allomengea dentisetis*, *Ozyptila sincera canadensis*, *Cybaeopsis euopla*, *Agroeca ornata*, *Trochosa terricola*, *Pardosa mackenziana*, and *Xysticus luctuosus*. Similarly, from the understory vegetation, 18 species were frequent, but only three (*Helophora insignis*, *Dismodicus alticeps*, *Pityohyphantes subarcticus*) were common, accounting, respectively, for 26.7% and 67.7% of the total sample of individuals.

The George Lake studies mentioned earlier are relevant to the Aspen Parkland Ecoregion, since George Lake is located only about 20 km west of the northern edge of the Aspen Parkland (Fig. 5), and the assemblages cluster with other aspen parkland assemblages (Fig. 6). However, Graham (2002) documented the spider assemblages directly inside the Aspen Parkland Ecoregion in and around natural and restored ponds near Camrose from mid-May to August 2004 (Fig. 5, Table 4). Much of this ecoregion has been converted to agriculture, as it is ideal for growing canola and very little pristine aspen habitat remains in any of the three Prairie Provinces. Graham collected 65 species from 6,902 adults from pitfall traps adjacent to ponds and 15 species from 812 individuals from floating traps on the ponds. In the pitfall trap sample, *Pardosa fuscula* was abundant and was clearly the dominant species, with a frequency of 54%; *P. modica* and *Alopecosa aculeata* were common (Table 4). Nine species were frequent, including four other lycosids (*P. groenlandica*, *P. moesta*, *Pirata piraticus*, *Trochosa terricola*), along with *Gnaphosa parvula*, *Neoantistea magna*, *Pachygnatha clercki*, *Xysticus emertoni*, and *X. ferox*. Samples from the floating traps were dominated by *Pirata piraticus*, but *Dolomedes triton*, *Tetragnatha clercki*, and *T. dorothea* were also common (see ACFOR designations in Table 4). *Pardosa fuscula* represented only 4% of the spider catch in the floating traps, which was clearly far less common than in riparian habitats. Two other species were frequently captured by floating traps in the pond microhabitat: *Bathyphantes pallidus* and *Clubiona norvegica*.

Studies in the Suffield National Wildlife Area (within the Canadian Forces Base) are among the few to provide information on spiders in the Mixed Grassland Ecoregion in Alberta. This site comprises one of the few remaining patches of pristine grassland habitat in Canada. The reserve is 2,690 km<sup>2</sup> and is located northwest of Medicine Hat. Finnermore and Buckle (1999) documented the spider assemblages from the reserve as part of a multi-agency effort to document its wildlife. They sampled a gradient from black soils with relatively high moisture and tall vegetation, to aeolian (wind-deposited) drier soil types and

shorter vegetation from 17 July to 15 August 1995, using mainly pitfall traps. Ninety-seven species were identified from 1,700 specimens (Table 4). In addition to high richness, the assemblage was characterized by high evenness: 40 species were frequent and no species was considered abundant ( $>0.5\%$  and  $>50\%$ , respectively). Only two (Lycosidae) were common in the collections (5–50%): *Schizocosa mccooki* (18%) and *P. distincta* (6%). Five species were undescribed. High evenness of Carabidae (Coleoptera) from this same study is also reported in Chapter 1 of Volume 4.

Another grassland ecoregion in Alberta where spiders have been studied is within the Moist Mixed Grassland Ecoregion, near Lethbridge in the southern part of the province (HC and RL, unpublished data). The spider fauna was studied in and adjacent to canola (*Brassica napus* L.) as part of a larger effort led by L. Dosdall (unpublished data) to improve knowledge of arthropod biodiversity in this crop and to integrate natural enemies into sustainable pest management systems. Spiders were collected from over 4,000 sweeps taken from May to August 2010–2012 at various canola fields or plots around Lethbridge. Only 328 specimens (ca. 23 species) were collected from the canola canopy despite the large number of sweeps. The three common species were *Tetragnatha laboriosa* (38%), *Dictyna major* (21%), and *Neoscona arabesca* (5%). A number of species collected from the crop were not reported in the other prairie studies and some new records are noted: *D. major*, *Islandiana holmi* (Alberta), *Araniella* sp., *Habronattus borealis* (Alberta), *Hypsosinga* sp., *Mecaphesa celer*, *Misumenoides formosipes* (new record outside Ontario), *Phidippus johnsoni*, *Asagena (Steatoda) medialis* (new record for Canada), *Thanatus* sp. (immature), and *Xysticus banksi*. Spiders were also collected from pitfall traps in adjacent wheat fields, a tree shelter, and a grassy alkaline margin to identify potential predators of diamond back moth in the canola crop (Mauduit 2012). Only some of the more common spiders from these samples, which included 756 spiders, had been identified to species from the latter study at the time of writing this chapter. Nevertheless, based on the identifications to date, the most common species in pitfall traps were *Pardosa dromaea* (20%), *Xysticus cunctor* (13%), and *Schizocosa mccooki* (12%). These species were also reported from the drier Mixed Grassland Ecoregion at Suffield in Alberta (Finnamore and Buckle 1999) and Grasslands National Park (Finnamore *et al.* 2000 and see below in this section) in Saskatchewan. Other frequent species were *Pardosa tesquorum* (3%) and *P. sternalis* (1%); the latter species was not reported in the other faunistic investigations in the ecozone listed in Table 4. The crab spider, *Xysticus cunctor*, was the only species that was collected by both methods used in the study; it was frequent in sweep nets and common in traps. Stjenberg (2011) also collected far fewer spiders by sweeping than by pitfall trapping in a mixed prairie reserve in southern Manitoba.

In Saskatchewan, two studies have provided information about spiders in the Mixed Grassland Ecoregion. Pepper (1999) conducted pitfall trapping from May to August 1995 to assess effects of pasture size on spiders as well as on ground-dwelling beetles (see Chapter 1, Volume 4) in the Shaunavon area, west of Val Marie. She reported 118 species in a collection of 3,092 spiders. Thirty-two species were frequent and three were common (*Pardosa distincta*, *P. ontariensis*, *P. concinna*). Species richness increased with pasture size, and the characteristics of the spider assemblages were associated with range condition. In addition, many species were classified as “rare” (using the ACFOR classification), and only two species were found in all seven pastures. Finnamore *et al.* (2000) assessed arthropod diversity patterns at Grasslands National Park, located just north of the USA border, east of Val Marie. They used similar collecting methods as those reported for their Suffield study (Finnamore and Buckle 1999) and selected the spiders collected in July of

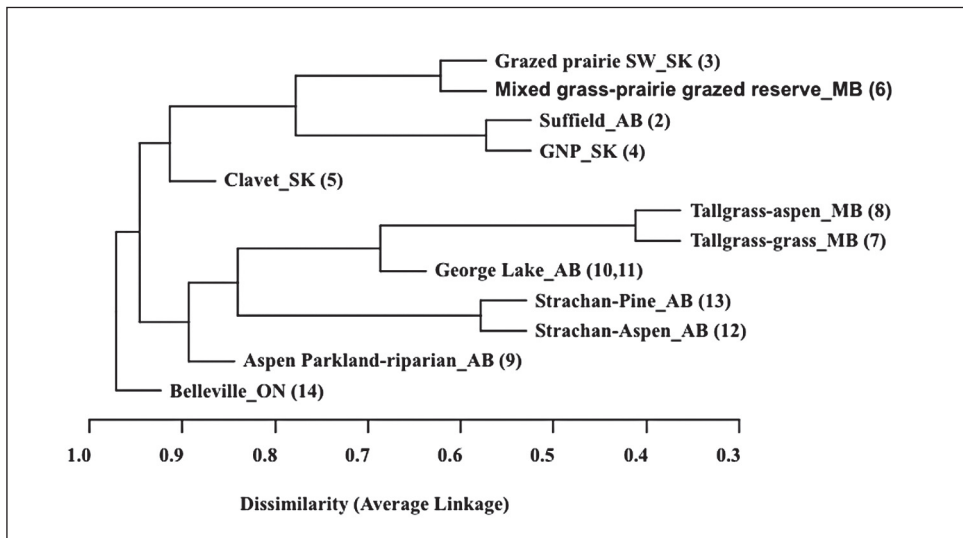
1996 for quantitative diversity analysis. They found 109 species in a sample of 25,594 spiders (Table 4). The assemblage included 24 frequent species (>0.5%) and six common (>5%). The two most common species were *Zelotes lasalanus* (14%) and *Thanatus coloradensis* (11%); the two most common lycosids at Suffield (*Schizocosa mccooki* and *P. distincta*) ranked fifth and sixth in this study. About 20 of the species recorded could not be determined accurately because of the lack of taxonomic resources or because they were new to science (Table 4).

Spiders have also been studied in the Moist Mixed Grassland Ecoregion in Saskatchewan. Doane and Dondale (1979) found 47 species among 1,125 spiders collected in and adjacent to a wheat field near Clavet in central Saskatchewan from April to October in 1975 and 1976. Twenty-two species were frequent and four were common. *Pardosa dromaea* and *Arctosa emertoni* ranked first and second overall, at 21 and 20%, respectively, while *Hogna frondicola* and *Pardosa* nr. *tesquorum* ranked third and fourth at 7%. Another lycosid, *Pirata piraticus*, was frequent (4%) and favoured the border of the field, perhaps reflecting a similar moisture gradient as that observed by Graham *et al.* (2003). Peak seasonal activity for *A. emertoni* adults occurred from late April to mid-July and about a week later for *P. dromaea*. No known spider biodiversity studies have been conducted in the Aspen Parkland Ecoregion of Saskatchewan or in the Cypress Uplands.

In Manitoba, Stjernberg (2011) studied spider assemblages in 2005 and 2006 in the Yellow Quill Mixed Grass Prairie Preserve, located in the Aspen Parkland Ecoregion, in relation to cattle grazing (30 km SE of Brandon; Fig. 5). She reported 143 species from 24,685 spiders in pitfall traps and 41 species from 274 spiders in sweep nets. Ten of the species were found only by sweeping, including *Argiope trifasciata*, which was common at the site. *Tetragnatha laboriosa*, *Dictyna volucripes*, and *Misumenops celer* were the three most common species collected by sweeping (34, 12, and 11% of the sweep total net catch, respectively); they were also caught in pitfalls but at low frequencies (<0.05%). Only *Xysticus triguttatus* was frequent in sweep net samples and common in pitfalls (Table 4). *Pardosa distincta* was by far the most abundant species caught in traps (60%), and it was associated with ungrazed grass paddocks; *Alopecosa aculeata* (9% of trap catch) was associated with grazed paddocks (Stjernberg 2011). *Schizocosa mccooki*, a species common in the Mixed Grassland Ecoregion, was frequently collected in this prairie reserve in southwestern Manitoba (Stjernberg 2011; Table 4). Farther northeast, in tallgrass prairie habitat near Winnipeg, this species was absent (Wade 2002; Roughley *et al.* 2006; Wade and Roughley 2010).

Although tallgrass prairie once covered thousands of square kilometres in southeastern Saskatchewan, Manitoba, and southern Ontario, <1% remains (Noss *et al.* 1995). A detailed account of the effect of fire on tallgrass prairie spiders near Winnipeg can be found in Wade (2002) and in a summary in Wade and Roughley (2010). In a related study summarized here, these authors (Roughley *et al.* 2006) used pitfall trap sampling to study the spider (and ground beetle) fauna in a tallgrass reserve near Winnipeg along a tallgrass–aspen ecotone from 1998 to 2000. They identified 92 species from a catch of 4,999 individuals. Twenty species were frequent, and three lycosids were common in the tallgrass habitat: *P. moesta* (33%), *P. distincta* (17%), and *Alopecosa aculeata* (8%). In the adjacent aspen habitat, *P. moesta* was abundant (54%), but *P. distincta* was captured only occasionally (0.09%). *Agroeca ornata* (10%) and *Centromerus sylvaticus* (7%) were the other two common species in the aspen site, with another 18 species considered frequent (0.5 to 5%). Fifty-two species were shared between the two habitats, but 25 and 15 were restricted to the tallgrass and aspen sites, respectively.

Although relatively few spider studies have been conducted in the Prairies Ecozone, results from studies from outside this zone can help interpret patterns in the studies that are available (Fig. 6). Dondale (1970) conducted a study using quick “trap and vacuum” sampling from 1965 to 1970 in a meadow (Heasman field) near Belleville in southern Ontario. This is a departure from more standard pitfall or sweep sampling used in many other studies, and so allows comparison of biodiversity obtained with different sampling methods. A total of 150 species were collected, and the investigator estimated the total density of all spiders at 53.3 individuals/m<sup>2</sup> from the collections. The relative abundances can be reconstructed as follows, based on the information presented in one of Dondale’s (1970) tables: four species were common (*Erigone autumnalis*: 24%, *Ceraticelus emertoni*: 20%, *Pirata minutus*: 7%, *Eperigone trilobata*: 6%), 17 frequent (0.5–5%), 21 occasional (average frequency of 0.33%), and 108 rare (average frequency of 0.04%). Interestingly, none of the species considered common or frequent in Dondale’s (1970) study was shared with any of the prairie grassland sites considered in our review, and the Ontario site clustered well away from the Prairies sites (Fig. 6); this shows that eastern and western spider communities are unique. Of the 41 species that were shared with the Prairies Ecozone, 12 were considered occasional at the Heasman field, with an estimated frequency



**Fig. 6.** Species composition patterns for spider assemblages from different habitats from the Prairies Ecozone, adjacent transition ecoregions, and a meadow in southern Ontario. The dendrogram (average linkage cluster analysis) depicts dissimilarities among assemblages collected through pitfall trapping (studies 1–13) and a vacuum quadrat collection (study 14), so that sites that group most closely together have the most similar spider community. **Study references and ecoregion** (numbers correspond to sites in Fig. 5 and Table 4): Grazed prairie SW\_SK (3) = Pepper (1999), Mixed Grassland; Mixed grass-prairie grazed reserve\_MB (6) = Stjernberg (2011), Aspen Parkland; Suffield\_AB (2) = Finnamore and Buckle (1999), Mixed Grassland; GNP\_SK (4) = Grasslands National Park in Saskatchewan (Finnamore *et al.* 2000), Mixed Grassland; Clavet\_SK (5) = Doane and Dondale (1979); Tallgrass\_aspen MB (8) and Tallgrass-grass\_MB (7) = Roughley *et al.* (2006), Lake Manitoba Plain Ecoregion; George Lake\_AB = averages for Graham *et al.* (2003) (10) and Pinzón and Spence (unpublished data) (11), Boreal Transition near Prairies Ecozone; Strachan-Pine (13) and Strachan-Aspen (12) = Cárcamo’s (1997) pine and aspen sites in Western Alberta Uplands; Aspen Parkland riparian AB (9) = Graham (2002) prairie pond studies, Aspen Parkland; Belleville\_ON (14) = Heasman meadow (Dondale 1970), eastern mixedwood forest.

of 0.34%, and the rest were rare, with a mean frequency of <0.05%. These differences relate both to differences in sample methodology and in habitat, since Belleville is located in the Mixedwood Plains Ecozone in Ontario.

The prairie grassland spider assemblage also showed considerable differences from assemblages from the aspen and pine forests at the boreal foothills in the transition of the Montane Cordillera and Prairies ecozones (Western Alberta Uplands) near Strachan (Fig. 6; see Fig. 4 for location) studied by Cárcamo (1997). Only two of the frequent lycosid species (*Pardosa moesta* and *Alopecosa aculeata*) were shared with the assemblages from the Mixed Grassland Ecoregion about 400 km to the southeast. The foothills assemblage shared more species of frequent abundance with other transition ecoregions from Alberta and Manitoba: *Trochosa terricola*, *Bathypantes pallidus*, *Agroeca ornata*, and *Diplocentria bidentata*. The aspen assemblage had low similarity with the pine assemblage, which could be explained by higher frequencies of *Allomengea dentisetis* (38% vs. 1%) in aspen than in pine and the reverse pattern with *D. bidentata* (1% vs. 11%) (both Linyphiidae) (HC and D. Buckle, unpublished data).

### Patterns of Species Assemblages

Although some ecoregions are understudied, distinct species assemblages are suggested by the faunistic studies reported from the Prairies Ecozone, particularly for the drier or mesic grassland regions (Table 4, Fig. 6). A high degree of affinity was observed for the Mixed Grassland sites. Twenty-nine frequent species were collected only in this ecoregion. *Schizocosa mccooki* and *Zelotes lasalanus* were the two most commonly reported species in this region. The only other site where they were reported, though at lower frequencies (1–2%) was at the Yellow Quill Mixed Grass Prairie Preserve in southwest Manitoba (Table 4). We found only two studies in the Moist Mixed Grassland Ecoregion. In both, *Pardosa dromaea* and *P. nr. tesquorum* were commonly collected and these species appear to be unique to this ecoregion. Only three other species qualified as frequent residents of this ecoregion, including another undetermined or undescribed *Micaria* sp. (Table 4). Spider assemblages from these two grassland ecoregions are clearly distinctive from those of the Boreal Ecozone. Only two of the 75 frequent grassland species (*Pardosa fuscula* and *Alopecosa aculeata*, both widespread) were also frequent in an intensive boreal study site near Peace River in northwestern Alberta (Pinzón 2011). Twelve other species among these 75 were shared but accounted for less than 0.5% of the boreal spiders in Pinzón's data.

Assemblages from the transitional more humid ecoregion of Manitoba were less distinct than those of the transition ecoregions of Alberta (Fig. 6). None of the common spiders collected in either tallgrass or aspen habitat at the St. Charles Rifle Range tallgrass prairie reserve near Winnipeg were unique to that ecoregion (Table 4). However, some of those considered frequent were not reported from other ecoregions. For example, *Grammonota pictilis* was frequent in the tallgrass habitat and absent from the aspen habitat in that reserve (Roughley *et al.* 2006). There were three other species that were shared with the assemblage from the Heasman meadow in southern Ontario (Dondale 1970), and these might prove to be characteristic of tallgrass habitats, but further study is required. The Yellow Quill Mixed Grass Prairie Preserve, despite its location within the Aspen Parkland Ecoregion in Manitoba, had a community that was more similar to that of the site near Clavet in the Moist Mixed Grassland Ecoregion of Saskatchewan than the only other Aspen Parkland site in central Alberta (Fig. 6). In addition, some of the frequent species, such as *S. mccooki* and *Z. lasalanus*, were more typical of “true” prairie grassland. This



pattern is likely related to the fact that the Alberta study was conducted in riparian habitats, whereas the Manitoba study took place in more arid, grassland habitats.

The riparian spider assemblage in the Aspen Parkland Ecoregion studied by Graham (2002) appears to be more similar to those from the other transition forested ecoregions than to those from grassland sites (Fig. 6). However, Graham's study focused on riparian habitats near ponds, and this may explain the higher similarity of the assemblage to those from the more humid transition ecoregion. Although the pond riparian study shared more species with the forested sites than with the grassland sites, none of these shared species were frequent near the prairie ponds. The majority of the species near the prairie pond aspen sites were shared between the grassland ecoregions and the forest transition ecoregions within the Boreal Ecozone. The only exception was *Pardosa modica*, which was the second most common species near ponds, and seems to favour grasslands. This species was not reported from any of the other forested sites near the Prairies Ecozone (Table 4) nor in Pinzón's (2011) intensive boreal studies in northwestern Alberta, although the species has been collected in the southern Yukon, and it occurs as far east as Nova Scotia (Dondale and Redner 1990).

The transition forest habitats had several frequent species in common that were not (or rarely) collected in the Prairies Ecozone (Table 4, Fig. 6). These species included *Bathypantes pallidus*, *Ozyptila sincera canadensis*, all *Lepthyphantes*, *Xysticus luctuosus*, *X. obscurus*, *X. ellipticus*, *X. canadensis*, *Allomengea dentisetis*, *Cybaeopsis euopla* (and all the other amaurobiids), *Agroeca ornata*, *Trochosa terricola*, and *Pardosa mackenziana*. The latter six species are boreal elements that were frequent in Pinzón's (2011) intensive study in northwestern Alberta (near Peace River). The foothills (Boreal Ecozone) assemblage southwest of Rocky Mountain House (Cárcamo 1997) had a typical boreal spider fauna: all 30 species that represented at least 0.5% of the fauna were shared with the assemblage reported from the more northern boreal site in Pinzón (2011). No studies from the Montane Cordillera Ecozone are available for comparison, but some of the less frequent species in the genera *Lepthyphantes* and *Walckenaeria* might be representatives of that ecozone. Although transition ecoregions appear to lack a distinctive spider assemblage, the community structure is certainly distinctive, as illustrated by the high abundance of *Allomengea dentisetis* in mixedwood aspen habitats. A few spider species are widespread throughout the Prairies Ecozone. *Hogna frondicola* was common in collections from at least one grassland site in all ecoregions, including southern Ontario, but not in any of the sites under tree cover (Table 3). The only other common widespread grassland species was *Pardosa distincta*; however, it also occurred in aspen habitats, although not apparently in the foothills region. *Enoplognatha marmorata*, *Xysticus ferox*, *Alopecosa aculeata*, *Pardosa modica*, and *Thanatus striatus* also occurred in all grassland sites, but at frequencies of less than 5%.

### Research Needs

The highest priority to advance knowledge of spiders in the Prairies Ecozone (and Canada), remains the same as that highlighted by Bennett (1999) more than a decade ago. There remains a severe shortage of professional opportunities for systematic araneologists in Canada. Although there are trained systematists and no shortage of urgent taxonomic work required, there have been no recent opportunities in academia or public institutions to support their work and replace retired systematists. Without basic alpha taxonomy and revisionary work, advancing the understanding of biodiversity and conservation issues will remain a serious challenge.

The spider taxa that urgently require revision and development of keys to support identification are easy to discern from the number of undetermined species listed in Table 4. Most obvious among these is the Linyphiidae—by far the most speciose and least understood family of spiders in Canada. Currently, identifying species in this family, particularly in the Erigoninae, requires searching through species descriptions scattered in various publications that span more than 150 years (Draney and Buckle 2005). For Alberta linyphiids, Pinzón (2011) has compiled relevant images to identify the known species from the province. However, no effective regional keys that include both sexes are available for most genera. At least 15% of the linyphiids reported from biodiversity studies in the region (Table 4) could not be determined to species, despite efforts by Don Buckle, one of the few world experts of this family, who examined the specimens. In fact, assigning linyphiids even to genus is a major challenge for non-taxonomists or even for taxonomists without specific expertise for this family. Clearly the Linyphiidae should be the top priority for future Canadian araneologists.

Surprisingly, the so-called charismatic megafauna of the spiders, the Salticidae, are also poorly known. Of the 38 taxa reported from the biodiversity investigations in the Prairies Ecozone (Table 4), 10 were not determined to species. Ongoing efforts are targeting this group and it is hoped that this group of spiders will be identifiable in the near future (Buddle and Shorthouse 2000). Two other families urgently require attention. The Theridiidae, which also ranks among the top six families in terms of species richness, also includes a large proportion of undescribed species. The last major family without species keys is the Dictynidae—the third largest in the Prairies, but not a dominant group in terms of species richness in the grassland ecoregions. Only 16 species were reported from biodiversity studies in the ecozone, but some of the species (e.g., *Dictyna major*) were common at some sites, and at least one *Dictyna* species could not be determined in the sample of biodiversity of studies reported in Table 4.

The spider fauna in the Prairies Ecozone has been studied at only a few sites and has been mostly based on pitfall trap samples. A key objective in the future should be to supplement pitfalls with alternative methods that sample the web building or small spiders better than pitfalls. George Lake (Alberta) studies, for example, demonstrated large differences in species composition between the ground and understory layers of the forest (JP and JS, unpublished data), and similar results have been observed for canola near Lethbridge (HC and RL, unpublished data) and forested habitats in the boreal forest where ground, understory, and overstory layers have been compared (Pinzón *et al.* 2011). Key habitat types are also missing. Spider assemblages from the Cypress Hills Uplands of Alberta and Saskatchewan, the Fescue Grasslands Ecoregion in southern Alberta, most ecoregions in Manitoba, and the extensive Boreal Plains Lowlands of the Alberta Peace River Region have received no attention. This latter region would make for an interesting biogeographical study given the disjunct nature of the grasslands in that region (as shown with Lepidoptera by Schmidt *et al.* in Chapter 6, Volume 4). The Moist Mixed Grasslands are also poorly known, with only one study reported from Saskatchewan and one from a cultivated site in Alberta. The spider fauna of Aspen Parkland within the ecozone has also been poorly studied. However, the Boreal Transition Ecoregion, as studied at the University of Alberta Field Site at George Lake near the Aspen Parkland Ecoregion, is well-known. It would be of interest to see whether mesic habitats within the aspen forests of the Prairies Ecozone have more species in common with adjacent grasslands than with boreal mixedwood forests. Clearly, as with most invertebrates, there is no shortage of geographical gaps to fill.

Much basic ecological work remains to be done with spiders from grassland habitats, other than perhaps the fishing spiders (e.g., Zimmerman and Spence 1989, 1992, 1998; Spence *et al.* 1996), and little is known about spider assemblages, habitat associations, interactions, and the functional role of spiders in grassland habitats. In contrast, forested boreal habitats have been well studied (e.g., Buddle *et al.* 2000, 2006; Work *et al.* 2004; Buddle and Shorthouse 2008; Pinzón and Spence 2008, 2010; Pinzón *et al.* 2011, 2012, 2013*a*, 2013*b*; Bergeron *et al.* 2013). For example, from the eight faunistic studies described in this review from the Prairies Ecozone, just under 300 species have been reported (Table 4). This compares to close to 300 species that have been reported from just one locality in the forest foothills (Boreal Plains Ecozone) in northern Alberta (Pinzón 2011; D. Shorthouse, unpublished data). This situation clearly shows the need for conducting additional biodiversity research in the Prairies Ecozone that focuses on habitats that are presently understudied in order to better understand patterns in species composition and richness across this region.

Over the past several decades, there has been a strongly developing interest in sustainable agriculture and alternative pest management methods that rely less on pesticides and more on natural biological alternatives. Yet, other than a few groups of predators, such as carabid beetles (Holliday *et al.*; Chapter 1, Volume 4) and some specialized parasitoid taxa (e.g., Ichneumonidae and Braconidae; Chapters 9 and 10, respectively, Volume 4), not much is known about many of the generalist predators such as spiders, although ecological studies suggest that they play significant roles in bolstering natural resistance to pest damage (e.g., Snyder and Wise 1999). This knowledge gap stems from the lack of both human resources and taxonomic tools. Knowledge about the diversity of spiders and their life histories is essential to integrate them into pest control strategies for cropping systems, and doing this will likely advance progress toward a more sustainable agriculture.

## Conclusions

The most distinctive spider assemblage within the Prairies Ecozone occurs in the shortgrass prairies (Mixed Grassland Ecoregion). At least 35 species were unique to this ecoregion of Canada. These species are likely at the northern range of their larger geographical distribution in the Great Plains of North America. *Schizocosa mccooki* and *Zelotes lasalanus* are common representative species in these habitats. Seventy-five species have been collected frequently (>0.5% of the catches) in biodiversity studies from this grassland ecoregion, and only two of these species are also frequent in the adjacent Boreal Plains Ecozone. Other more humid ecoregions appear to harbour less distinctive assemblages, but most have been too poorly studied to draw firm conclusions.

Spiders are fascinating, unique organisms among the arthropods—few people are indifferent to them. It is this fascination that drives people (professionals, expert amateurs, or “dabblers”) to study them and contribute to making the group well-known in many places. Through the work of a small cadre of professional araneologists in Canada, considerable progress has been made to our knowledge of spiders in the Prairies, so that much of the prairie and Canadian spider fauna is known. Of the ca. 1,500 species expected to occur in Canada, we already know the identity of over 1,400 or almost 95% of them! This makes spiders one of the best known arthropod orders, comparable to the Lepidoptera, and far better known than some groups such as soil arthropods (e.g., Myriapoda or Collembola; see Chapters 2 and 6, respectively, this volume). But knowing the identity of the species in a group is only the first step along the road of biological knowledge, and that is as far as we

have come with spiders. Although most spider species are known, studying their diversity remains a major challenge due to the taxonomic challenges discussed earlier. Even basic biodiversity surveys that include comprehensive sampling (more than just pitfall trapping) and encompass diverse habitats (aquatic, riparian, sand dunes, grassy, forest, etc.) are lacking within any ecoregion. Until we have keys for the most diverse taxa, especially Linyphiidae, Salticidae, and Theridiidae, that dominate samples from most grassland habitats, progress in conservation biology and other applied fields of spider ecology will be limited in the Prairies Ecozone. Given the importance of spiders in ecological systems as general predators, and their fascinating biology, further investment in the study of spiders is warranted.

### Acknowledgements

Like most arachnologists in the Prairies, we are indebted to Donald J. Buckle for his generous, enthusiastic, indispensable assistance in determining species of the family Linyphiidae (and many others). The senior author also thanks Robb Bennett for help in determining Agelenidae and Cybaeidae. We gratefully acknowledge the taxonomic contributions of C. Dondale, P. Paquin, N. Dupérré, and D. Buckle because their Canadian checklist formed the basis for the preparation of the prairie checklist presented here. Comments by D. Shorthouse, an anonymous reviewer, and especially one of the editors (Donna Giberson), significantly improved a draft of this chapter. Finally, a huge thanks to C. Dondale and J. Redner for their numerous spider keys—without them, biodiversity studies in Canada would be impossible.

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## Chapter 5

# Chewing Lice (Insecta: Phthiraptera: Amblycera, Ischnocera) and Feather Mites (Acari: Astigmatina: Analgoidea, Pterolichoidea): Ectosymbionts of Grassland Birds in Canada

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**Abstract.** The diversity of bird species nesting in Canadian grasslands is high, and each of them is host to one or more species of lice and mites. A checklist of feather lice (Phthiraptera: Amblycera, Ischnocera) and feather mites (Acari: Analgoidea, Pterolichoidea) from 160 species of birds that nest in terrestrial and aquatic habitats in the grassland biome in Alberta, Saskatchewan, and Manitoba is provided here. The list includes known and expected records. In total, four families, 54 genera, and 183 named species and subspecies of chewing lice are known to occur on these hosts in the Prairie Provinces. At least an additional 63 species are expected to be found eventually, on the basis of records from these hosts elsewhere in North America. Twenty-seven species in six genera have been collected from hosts with no prior louse records; many of these species are undescribed. For feather mites, 20 families, 73 genera, 134 named species, and 38 undescribed species are known to occur, and an additional 13 genera and 39 species are expected to be found eventually on these hosts in Canadian grasslands. Many populations and species of grassland-breeding birds are endangered in North America, and it is clear that should they be lost, many species of lice and mites would disappear with them.

**Résumé.** De très nombreuses espèces d'oiseaux nichent dans les prairies canadiennes et chacune est l'hôte d'une ou de plusieurs espèces de poux et d'acariens. Ce chapitre présente une liste des espèces connues ou prévues de poux d'oiseaux (Phthiraptera : Amblycera, Ischnocera) et d'acariens (Acari : Analgoidea, Pterolichoidea) répertoriées chez 160 espèces d'oiseaux nichant dans les habitats terrestres ou aquatiques du biome des prairies, en Alberta, en Saskatchewan et au Manitoba. La liste recense au total quatre familles, 54 genres et 183 espèces et sous-espèces décrites. Compte tenu des données recueillies sur les hôtes ailleurs en Amérique du Nord, on s'attend par ailleurs à découvrir 63 espèces supplémentaires de ces insectes. Vingt-sept espèces et six genres ont été répertoriés sur des hôtes au sujet desquels il n'existait aucune donnée concernant les poux d'oiseaux. Plusieurs de ces espèces n'avaient jamais été décrites. S'agissant des acariens, on a confirmé la présence de 20 familles, 73 genres, 134 espèces décrites et 38 espèces non décrites, et on soupçonne la présence sur les hôtes aviaires des prairies canadiennes de 13 genres et de 39 espèces supplémentaires. Plusieurs des populations et des espèces d'oiseaux qui se reproduisent dans les Prairies sont menacées en Amérique du Nord, et il est clair que si ces espèces venaient à disparaître, de nombreuses espèces de poux et d'acariens disparaîtraient également.

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## Introduction

Many birds that are grassland specialists nest only in areas of continuous grass. However, grasslands offer a diversity of additional habitats, including bluffs of trees, coulees, wetlands, pothole lakes, streams, and rivers. In combination, this patchwork supports a considerable diversity of birds that nest in suitable habitat wherever it occurs. Cultivation for agricultural production and fragmentation of grassland ecosystems have had a major impact on the welfare of these nesting birds, and indeed, grassland specialists are among the species most seriously affected by human activity in North America (Herkert 1995).

As concerns for conservation of grassland birds increase, our understanding of factors affecting their populations has also increased (Koper and Nudds 2011). Considerable attention has been focused on nesting success as affected by habitat fragmentation, especially related to the impact of predation (see review by Stephens *et al.* 2003). However, the role played by parasites and other symbionts on breeding success and fitness in avian populations has largely been ignored. From the time it hatches until it dies, each bird is a flying menagerie of associated internal and external symbionts. It experiences a dynamic relationship with mites, lice, flies, fleas, bugs, protists, viruses, nematodes, trematodes, tapeworms, and acanthocephalans (Rothschild and Clay 1953), changing in species and numerical composition depending on the age and fitness of the host, nature of association with conspecifics, season, food, habitat, and attack by arthropod vectors. And of course, this impressive diversity of associates is largely unseen by most people, even many of those who work closely with the birds. Conversely, declining host populations may also play a role in the decline and even the extinction of ectosymbionts, but this aspect of the host–symbiont relationship has received relatively little attention (Rózsa 1992; Koh *et al.* 2004; Whiteman and Parker 2005) compared with that given to declines and extinctions in bird populations. Considering that each bird is host to such tremendous diversity of symbionts (Rothschild and Clay 1953), it is worthwhile to explore the status of this diversity in grassland birds in Canada.

Galloway and Danks (1990) emphasized the deficiency in our knowledge of ectosymbionts of birds in Canada, especially for feather mites and chewing lice. These two groups are taxonomically and ecologically diverse, with the potential to elucidate important evolutionary and phylogenetic relationships in their hosts (Marshall 1981; Johnson and Clayton 2003; Proctor 2003). Some species (i.e., ectoparasites) may affect the health and fitness of their hosts, an important consideration for host species at risk. Conversely, a reduction in bird host populations may have a major impact on the survival of host-dependent species of ectosymbionts. There has not been a review of species of these arthropod groups in Canada since Wheeler and Threlfall (1989). Given recent published and unpublished studies on the biodiversity of these important ectosymbionts, it is our objective to summarize the current status of our knowledge about chewing lice and feather mites known or likely to be associated with birds nesting in grasslands in the Canadian Prairie Provinces.

## Scope of the Study

The first challenge in this review was to decide what constitutes a “grassland” bird. We chose to include species that breed within areas of continuous grassland in Manitoba, Saskatchewan, and Alberta, including shortgrass, mixedgrass, and tallgrass prairie, as described by Shorthouse and Larson (2010: Fig. 1). We also include forest birds that breed

in shrubbery, bluffs, and coulees in grasslands, as well as water birds that breed in and along wetlands and waterways within grassland habitats. Species that migrate through grasslands to nest in the boreal, subarctic, or arctic regions are not included in this survey. Species introduced into North America (e.g., ring-necked pheasant, rock pigeon, house sparrow) are not included, though some do nest in our defined habitats in grasslands. Our species list was drawn from various sources, primarily Godfrey (1986), Carey *et al.* (2003), and Penner (2007). In total, we include lice and mites associated with 160 species of birds that nest in grasslands in Canada. Nomenclature for birds follows the American Ornithologists' Union (1998 and supplements).

### Sources of Data

Both published and new records for ectosymbionts are included in this review. Nomenclature for chewing lice follows Price *et al.* (2003). Undescribed louse species are included in our list; where genera are in need of extensive taxonomic revision (e.g., *Menacanthus* (from Galliformes), *Anaticola*, *Brueelia*, *Craspedorrhynchus*, *Philopterus*), species names for taxa known to occur on certain bird hosts are assigned on the basis of host association, with the understanding that nomenclatural changes are expected. Nomenclature for feather mites (Acari: Astigmatina: Analgoidea, Pterolichoidea) follows Gaud and Atyeo (1996) with these exceptions: recognition of Pteronyssidae as a family rather than as a subfamily of the Avenzoariidae (Mironov 2001), addition of genera described since 1996 (e.g., Mironov *et al.* 2007; Valim and Hernandez 2010), and placement of those families previously in the Freyanoidea within the Pterolichoidea (OConnor 2009). Feather mite records include described species, undescribed and clearly new species (indicated by “n. sp.” in tables), and genus-level records for species represented only by a stage or sex insufficient to assign to species (indicated by “sp.” in tables; e.g., most *Proctophyllodes* spp. can be identified only from adult males). Published records of feather mites and lice are not included for hosts where specific provincial locations are not cited in publications (e.g., “Canada”), with the exception of *Goniodes cupido*. This species was reported infesting Greater Prairie Chicken from Canada by Emerson (1951); since this species occurred almost entirely in prairie grasslands in Canada, it seems warranted to include it here, despite its host having been extirpated. All records are included for Alberta, Saskatchewan, and Manitoba, although collections may not necessarily have been from locations strictly speaking within grassland habitats, e.g., Winnipeg. New collections of ectosymbionts were gathered from 1991 to 2012 primarily in Manitoba and Alberta by TDG and HCP, respectively. Birds were salvaged from wildlife hospitals, from provincial and federal wildlife agencies, and from the general public and were held under research permits issued to TDG and HCP. Ectosymbionts were collected by washing birds in warm soapy water following the techniques described by Mironov and Galloway (2002). Ectosymbionts were sorted from washed samples and preserved in 70% or 95% ethanol. Lice were prepared onto microscope slides using the technique of Richards (1964) for identification. Feather mites were mounted in either Hoyer's medium or in polyvinyl alcohol (PVA; cat. #6371A, BioQuip, Rancho Dominguez, California) after clearing in 85% lactic acid for 12–24 hours. Voucher specimens for all taxa are variously deposited in the J.B. Wallis/R.E. Roughley Museum of Entomology (University of Manitoba, Winnipeg), the E.H. Strickland Museum (University of Alberta, Edmonton), the Canadian National Collection (Agriculture and Agri-Food Canada, Ottawa), and the Zoological Institute of Parasitology (St. Petersburg, Russia).

## Grassland Birds

From our criteria for grassland birds, we include 160 species representing 16 orders, 44 families, and 114 genera (see Tables 1–6). Only four orders include more than 10 species, the Passeriformes (77 spp.), Charadriiformes (19 spp.), Anseriformes (17 spp.), and Accipitriformes (13 spp.). Five orders are represented by only one species (Suliformes, Columbiformes, Cuculiformes, Apodiformes, and Coraciiformes). Five species are listed federally as endangered (Burrowing Owl, Greater Sage Grouse, Piping Plover, Mountain Plover, and Sage Thrasher), five as threatened (Peregrine Falcon, Sprague's Pipit, Barn Swallow, Bobolink, and Loggerhead Shrike), and two as species of special concern (Long-billed Curlew and McCown's Longspur) (Committee on the Status of Endangered Wildlife in Canada (COSEWIC): [http://www.cosewic.gc.ca/eng/sct5/index\\_e.cfm](http://www.cosewic.gc.ca/eng/sct5/index_e.cfm)). One species, the Greater Prairie Chicken, is listed as extirpated in Canada.

Most birds examined for this study were opportunistically salvaged and none were actively collected for this study. Consequently, diversity and sample sizes for each species vary widely; sample sizes range from one (e.g., Forster's Tern, Burrowing Owl, Ferruginous Hawk, Bobolink) to 504 (American Robin) and are much larger for birds from Manitoba than from Alberta. For those bird species included in the tables, 33 (20.6% of the 160 species included) were not sampled by TDG or HCP; ectosymbionts associated with these species are from records in the published literature. Some of these unexamined species are grassland specialists (e.g., Sage Grouse, Sage Thrasher, Sprague's Pipit), while others are uncommon or at the northern limit of their range (e.g., White-faced Ibis, Black-necked Stilt, Piping Plover).

## Phthiraptera (Lice)

Chewing lice are permanent ectoparasites that infest birds and mammals. Chewing lice of birds attach their eggs to the feathers of their hosts: the shafts, down, barbs, or in some cases, inserted between the barbs and even inside the shafts, depending on the species of lice. They are hemimetabolous (develop gradually with each moult), with three juvenile instars, not always overlapping exactly with the regions of the body occupied by adults. However, most species occupy specific regions of their host's body; some species apparently feed on feathers in one region of the body, while laying their eggs on feathers in another.

Chewing lice on birds belong to two suborders, Amblycera and Ischnocera. The breakdown of the taxa recorded here that infest grassland birds is shown in Table 1. In addition to the 183 species of lice recorded within the Prairies Ecozone, an additional 63 species are recorded in the literature from the grassland birds listed (Table 2). Therefore, the total of recorded plus expected species of chewing lice is 247. A brief account of each family follows.

### *Amblycera*

#### *Laemobothriidae*

There is only one genus in this family, *Laemobothrion*, revised in part by Nelson and Price (1965). Species in this family are the largest of lice, *L. vulturis* having a total body length >1.0 cm (Nelson and Price 1965). They infest Accipitriformes and Falconiformes (vultures, accipitrids, falconids, and pandionids, subgenus *Laemobothrion*) and Gruiformes (subgenus *Eulaemobothrion*) in Canada (Table 2) and are seldom collected in large

**Table 1.** Breakdown of chewing lice (Phthiraptera) recorded in the present study infesting grassland birds in Alberta, Saskatchewan, and Manitoba (see Table 5 for full list).

Suborder	Families	Number of Genera	Number of Species
Amblycera	Laemobothriidae	1	4
	Menoponidae	17	67
	Ricinidae	2	8
Ischnocera	Philopteridae	34	104
TOTAL		54	183

numbers. In particular, the prevalence and intensity of infestation for *Laemobothrion* spp. on hawks, eagles, and falcons in grassland regions seem to be extremely low.

### *Menoponidae*

Members of this family are relatively mobile lice, readily abandoning a dead host (Johnson and Clayton 2003). As a group, they have diverse feeding habits, as many feed not only on feathers, but on blood and serum as well. Some species (e.g., *Austromenopon*) may even serve as intermediate hosts for filarioid nematode parasites of their hosts (Bartlett and Anderson 1989). Host grooming usually keeps louse populations in check, but occasionally intensity of infestation can reach extraordinary numbers. For example, a Great Blue Heron from Manitoba was infested with nearly 25,000 *Ciconiphilus decimfasciatus* (TDG, unpublished).

Seventeen genera of menoponid chewing lice are recorded here from grassland birds (*Actornithophilus*, *Austromenopon*, *Bonomiella*, *Ciconiphilus*, *Colpocephalum*, *Cuculiphilus*, *Eidmanniella*, *Hohorstiella*, *Holomenopon*, *Kurodaia*, *Machaerilaemus*, *Menacanthus*, *Myrsidea*, *Nosopon*, *Piagetiella*, *Pseudomenopon*, and *Trinoton*; Table 2). The only two genera expected but not yet recorded are *Plegadiphilus* and *Amysrsidea*. The former is represented by *P. plegadis*, which infests White-faced Ibis, but to our knowledge, no specimens of this host have been examined for lice in Canada. *Amysrsidea perdicis* on the other hand, is known from a number of species of grouse (Price *et al.* 2003); only Sharp-tailed Grouse has been examined in this study, and none were infested with *A. perdicis*.

Five genera account for more than half (39) the recorded species of Menoponidae infesting grassland birds. Ten species of *Colpocephalum* are included here (Table 2), infesting the closely related hawks, eagles, falcons, and Turkey Vulture. Two species also infest birds in other orders, that is, *C. unciferum*, which infests American White Pelican, and *C. fregili*, which infests Common Raven. Some *Colpocephalum* spp. feed on feathers and act as predators (Nelson and Murray 1971). There are eight species each in the genera *Menacanthus* (many of which feed on blood) and *Myrsidea*, the former infesting passeriforms and piciforms, the latter infesting only passeriforms in Canadian grasslands. As is the case in many genera of lice, some species infest only one or a few related hosts. For example, *Kurodaia haliaeeti* infests only the Osprey; *M. tyranni*, reported here from two species of kingbirds on the Prairies, has been reported to infest five species of tyrannids (Price *et al.* 2003). At the opposite extreme, *M. eurysternus* infests at least

118 host species in 20 families worldwide (Price 1975, 1977). Seven species each are recorded for *Actornithophilus* and *Austromenopon*, infesting charadriiform birds. The remaining 26 species are distributed among 12 genera, with one to four species in each genus (Table 2). Among them are some of the most intriguing of chewing lice. Two species of *Trinoton* infest ducks and geese; they are heavily pigmented and among the largest and most conspicuous of lice. Some species of *Actornithophilus* live inside the feather quills on their charadriiform hosts (Rothschild and Clay 1953), though little is known about the role of this peculiar niche in the life cycle of the lice. There are two species of *Piagetiella*, the adults of which attach to the inner lining of the pouches of pelicans and some cormorants. *Machaerilaemus* spp. seem to infest various passeriform birds (Table 2) at very low levels of prevalence and intensity, which poses interesting questions about the sustainability of louse populations that typically exhibit low infestation parameters.

### ***Ricinidae***

There are only two genera of ricinids recorded from grassland birds, *Ricinus* and *Trochiloecetes*. The former was revised by Nelson (1972), and his monograph stands as the seminal work on this genus in North America. *Ricinus* spp. are relatively large and infest a variety of passeriforms, probably feeding largely on blood and serum. These lice are typically present at low levels of prevalence and intensity and are therefore seldom collected for some hosts, even when reasonable sample sizes are obtained. Seven species of *Ricinus* are recorded infesting grassland birds in this study, and at least 10 additional species are expected (Table 2).

One species of ricinid in the genus *Trochiloecetes* has been collected from Ruby-throated Hummingbird in Manitoba (TDG, unpublished). Another may be present: Osborn's original description of *Physostoma lineatum* was deficient and its types are most likely lost (Carriker 1960). However, we believe this species may belong to the genus *Trochiloecetes* and not *Trochiliphagus* where Carriker (1960) placed it, or *Ricinus*, where it was placed by Rheinwald (2007). A formal designation cannot be made until a detailed comparison of additional specimens is conducted. Virtually nothing is known about the biology of this species of *Trochiloecetes*, other than that it does not appear to feed on feathers.

### ***Ischnocera***

#### ***Philopteridae***

Members of this family exhibit an impressive range of anatomical and behavioural specialization. Although most seem to feed primarily on feathers, some regularly feed on blood (e.g., *Ornithobius goniopleurus* as adults and nymphs). Philopterids have a large crop extending from the posterior region of the foregut. This crop in many species is often found packed full of uniformly cut pieces of feathers (Johnson and Clayton 2003). This is particularly the case in species of *Philopterus* and *Strigiphilus*, to the point that preparation of clean specimens onto slides becomes a challenge. Many of these lice have transovarially transmitted endosymbiotic bacteria that may play a role in the digestion of these feather pieces (Johnson and Clayton 2003; Perotti *et al.* 2008). The body shape in some species of philopterids is elongate and associated with rapid movement over the surfaces of the body contour or wing feathers (e.g., *Anaticola* spp.), whereas others are rounded and slower moving (e.g., *Anatoecus* spp.) and may be largely restricted to the head and neck regions (Grossi *et al.* In press), where pressure from host grooming is less strenuous. Philopterids typically have simple, filiform antennae, compared with clubbed antennae in the Amblycera. However, in some genera of philopterids, the antennae are

sexually dimorphic (e.g., *Fulicoffula*, *Pectinopygus*), the males having modified segments to accommodate grasping the base of the abdomen of females during copulation (Séguy 1944; TDG, unpublished).

This family of lice is the most diverse on grassland birds examined here, with 34 genera and 105 species reported. The genus *Brueelia* infests woodpeckers and perching birds and is the most species rich, with 18 species recorded on our grassland birds, followed by the genus *Philopterus*, with 11 species (Tables 2 and 5). These two genera also account for the greatest number of new host records and undescribed species in the current survey. Most philopterids are relatively host specific, with only one species of each genus associated with a host or group of related hosts. However, in some cases, there are two species in the same genus that infest the same host individual: *Anatoecus dentatus* and *A. penicillatus* (the only species of louse in this study that appears to be an introduced, exotic species to North America) infesting Canada Goose (Grossi *et al.* In press); *Columbicola baculoides* and *C. macrourae* infesting Mourning Dove (Galloway and Palma 2008); *Degeeriella fulva* and *D. regalis* infesting Red-tailed Hawk (Clay 1958; TDG, unpublished); *Strigiphilus cursor* and *S. oculatus* infesting Great Horned Owl (Clayton and Price 1984; TDG, unpublished). In one particularly interesting case, two pairs of species in each of two genera infest the same host, the Sora: *Fulicoffula americana* and *F. distincta*; *Rallicola mystax* and *R. subporzanae* (Galloway 2004).

### Feather Mites

Like feather lice, feather mites are permanent ectosymbionts of birds and do not have any life history stage living off of the host. They have been found from all orders of birds with the exception of Rheiformes. Depending on the taxon, they occupy the vanes of flight feathers, downy parts of flight and contour feathers, insides of quills, or surface layers of the skin (Dabert and Mironov 1999). Most feather mites appear to be commensals, neither harming nor benefiting the host, that feed on secretions from the preen gland (uropygial oil) that the host spreads on the feather while grooming, together with whatever small particles are caught on the feather barbs (e.g., fungal spores, pollen, algae, diatoms: Dubinin 1951; Proctor 2003; Galván *et al.* 2012). Some species of quill-dwelling feather mites may cause damage by chewing on the spongy material inside the rachis (central feather shaft) and weakening the feathers, and vane-dwelling mites can cause irritation in captive hosts if these mites develop large population sizes (Gaud and Atyeo 1996).

Feather mites belong to two superfamilies, Analgoidea and Pterolichoidea, within the unranked clade Psoroptidia of Astigmatina (OConnor 2009). Pterolichoidea are found mainly on non-passerine birds, whereas analgoidea are diverse on both passerines and non-passerines. The breakdown of the taxa recorded from Canadian grassland birds is shown in Table 3 (species not found but expected to occur are listed in Tables 4 and 6). Given that almost half of the host species examined are from the Passeriformes, it is not surprising that we recorded more analgoidea (94 spp.) than pterolichoidea (39 spp.). Besides the 73 genera and 134 species of mites recorded from birds examined in this study, an additional 13 genera and 39 species are noted in the literature from the birds listed, bringing the total of recorded plus expected species of feather mites to 86 genera and 173 species. Little is known about the biology of feather mites (Proctor 2003), and so the following summary is more taxonomically than ecologically focused, with host ranges coming mainly from Gaud and Atyeo (1996).



**Table 2.** Published records, new records, and expected records for chewing lice on birds breeding in grassland biomes of Alberta (A), Saskatchewan (S), and Manitoba (M). Numerical superscripts for recorded species coincide with provinces (this study) and with references provided at the end of the table; numerical superscripts for expected records are for species other than those provided in Price *et al.* (2003). n/a indicates that no information is available. The four-letter acronym follows in parentheses after the common name of each bird ([http://www.birdpop.org/DownloadDocuments/Alpha\\_codes\\_english.pdf](http://www.birdpop.org/DownloadDocuments/Alpha_codes_english.pdf)).

Bird Hosts	Recorded and Expected Species
<b>PODICIPEDIFORMES</b>	
<b>Podicipedidae</b>	
<i>Podilymbus podiceps</i> (Linnaeus), Pied-billed Grebe (PBGR)	<b>Recorded:</b> <i>Pseudomenopon dolium</i> (Rudow) <sup>M</sup> ; <i>Aquanirmus podilymbus</i> Edwards <sup>M</sup> <b>Expected:</b> n/a
<i>Podiceps grisegena</i> (Boddaert), Red-necked Grebe (RNGR)	<b>Recorded:</b> <i>Pseudomenopon dolium</i> (Rudow) <sup>M</sup> <b>Expected:</b> <i>Aquanirmus emersoni</i> Edwards
<i>Podiceps auritus</i> (Linnaeus), Horned Grebe (HOGR)	<b>Recorded:</b> <i>Aquanirmus bucomfishi</i> Edwards <sup>M</sup> <b>Expected:</b> <i>Pseudomenopon dolium</i> (Rudow)
<i>Podiceps nigricollis</i> Brehm, Eared Grebe (EAGR)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Laemobothrion (Eulaemobothrion) simile</i> Kellogg; <i>Pseudomenopon dolium</i> (Rudow); <i>Aquanirmus americanus</i> (Kellogg & Chapman)
<i>Aechmophorus occidentalis</i> (Lawrence), Western Grebe (WEGR)	<b>Recorded:</b> <i>Pseudomenopon dolium</i> (Rudow) <sup>M</sup> ; <i>Aquanirmus occidentalis</i> Edwards <sup>A,1,A,M</sup> <b>Expected:</b>
<i>Aechmophorus clarkii</i> (Lawrence), Clark's Grebe* (CLGR)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<b>SULIFORMES</b>	
<b>Phalacrocoracidae</b>	
<i>Phalacrocorax auritus</i> (Lesson), Double-crested Cormorant (DCCO)	<b>Recorded:</b> <i>Eidmanniella pellucida</i> (Rudow) <sup>A;S,2,M</sup> ; <i>Piagetiella incomposita</i> (Kellogg & Chapman) <sup>S,2</sup> ; <i>Pectinopygus farallonii</i> (Kellogg) <sup>A;S,2,M</sup> <b>Expected:</b>
<b>PELECANIFORMES</b>	
<b>Pelecanidae</b>	
<i>Pelecanus erythrorhynchos</i> Gmelin, American White Pelican (AWPE)	<b>Recorded:</b> <i>Colpocephalum unciferum</i> Kellogg <sup>M</sup> ; <i>Piagetiella peralis</i> (Leidy) <sup>A,4,A;S,3,4;M,21,M</sup> ; <i>Pectinopygus tordoffi</i> Elbel & Emerson <sup>M</sup> <b>Expected:</b>
<b>Ardeidae</b>	
<i>Botaurus lentiginosus</i> (Rackett) American Bittern (AMBI)	<b>Recorded:</b> <i>Ciconiphilus decimfasciatus</i> (Boisduval & Lacordaire) <sup>M</sup> ; <i>Ardeicola botauri</i> (Osborn) <sup>M</sup> <b>Expected:</b>
<i>Ardea herodias</i> Linnaeus, Great Blue Heron (GBHE)	<b>Recorded:</b> <i>Ciconiphilus decimfasciatus</i> (Boisduval & Lacordaire) <sup>M</sup> ; <i>Ardeicola cruscula</i> (Linnaeus) <sup>M</sup> <b>Expected:</b>
<i>Butorides virescens</i> (Linnaeus), Green Heron (GRHE)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Ciconiphilus butoridiphagus</i> Carriker; <i>Ardeicola nigra</i> Tuff
<i>Nycticorax nycticorax</i> (Linnaeus), Black-crowned Night-Heron (BCNH)	<b>Recorded:</b> <i>Ciconiphilus decimfasciatus</i> (Boisduval & Lacordaire) <sup>M</sup> <b>Expected:</b>

**Threskiornithidae**

*Plegadis chihi* (Vieillot),  
White-faced Ibis\* (WFIB)

**Recorded:** n/a  
**Expected:** *Colpocephalum leptopygos* Nitzsch; *Plegadiphilus plegadis* (Dubinin); *Ardeicola raphidius* (Nitzsch); *Ibidoecus bisignatus* (Nitzsch)

**ANSERIFORMES**

**Anatidae**

*Branta canadensis* (Linnaeus),  
Canada Goose (CAGO)

**Recorded:** *Ciconiphilus pectiniventris* (Harrison)<sup>M</sup>; *Holomenopon leucoxanthum* (Burmeister)<sup>M</sup>; *Trinoton anserinum* (Fabricius)<sup>M</sup>; *Anaticola anseris* (Linnaeus)<sup>M</sup>; *Anatoecus dentatus* (Scopoli)<sup>M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>M</sup>; *Anatoecus penicillatus* Kéler<sup>M</sup>; *Ornithobius goniopleurus* Denny<sup>A; M</sup>  
**Expected:**

*Aix sponsa* (Linnaeus),  
Wood Duck (WODU)

**Recorded:** *Holomenopon clauseni* Price<sup>M</sup>; *Holomenopon clypeilargum* Eichler<sup>M</sup>; *Trinoton querquedulae* (Linnaeus)<sup>A; 5; M</sup>; *Anaticola mergiserrati* (DeGeer)<sup>M</sup>; *Anatoecus dentatus* (Scopoli)<sup>M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>M</sup>  
**Expected:**

*Anas strepera* Linnaeus,  
Gadwall (GADW)

**Recorded:** *Trinoton querquedulae* (Linnaeus)<sup>A; M; 6; M</sup>; *Anaticola crassicornis* (Scopoli)<sup>A; M; 6; M</sup>; *Anatoecus dentatus* (Scopoli)<sup>M; 6; M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>M; 6; M</sup>  
**Expected:** *Holomenopon clypeilargum* Eichler; *Holomenopon leucoxanthum* (Burmeister); *Holomenopon setigerum* (Blagoveshtchensky)

*Anas americana* Gmelin,  
American Wigeon (AMWI)

**Recorded:** *Trinoton querquedulae* (Linnaeus)<sup>M</sup>; *Anaticola crassicornis* (Scopoli)<sup>A; 7; 5; M; 6</sup>; *Anatoecus dentatus* (Scopoli)<sup>M; 6</sup>  
**Expected:** *Holomenopon clypeilargum* Eichler; *Holomenopon leucoxanthum* (Burmeister)

*Anas platyrhynchos* Linnaeus  
Mallard (MALL)

**Recorded:** *Holomenopon leucoxanthum* (Burmeister)<sup>M</sup>; *Holomenopon maxbeieri* Eichler<sup>M</sup>; *Trinoton querquedulae* (Linnaeus)<sup>A; 7; 5; A; M; 6; M</sup>; *Anaticola crassicornis* (Scopoli)<sup>A; M; 6; M</sup>; *Anatoecus dentatus* (Scopoli)<sup>A; 5; M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>M</sup>  
**Expected:**

*Anas discors* Linnaeus,  
Blue-winged Teal (BWTE)

**Recorded:** *Holomenopon clauseni* Price<sup>M</sup>; *Holomenopon clypeilargum* Eichler<sup>M</sup>; *Trinoton querquedulae* (Linnaeus)<sup>M; 6; M</sup>; *Anaticola crassicornis* (Scopoli)<sup>A; M; 6; M</sup>; *Anatoecus dentatus* (Scopoli)<sup>M; 6; M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>A; M</sup>  
**Expected:** *Holomenopon setigerum* (Blagoveshtchensky)

*Anas clypeata* Linnaeus, Northern  
Shoveler (NOSH)

**Recorded:** *Trinoton querquedulae* (Linnaeus)<sup>M; 6</sup>; *Holomenopon setigerum* (Blagoveshtchensky)<sup>M</sup>; *Anaticola crassicornis* (Scopoli)<sup>M; 6</sup>; *Anatoecus dentatus* (Scopoli)<sup>M; 6; M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>M</sup>  
**Expected:** *Holomenopon clypeilargum* Eichler; *Holomenopon leucoxanthum* (Burmeister)

*Anas acuta* Linnaeus,  
Northern Pintail (NOPI)

**Recorded:** *Trinoton querquedulae* (Linnaeus)<sup>M; 6; M</sup>; *Anaticola crassicornis* (Scopoli)<sup>M; 6; M</sup>; *Anatoecus dentatus* (Scopoli)<sup>M; 6</sup>  
**Expected:** *Holomenopon acutae* Price; *Holomenopon clypeilargum* Eichler; *Holomenopon leucoxanthum* (Burmeister); *Holomenopon setigerum* (Blagoveshtchensky); *Anatoecus icterodes* (Nitzsch)

*Anas crecca* Linnaeus,  
American Green-winged Teal  
(AGWT)

**Recorded:** *Holomenopon clypeilargum* Eichler<sup>M</sup>; *Holomenopon leucoxanthum* (Burmeister)<sup>M</sup>; *Trinoton querquedulae* (Linnaeus)<sup>M; 6; M</sup>; *Anaticola crassicornis* (Scopoli)<sup>M; 6; M</sup>; *Anatoecus dentatus* (Scopoli)<sup>M; 6; M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>M</sup>  
**Expected:** *Holomenopon setigerum* (Blagoveshtchensky)

- Anas cyanoptera* Vieillot,  
Cinnamon Teal\* (CITE)  
**Recorded:** n/a  
**Expected:** *Holomenopon clypeilargum* Eichler; *Holomenopon leucoxanthum* (Burmeister); *Holomenopon setigerum* (Blagoveshtchensky); *Trinoton querquedulae* (Linnaeus); *Anaticola crassicornis* (Scopoli); *Anatoecus dentatus* (Scopoli); *Anatoecus icterodes* (Nitzsch)
- Aythya valisineria* (Wilson),  
Canvasback (CANV)  
**Recorded:** *Holomenopon leucoxanthum* (Burmeister)<sup>M</sup>; *Trinoton querquedulae* (Linnaeus)<sup>M</sup>; *Acidoproctus moschati* (Linnaeus)<sup>M</sup>; *Anaticola mergiserrati* (De Geer)<sup>M</sup>; *Anatoecus dentatus* (Scopoli)<sup>M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>M</sup>  
**Expected:** *Holomenopon clypeilargum* Eichler
- Aythya americana* (Eyton),  
Redhead (REDH)  
**Recorded:** *Holomenopon leucoxanthum* (Burmeister)<sup>M,6,M</sup>; *Trinoton querquedulae* (Linnaeus)<sup>M,6,M</sup>; *Acidoproctus moschati* (Linnaeus)<sup>M</sup>; *Anaticola mergiserrati* (De Geer)<sup>M,6,M</sup>; *Anatoecus dentatus* (Scopoli)<sup>M,6,M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>M</sup>  
**Expected:**
- Aythya affinis* (Eyton),  
Lesser Scaup (LESC)  
**Recorded:** *Holomenopon leucoxanthum* (Burmeister)<sup>M</sup>; *Anaticola mergiserrati* (DeGeer)<sup>M</sup>; *Anatoecus dentatus* (Scopoli)<sup>M</sup>  
**Expected:** *Trinoton querquedulae* (Linnaeus); *Acidoproctus moschati* (Linnaeus)
- Bucephala albeola* (Linnaeus),  
Bufflehead (BUFF)  
**Recorded:** *Anaticola clangulae* (Fabricius [O.]<sup>M</sup>); *Anatoecus icterodes* (Nitzsch)<sup>M</sup>  
**Expected:** *Holomenopon bucephalae* Price; *Holomenopon clauseni* Price; *Holomenopon leucoxanthum* (Burmeister); *Trinoton querquedulae* (Linnaeus); *Anatoecus dentatus* (Scopoli)
- Bucephala clangula* (Linnaeus),  
Common Goldeneye (COGO)  
**Recorded:** *Trinoton querquedulae* (Linnaeus)<sup>A</sup>; *Anaticola clangulae* (Fabricius [O.]<sup>M</sup>); *Anatoecus dentatus* (Scopoli)<sup>M</sup>; *Anatoecus dentatus* (Scopoli)<sup>M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>A,M</sup>  
**Expected:** *Holomenopon bucephalae* Price; *Ciconiphilus cygni* Price & Beer
- Melanitta fusca* (Linnaeus),  
White-winged Scoter (WWSC)  
**Recorded:** *Trinoton querquedulae* (Linnaeus)<sup>M</sup>; *Anaticola mergiserrati* (De Geer)<sup>M</sup>  
**Expected:** *Holomenopon loomisii* (Kellogg); *Anatoecus dentatus* (Scopoli); *Anatoecus icterodes* (Nitzsch)
- Oxyura jamaicensis* (Gmelin),  
Ruddy Duck (RUDU)  
**Recorded:** *Holomenopon leucoxanthum* (Burmeister)<sup>M</sup>; *Anaticola crassicornis* (Scopoli); *Anatoecus dentatus* (Scopoli)<sup>M</sup>; *Anatoecus icterodes* (Nitzsch)<sup>M</sup>  
**Expected:** *Trinoton querquedulae* (Linnaeus)

## ACCIPITRIFORMES

### Cathartidae

- Cathartes aura* (Linnaeus),  
Turkey Vulture (TUVU)  
**Recorded:** *Colpocephalum kelloggi* Osborn<sup>M</sup>; *Cuculiphilus alternatus* (Osborn)<sup>M</sup>; *Laemobothrion glutinans* Nitzsch [In Giebel]<sup>M</sup>; *Falcolipeurus marginalis* (Osborn)<sup>M</sup>  
**Expected:**

### Accipitridae

- Circus cyaneus* (Linnaeus),  
Northern Harrier (NOHA)  
**Recorded:** *Colpocephalum turbinatum* Denny<sup>M</sup>; *Nosopon lucidum* (Rudow)<sup>M</sup>; *Degeeriella fusca* (Denny)<sup>M</sup>  
**Expected:** *Laemobothrion maximum* (Scopoli); *Kurodaia fulvofasciata* (Piaget)
- Accipiter striatus* Vieillot,  
Sharp-shinned Hawk (SSHA)  
**Recorded:** *Colpocephalum nanum* Piaget<sup>M</sup>; *Craspedorrhynchus* sp. 3<sup>M</sup>; *Degeeriella nisus* (Giebel)<sup>A,M</sup>  
**Expected:** *Nosopon lucidum* (Rudow)<sup>8</sup>

*Accipiter cooperii* (Bonaparte),  
Cooper's Hawk (COHA)

**Recorded:** *Colpocephalum nanum* Piaget<sup>M</sup>; *Nosopon lucidum* (Rudow)<sup>M</sup>; *Craspedorrhynchus subhaematopus* Emerson<sup>M</sup>; *Degeeriella vagans* (Giebel)<sup>M</sup>  
**Expected:** *Laemobothrion maximum* (Scopoli)

*Buteo swainsoni* Bonaparte,  
Swainson's Hawk (SWHA)

**Recorded:** *Laemobothrion maximum* (Scopoli)<sup>M</sup>; *Colpocephalum turbinatum* Denny<sup>M</sup>; *Craspedorrhynchus* sp. 4<sup>M</sup>; *Degeeriella regalis* (Giebel)<sup>M</sup>  
**Expected:** *Kurodaia fulvofasciata* (Piaget)

*Buteo jamaicensis* (Gmelin),  
Red-tailed Hawk (RTHA)

**Recorded:** *Colpocephalum nanum* Piaget<sup>M</sup>; *Colpocephalum turbinatum* Denny<sup>M</sup>; *Kurodaia fulvofasciata* (Piaget)<sup>M</sup>; *Nosopon lucidum* (Rudow)<sup>M</sup>; *Laemobothrion maximum* (Scopoli)<sup>A,8;M</sup>; *Craspedorrhynchus americanus* Emerson<sup>M</sup>; *Degeeriella fulva* (Giebel)<sup>A,M</sup>; *Degeeriella regalis* (Giebel)<sup>A,8;M</sup>  
**Expected:** *Colpocephalum napiforme* Rudow

*Buteo regalis* (Gray),  
Ferruginous Hawk (FEHA)

**Recorded:** *Craspedorrhynchus hirsutus* Carriker<sup>A</sup>; *Degeeriella fulva* (Giebel)<sup>A</sup>  
**Expected:** *Laemobothrion maximum* (Scopoli)

*Haliaeetus leucocephalus* (Linnaeus),  
Bald Eagle (BAEA)

**Recorded:** *Colpocephalum flavescens* (De Haan)<sup>M</sup>; *Colpocephalum turbinatum* Denny<sup>M</sup>; *Kurodaia fulvofasciata* (Piaget)<sup>M</sup>; *Craspedorrhynchus halietai* (Osborn)<sup>M</sup>; *Degeeriella discocephalus* (Burmeister)<sup>M</sup>  
**Expected:** *Laemobothrion vulturis* (Fabricius)

*Aquila chrysaetos* (Linnaeus),  
Golden Eagle (GOEA)

**Recorded:** *Colpocephalum flavescens* (De Haan)<sup>A,8</sup>; *Degeeriella discocephalus* (Burmeister)<sup>M</sup>  
**Expected:** *Colpocephalum impressum* Rudow; *Laemobothrion maximum* (Scopoli); *Laemobothrion vulturis* (Fabricius); *Degeeriella aquilarum* Eichler; *Degeeriella fulva* (Giebel); *Falcolipeurus suturalis* (Rudow)

#### Pandionidae

*Pandion haliaetus* (Linnaeus),  
Osprey (OSPR)

**Recorded:** *Kurodaia haliaeeti* (Denny)<sup>M</sup>  
**Expected:** *Colpocephalum napiforme* Rudow; *Colpocephalum turbinatum* Denny; *Laemobothrion maximum* (Scopoli)

#### FALCONIFORMES

##### Falconidae

*Falco sparverius* Linnaeus,  
American Kestrel (AMKE)

**Recorded:** *Colpocephalum subzerafae* Tendeiro<sup>A,5,A</sup> (as *C. flavescens* (De Haan); <sup>M</sup>;  
*Nosopon lucidum* (Rudow)<sup>M</sup>; *Degeeriella carruthi* Emerson<sup>A,M</sup>  
**Expected:** *Laemobothrion tinnunculi* (Linnaeus)

*Falco columbarius* Linnaeus,  
Merlin (MERL)

**Recorded:** *Colpocephalum subzerafae* Tendeiro<sup>M</sup>; *Nosopon lucidum* (Rudow)<sup>M</sup>; *Craspedorrhynchus* sp. 1<sup>M</sup>; *Degeeriella rufa* (Burmeister)<sup>M</sup>  
**Expected:** *Laemobothrion tinnunculi* (Linnaeus)

*Falco mexicanus* Schlegel,  
Prairie Falcon (PRFA)

**Recorded:** *Laemobothrion tinnunculi* (Linnaeus)<sup>M</sup>; *Colpocephalum zerafae* Ansari<sup>M</sup>; *Nosopon lucidum* (Rudow)<sup>M</sup>; *Craspedorrhynchus* sp. 2<sup>M</sup>; *Degeeriella rufa* (Burmeister)<sup>M</sup>  
**Expected:** *Colpocephalum turbinatum* Denny

#### GALLIFORMES

##### Phasianidae

*Centrocercus urophasianus*  
(Bonaparte),  
Sage Grouse\* (SAGR)

**Recorded:** n/a  
**Expected:** *Goniodes centrocerci* Simon; *Lagopoecus gibsoni* Hopkins

*Tympanuchus cupido* (Linnaeus), Greater Prairie Chicken\* (GPRC) **Recorded:** n/a  
**Expected:** *Amyrsidea perdicis* (Denny); *Goniodes cupido* Rudow

*Tympanuchus phasianellus* (Linnaeus), Sharp-tailed Grouse (STGR) **Recorded:** *Goniodes nebraskensis* Carriker<sup>M,9,10,M</sup>; *Lagopoecus gibsoni* Hopkins (?)<sup>M,10</sup>  
**Expected:** *Amyrsidea perdicis* (Denny); *Lagopoecus perplexus* (Kellogg & Chapman)

## GRUIFORMES

### Rallidae

*Rallus limicola* Vieillot Virginia Rail (VIRA) **Recorded:** *Pseudomenopon scopulacorne* (Denny)<sup>M</sup>; *Rallicola kelloggi* Emerson<sup>M</sup>  
**Expected:** *Fulicoffula comstocki* (Kellogg & Chapman); *Incidifrons monachus* (Kellogg & Paine)

*Porzana carolina* (Linnaeus), Sora (SORA) **Recorded:** *Pseudomenopon scopulacorne* (Denny)<sup>A,M,11</sup>; *Fulicoffula americana* Emerson<sup>M,11</sup>; *Fulicoffula distincta* Emerson<sup>M,11</sup>; *Rallicola mystax* (Giebel)<sup>M,11</sup>; *Rallicola subporzanae* Emerson<sup>M,11</sup>  
**Expected:**

*Fulica americana* Gmelin, American Coot (AMCO) **Recorded:** *Laemobothrion atrum* (Nitzsch)<sup>A,12,M,12,M</sup>; *Pseudomenopon pilosum* (Scopoli)<sup>A,12,A,M,12,M</sup>; *Fulicoffula longipila* (Kellogg)<sup>A,12,A,M,12,M</sup>; *Incidifrons transpositus* (Kellogg)<sup>A,12,A,M,12,M</sup>; *Rallicola advenus* (Kellogg)<sup>A,12,A,M,12,M</sup>  
**Expected:**

## CHARADRIIFORMES

### Charadriidae

*Charadrius vociferus* Linnaeus, Killdeer (KILL) **Recorded:** *Actornithophilus hoplopteri* (Mjöberg)<sup>M</sup>; *Austromenopon aegialitidis* (Durrant)<sup>M</sup>; *Quadriceps boeophilus* (Kellogg)<sup>M</sup>  
**Expected:** *Saemundssonina conica conica* (Denny)

*Charadrius melodus* Ord, Piping Plover\* (PIPL) **Recorded:** n/a  
**Expected:** *Actornithophilus ochraceus* (Nitzsch); *Austromenopon aegialitidis* (Durrant); *Quadriceps macrocephalus* (Waterston); *Saemundssonina platygaster platygaster* (Denny)

*Charadrius montanus* Townsend, Mountain Plover\* (MNPL) **Recorded:** n/a  
**Expected:** *Actornithophilus ochraceus* (Nitzsch); *Quadriceps assimilis* (Piaget)

### Recurvirostridae

*Himantopus mexicanus* (Müller), Black-necked Stilt\* (BNST) **Recorded:** n/a  
**Expected:** *Actornithophilus mexicanus* Emerson; *Austromenopon himantopi* Timmermann; *Quadriceps hemichrous* (Nitzsch (In Giebel)); *Quadriceps semifissus* (Nitzsch (In Giebel))

*Recurvirostra americana* Gmelin, American Avocet (AMAV) **Recorded:** *Actornithophilus uniseriatus* (Piaget)<sup>A,5,M</sup>; *Austromenopon micrandrum* (Nitzsch (In Giebel))<sup>M</sup>; *Cirrophthirius testudinarius* (Children)<sup>A,5,M</sup>; *Quadriceps semifissus* (Nitzsch (In Giebel))<sup>M</sup>  
**Expected:** *Quadriceps zephyra* (Timmermann)

### Scolopacidae

*Gallinago delicata* (Ord), Wilson's Snipe (WISN) **Recorded:** *Austromenopon durisetosum* (Blagoveshchensky)<sup>A,M</sup>; *Rhynonirmus scolopacis* (Denny)<sup>A,M</sup>  
**Expected:** *Actornithophilus stictus* (Kellogg & Paine); *Cummingsiella ambigua* (Burmeister); *Saemundssonina kratochvili* Balát

<i>Limosa fedoa</i> (Linnaeus), Marbled Godwit (MAGO)	<b>Recorded:</b> <i>Actornithophilus limosae</i> (Kellogg) <sup>M</sup> ; <i>Austromenopon limosae</i> Timmermann <sup>M</sup> ; <i>Carduceps clayae</i> Timmermann <sup>M</sup> ; <i>Lunaceps clayae</i> Timmermann <sup>M</sup> ; <i>Rotundiceps cordatus</i> (Osborn) <sup>M</sup> ; <i>Saemundssonina</i> sp. 2 <sup>M</sup> <b>Expected:</b>
<i>Numenius americanus</i> Bechstein, Long-billed Curlew (LBCU)	<b>Recorded:</b> <i>Cummingsiella longirostricola</i> (Wilson) <sup>A,M</sup> ; <i>Lunaceps kukri</i> Gustafsson & Olsson; <i>Saemundssonina scolopacisphaeopodis humeralis</i> (Denny) <sup>A,M</sup> <b>Expected:</b> <i>Actornithophilus patellatus</i> (Piaget)
<i>Bartramia longicauda</i> (Bechstein), Upland Sandpiper* (UPSA)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Rhynonirmus infuscatus</i> (Osborn); <i>Saemundssonina scolopacisphaeopodis nearctica</i> Timmermann
<i>Actitis macularia</i> (Linnaeus), Spotted Sandpiper (SPSA)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Actornithophilus umbrinus</i> (Burmeister); <i>Quadraceps ravus</i> (Kellogg); <i>Saemundssonina platygaster frater</i> (Giebel)
<i>Catoptrophorus semipalmatus</i> (Gmelin), Willet (WILL)	<b>Recorded:</b> <i>Actornithophilus lacustris</i> Clay <sup>M</sup> ; <i>Austromenopon sachtlebeni</i> Timmermann <sup>M</sup> ; <i>Quadraceps carrikeri</i> Hopkins & Timmermann <sup>S,8</sup> ; <i>Saemundssonina</i> sp. 1 <sup>M</sup> <b>Expected:</b>
<b>Phalaropidae</b>	
<i>Phalaropus tricolor</i> (Vieillot), Wilson's Phalarope (WIPH)	<b>Recorded:</b> <i>Actornithophilus umbrinus</i> (Burmeister) <sup>A,5,M</sup> ; <i>Quadraceps fimbriatus</i> (Giebel) <sup>M</sup> <b>Expected:</b> <i>Saemundssonina tricolor</i> Carriker
<b>Laridae</b>	
<i>Larus delawarensis</i> Ord, Ring-billed Gull (RBGU)	<b>Recorded:</b> <i>Actornithophilus piceus lari</i> (Packard) <sup>M</sup> ; <i>Austromenopon transversum</i> (Denny) <sup>M</sup> ; <i>Quadraceps punctatus sublingulatus</i> Timmermann <sup>A,M</sup> ; <i>Saemundssonina lari</i> (Fabricius) <sup>A,M</sup> <b>Expected:</b>
<i>Larus californicus</i> Lawrence, California Gull* (CAGU)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Actornithophilus piceus lari</i> (Packard); <i>Austromenopon transversum</i> (Denny); <i>Quadraceps punctatus sublingulatus</i> Timmermann; <i>Saemundssonina lari</i> (Fabricius)
<i>Leucophaeus pipixcan</i> Wagler, Franklin's Gull (FRGU)	<b>Recorded:</b> <i>Actornithophilus piceus lari</i> (Packard) <sup>A,M</sup> ; <i>Austromenopon transversum</i> (Denny) <sup>M</sup> ; <i>Quadraceps punctatus sublingulatus</i> Timmermann <sup>M</sup> ; <i>Saemundssonina lari</i> (Fabricius) <sup>M</sup> <b>Expected:</b>
<b>Sternidae</b>	
<i>Sterna hirundo</i> Linnaeus, Common Tern (COTE)	<b>Recorded:</b> <i>Actornithophilus piceus piceus</i> (Denny) <sup>M</sup> ; <i>Quadraceps sellatus</i> (Burmeister) <sup>M</sup> ; <i>Saemundssonina sterna</i> (Linnaeus) <sup>M,13,M</sup> <b>Expected:</b> <i>Austromenopon atrofulvum</i> (Piaget)
<i>Sterna forsteri</i> Nuttall, Forster's Tern (FOTE)	<b>Recorded:</b> <i>Quadraceps</i> sp. <sup>M</sup> <b>Expected:</b> <i>Actornithophilus piceus piceus</i> (Denny); <i>Austromenopon atrofulvum</i> (Piaget); <i>Saemundssonina parvigenitalis</i> Ward
<i>Hydroprogne caspia</i> Pallas, Caspian Tern (CATE)	<b>Recorded:</b> <i>Actornithophilus piceus piceus</i> (Denny) <sup>M</sup> ; <i>Austromenopon atrofulvum</i> (Piaget) <sup>M</sup> ; <i>Quadraceps caspius</i> (Giebel) <sup>M</sup> ; <i>Saemundssonina laticaudata</i> (Rudow) <sup>M</sup> <b>Expected:</b> <i>Quadraceps punctatus regressus</i> Timmermann
<i>Chlidonias niger</i> (Linnaeus), Black Tern (BLTE)	<b>Recorded:</b> <i>Actornithophilus piceus piceus</i> (Denny) <sup>M</sup> ; <i>Austromenopon atrofulvum</i> (Piaget) <sup>M</sup> ; <i>Quadraceps phaeonotus</i> (Nitzsch (In Giebel)) <sup>A,M</sup> ; <i>Saemundssonina lobaticeps</i> (Giebel) <sup>A,M</sup> <b>Expected:</b>

## COLUMBIFORMES

## Columbidae

*Zenaida macroura* (Linnaeus),  
Mourning Dove (MODO)

**Recorded:** *Bonomiella columbae* Emerson<sup>M,14</sup>; *Hohorstiella paladinella* Hill & Tuff<sup>M,14</sup>; *Columbicola baculoides* (Paine)<sup>M,14</sup>; *Columbicola macrourae* (Wilson)<sup>M,14</sup>; *Physconelloides zenaidurae* (McGregor)<sup>M,14</sup>

**Expected:** *Bonomiella zenaidae* Cicchino & González-Acuña

## CUCULIFORMES

## Cuculidae

*Coccyzus erythrophthalmus* (Wilson),  
Black-billed Cuckoo (BBCU)

**Recorded:** *Cuculoecus coccygii* (Osborn)<sup>M</sup>; *Cuculicola erythrophthalmus* Emerson<sup>M</sup>

**Expected:**

## STRIGIFORMES

## Strigidae

*Bubo virginianus* (Gmelin),  
Great Horned Owl (GHOW)

**Recorded:** *Colpocephalum brachysomum* Kellogg & Chapman<sup>M</sup>; *Kurodaia magna* Emerson<sup>S,15,M</sup>; *Strigiphilus oculus* (Rudow)<sup>S,16,M</sup>; *Strigiphilus syrnii* (Packard)<sup>S,15,16,M</sup>

**Expected:**

*Speotyto cunicularia* (Molina),  
Burrowing Owl (BUOW)

**Recorded:** *Strigiphilus speotyti* (Osborn)<sup>S,16</sup>

**Expected:** *Colpocephalum pectinatum* Osborn

*Aegolius acadicus* (Gmelin),  
Northern Saw-whet Owl (NSWO)

**Recorded:** *Kurodaia acadicae* Price & Beer<sup>M</sup>; *Strigiphilus acadicus* Emerson & Price<sup>A,M</sup>

**Expected:**

*Asio otus* (Linnaeus),  
Long-eared Owl (LEOW)

**Recorded:** *Strigiphilus barbatus* (Osborn)<sup>M</sup>

**Expected:**

*Asio flammeus* (Pontoppidan),  
Short-eared Owl (SEOW)

**Recorded:** *Strigiphilus cursor* (Burmeister)<sup>A,M</sup>

**Expected:** *Colpocephalum brachysomum* Kellogg & Chapman;  
*Kurodaia flammei* Price & Beer

## CAPRIMULGIFORMES

## Caprimulgidae

*Chordeiles minor* (Forster),  
Common Nighthawk (CONI)

**Recorded:** *Multicola macrocephalus* (Kellogg)<sup>M,17</sup>

**Expected:**

*Phalaenoptilus nuttallii* (Audubon),  
Common Poorwill\* (COPO)

**Recorded:** n/a

**Expected:** n/a

## APODIFORMES

## Trochilidae

*Archilochus colubris* (Linnaeus),  
Ruby-throated Hummingbird (RTHU)

**Recorded:** *Trochiloecetes* sp.<sup>M</sup>

**Expected:** *Ricinus lineatus* (Osborn)

## CORACIIFORMES

## Alcedinidae

*Megasceryle alcyon* (Linnaeus),  
Belted Kingfisher (BEKI)

**Recorded:** *Alcedoffula alcyonae* Carriker<sup>M</sup>

**Expected:**

## PICIFORMES

### Picidae

*Picoides pubescens* (Linnaeus),  
Downy Woodpecker (DOWO)

**Recorded:** *Menacanthus pici* (Denny)<sup>M</sup>; *Brueelia straminea* (Denny)<sup>A;M</sup>; *Penenirmus auritus* (Scopoli)<sup>A;M</sup>; *Picicola snodgrassi* (Kellogg)<sup>M</sup>  
**Expected:** *Menacanthus eurysternus* (Burmeister)

*Picoides villosus* (Linnaeus),  
Hairy Woodpecker (HAWO)

**Recorded:** *Menacanthus pici* (Denny)<sup>A;M</sup>; *Brueelia straminea* (Denny)<sup>A</sup>; *Penenirmus auritus* (Scopoli)<sup>M</sup>  
**Expected:** *Picicola snodgrassi* (Kellogg)

*Colaptes auratus* (Linnaeus),  
Northern Flicker (NOFL)

**Recorded:** *Menacanthus eurysternus* (Burmeister)<sup>A;M</sup>; *Menacanthus pici* (Denny)<sup>A;M</sup>; *Penenirmus jungens* (Kellogg)<sup>A;S,A;M</sup>; *Picicola porisma* Dalglish<sup>A;M</sup>  
**Expected:** *Brueelia straminea* (Denny)

*Sphyrapicus varius* (Linnaeus),  
Yellow-bellied Sapsucker (YBSA)

**Recorded:** *Menacanthus pici* (Denny)<sup>M</sup>; *Penenirmus auritus* (Scopoli)<sup>A;M</sup>  
**Expected:** *Brueelia straminea* (Denny)

## PASSERIFORMES

### Tyrannidae

*Contopus sordidulus* Sclater,  
Western Wood-Pewee\* (WEWP)

**Recorded:** n/a  
**Expected:** *Ricinus marginatus* (Children)

*Empidonax alnorum* Brewster,  
Alder Flycatcher (ALFL)

**Recorded:** n/a  
**Expected:** n/a

*Empidonax traillii* (Audubon),  
Willow Flycatcher (WIFL)

**Recorded:** n/a  
**Expected:** *Ricinus marginatus* (Children); *Ricinus sucinaceus* (Kellogg)

*Empidonax minimus* Baird & Baird,  
Least Flycatcher (LEFL)

**Recorded:** *Ricinus marginatus* (Children)<sup>A;M</sup>  
**Expected:**

*Empidonax occidentalis* Nelson,  
Cordilleran Flycatcher\* (COFL)

**Recorded:** n/a  
**Expected:** n/a

*Sayornis phoebe* (Latham),  
Eastern Phoebe (EAPH)

**Recorded:** *Philopterus* sp. 5<sup>M</sup>; *Picicola foedus* (Kellogg & Chapman)<sup>M</sup>; *Ricinus marginatus* (Children)<sup>M</sup>  
**Expected:**

*Sayornis saya* (Bonaparte),  
Say's Phoebe\* (SAPH)

**Recorded:** n/a  
**Expected:** *Picicola foedus* (Kellogg & Chapman); *Ricinus sucinaceus* (Kellogg)

*Tyrannus verticalis* Say,  
Western Kingbird (WEKI)

**Recorded:** *Menacanthus tyranni* Price<sup>M,18,M</sup>; *Picicola foedus* (Kellogg & Chapman)<sup>M,18,M</sup>; *Ricinus arcuatus* (Kellogg & Mann)<sup>M,18,M</sup>  
**Expected:** *Ricinus marginatus* (Children)

*Tyrannus tyrannus* (Linnaeus),  
Eastern Kingbird (EAKI)

**Recorded:** *Menacanthus tyranni* Price<sup>M,18,M</sup>; *Brueelia parabolycebe* (Carriker)<sup>M</sup>; *Philopterus* sp. 4<sup>M</sup>; *Picicola foedus* (Kellogg & Chapman)<sup>A;M,18,M</sup>; *Ricinus arcuatus* (Kellogg & Mann)<sup>M</sup>; *Ricinus marginatus* (Children)<sup>M,18,M</sup>  
**Expected:**

### Alaudidae

*Eremophila alpestris* (Linnaeus),  
Horned Lark (HOLA)

**Recorded:** n/a  
**Expected:** *Menacanthus alaudae* (Schrank); *Ricinus serratus* (Durrant)

### Hirundinidae

*Tachycineta bicolor* (Vieillot),  
Tree Swallow (TRES)

**Recorded:** *Brueelia* sp. 6<sup>M</sup>; *Philopterus major* (Kellogg)<sup>M</sup>  
**Expected:**



<i>Tachycineta thalassina</i> (Swainson), Violet-green Swallow* (VGSW)	<b>Recorded:</b> n/a <b>Expected:</b>
<i>Progne subis</i> (Linnaeus), Purple Martin (PUMA)	<b>Recorded:</b> <i>Machaerilaemus americanus</i> (Ewing) <sup>M</sup> ; <i>Myrsidea dissimilis</i> (Kellogg) <sup>A; M</sup> ; <i>Brueelia subis</i> (Carriker) <sup>A; M</sup> ; <i>Philoaterus domesticus</i> (Kellogg) <sup>M</sup> <b>Expected:</b>
<i>Stelgidopteryx serripennis</i> (Audubon), Northern Rough-winged Swallow* (NRWS)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Philoaterus tropicalis</i> Carriker
<i>Riparia riparia</i> (Linnaeus), Bank Swallow (BNSW)	<b>Recorded:</b> <i>Myrsidea latifrons</i> (Carriker [& Shull]) <sup>A; M</sup> ; <i>Brueelia tenuis</i> (Burmeister) <sup>M</sup> <b>Expected:</b> <i>Machaerilaemus clayae</i> (Balát); <i>Philoaterus microsomaticus</i> Tandan; <i>Ricinus fringillae</i> De Geer
<i>Hirundo rustica</i> Linnaeus, Barn Swallow (BARS)	<b>Recorded:</b> <i>Machaerilaemus malleus</i> (Burmeister) <sup>M</sup> ; <i>Myrsidea rustica</i> (Giebel) <sup>M</sup> ; <i>Brueelia domestica</i> (Kellogg & Chapman) <sup>M</sup> ; <i>Philoaterus microsomaticus</i> Tandan <sup>M</sup> <b>Expected:</b> n/a
<i>Petrochelidon pyrrhonota</i> Vieillot, Cliff Swallow (CLSW)	<b>Recorded:</b> <i>Machaerilaemus malleus</i> (Burmeister) <sup>M</sup> ; <i>Brueelia longa</i> (Kellogg) <sup>M</sup> <b>Expected:</b> <i>Philoaterus major</i> (Kellogg)
<b>Corvidae</b>	
<i>Cyanocitta cristata</i> , Blue Jay (BLJA)	<b>Recorded:</b> <i>Menacanthus eurysternus</i> (Burmeister) <sup>M</sup> ; <i>Machaerilaemus cyanocittae</i> Price, Hellenthal & Dalglish <sup>M</sup> ; <i>Brueelia clayae</i> Ansari <sup>M</sup> ; <i>Philoaterus crassipes</i> (Burmeister) <sup>A; M</sup> <b>Expected:</b>
<i>Pica hudsonia</i> , Black-billed Magpie (BBMA)	<b>Recorded:</b> <i>Menacanthus eurysternus</i> (Burmeister) <sup>A; S</sup> ; <i>Myrsidea piccae</i> (Linnaeus) <sup>M</sup> ; <i>Brueelia biocellata</i> (Piaget) <sup>A; M</sup> ; <i>Philoaterus piccae</i> (Denny) <sup>A; S; A; M</sup> <b>Expected:</b>
<i>Corvus brachyrhynchos</i> , American Crow (AMCR)	<b>Recorded:</b> <i>Myrsidea interrupta</i> (Osborn) <sup>S19; M</sup> ; <i>Brueelia rotundata</i> (Osborn) <sup>A; S; A; S; 20; M</sup> ; <i>Philoaterus osborni</i> Edwards <sup>A; S</sup> (as <i>P. corvi</i> (L.)); <sup>M</sup> <b>Expected:</b>
<i>Corvus corax</i> , Common Raven (CORA)	<b>Recorded:</b> <i>Colpocephalum fregili</i> Denny <sup>M</sup> ; <i>Menacanthus gonophaeus</i> (Burmeister) <sup>M</sup> ; <i>Myrsidea vinlandica</i> Klockenhoff & Schirmers <sup>A; M</sup> ; <i>Brueelia biocellata</i> (Piaget) <sup>A; M</sup> ; <i>Philoaterus corvi</i> (Linnaeus) <sup>M</sup> <b>Expected:</b> <i>Philoaterus osborni</i> Edwards
<b>Paridae</b>	
<i>Poecile atricapillus</i> (Linnaeus), Black-capped Chickadee (BCCH)	<b>Recorded:</b> <i>Brueelia longifrons</i> Carriker <sup>M</sup> ; <i>Philoaterus</i> sp. 1 <sup>M</sup> ; <i>Ricinus fringillae</i> De Geer <sup>M</sup> <b>Expected:</b>
<b>Sittidae</b>	
<i>Sitta canadensis</i> Linnaeus, Red-breasted Nuthatch (RBNU)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Ricinus sittae</i> Nelson
<b>Troglodytidae</b>	
<i>Salpinctes obsoletus</i> (Say), Rock Wren* (ROWR)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Menacanthus obsoleti</i> Price
<i>Cistothorus platensis</i> (Latham), Sedge Wren* (SEWR)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Menacanthus tenuifrons</i> (Blagoveshtchensky)
<i>Cistothorus palustris</i> (Wilson), Marsh Wren (MAWR)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Menacanthus tenuifrons</i> (Blagoveshtchensky)

*Troglodytes aedon* Vieillot,  
House Wren (HOWR)

**Recorded:** *Menacanthus aedonis* Price<sup>A;M</sup>  
**Expected:** *Penenirmus albiventris* (Scopoli)

**Turdidae**

*Sialia sialis* (Linnaeus),  
Eastern Bluebird (EABL)

**Recorded:** *Philoaterus sialii* (Osborn)<sup>M</sup>  
**Expected:**

*Sialia currucoides* (Bechstein),  
Mountain Bluebird (MOBL)

**Recorded:** n/a  
**Expected:** n/a

*Turdus migratorius* Linnaeus,  
American Robin (AMRO)

**Recorded:** *Menacanthus eurysternus* (Burmeister)<sup>M</sup>; *Myrsidea emersoni* Clay<sup>M</sup>; *Brueelia iliaci* (Denny)<sup>A;M</sup>; *Sturnidoecus simplex* (Kellogg)<sup>A;M</sup>; *Ricinus elongatus* (Olfers)<sup>M</sup>  
**Expected:**

**Mimidae**

*Dumetella carolinensis* (Linnaeus),  
Grey Catbird (GRCA)

**Recorded:** *Brueelia brunneinucha* Cicchino<sup>A;M</sup>; *Picicola orpheus* (Osborn)<sup>M</sup>  
**Expected:**

*Mimus polyglottos* (Linnaeus),  
Northern Mockingbird (NOMO)

**Recorded:** n/a  
**Expected:** *Menacanthus eurysternus* (Burmeister); *Brueelia brunneinucha* Cicchino

*Oreoscoptes montanus* (Townsend),  
Sage Thrasher\* (SATH)

**Recorded:** n/a  
**Expected:** *Brueelia rotundifrons* Cicchino

*Toxostoma rufum* (Linnaeus),  
Brown Thrasher (BRTH)

**Recorded:** n/a  
**Expected:** *Machaerilaemus maestus* (Kellogg & Chapman); *Menacanthus eurysternus* (Burmeister); *Brueelia dorsale* Williams

**Motacillidae**

*Anthus spragueii* (Audubon),  
Sprague's Pipit\* (SPPI)

**Recorded:** n/a  
**Expected:** n/a

**Bombycillidae**

*Bombycilla cedrorum* Vieillot,  
Cedar Waxwing (CEDW)

**Recorded:** *Brueelia cedrorum* (Piaget)<sup>M</sup>; *Philoaterus* sp. 2<sup>M</sup>  
**Expected:** *Menacanthus sturnellae* Price; *Ricinus dalgleishi* Nelson

**Laniidae**

*Lanius ludovicianus* Linnaeus,  
Loggerhead Shrike (LOSH)

**Recorded:** *Philoaterus coarctatus* (Scopoli)<sup>M</sup>  
**Expected:** *Menacanthus camelinus* (Nitzsch (In Giebel))

**Vireonidae**

*Vireo gilvus* (Vieillot),  
Warbling Vireo (WAVI)

**Recorded:** n/a  
**Expected:** n/a

*Vireo olivaceus* (Linnaeus),  
Red-eyed Vireo (REVI)

**Recorded:** *Philoaterus* sp. 7<sup>M</sup>; *Ricinus vireoensis* Nelson<sup>M</sup>  
**Expected:** *Menacanthus currucae* (Schrank)

**Parulidae**

*Geothlypis trichas* (Linnaeus),  
Common Yellowthroat (COYE)

**Recorded:** *Brueelia* sp. 8<sup>M</sup>; *Ricinus dalgleishi* Nelson<sup>M</sup>  
**Expected:** *Menacanthus geothlypis* Price

*Setophaga coronata* (Linnaeus),  
Yellow-rumped Warbler (YRWA)

**Recorded:** *Menacanthus dendroicae* Price<sup>M</sup>; *Philoaterus* sp. 9<sup>M</sup>  
**Expected:** *Ricinus dendroicae* Nelson

*Setophaga petechia* (Linnaeus),  
Yellow Warbler (YEWA)

**Recorded:** n/a  
**Expected:** *Myrsidea ridulosa* (Kellogg & Chapman); *Brueelia interposita* (Kellogg); *Ricinus dendroicae* Nelson

*Setophaga ruticilla* (Linnaeus),  
American Redstart (AMRE)

**Recorded:** *Myrsidea* sp.<sup>M</sup>  
**Expected:** *Menacanthus eurysternus* (Burmeister)

*Icteria virens*,  
Yellow-breasted Chat\* (YBCH)

**Recorded:** n/a  
**Expected:** n/a

**Cardinalidae**

*Pheucticus melanocephalus*  
(Swainson),  
Black-headed Grosbeak (BHGR)

**Recorded:** n/a  
**Expected:** n/a

*Spiza americana* (Gmelin),  
Dickcissel\* (DICK)

**Recorded:** n/a  
**Expected:** n/a

*Passerina amoena* (Say),  
Lazuli Bunting\* (LAZB)

**Recorded:** n/a  
**Expected:** *Ricinus australis* (Kellogg)

*Passerina cyanea* (Linnaeus),  
Indigo Bunting (INBU)

**Recorded:** *Brueelia* sp. 5<sup>M</sup>; *Philopterus* sp. 6<sup>M</sup>  
**Expected:** *Ricinus australis* (Kellogg)

**Emberizidae**

*Pipilo erythrophthalmus* (Linnaeus),  
Eastern Towhee\* (EATO)

**Recorded:** n/a  
**Expected:** *Machaerilaemus maestus* (Kellogg); *Myrsidea melanorum* (Kellogg); *Penenirmus quadripustulatus* (Kellogg & Mann); *Ricinus fringillae* De Geer; *Ricinus subhastatus* (Durrant)

*Pipilo maculatus* Swainson,  
Spotted Towhee\* (SPTO)

**Recorded:** n/a  
**Expected:** n/a

*Spizella passerina* (Bechstein),  
Chipping Sparrow (CHSP)

**Recorded:** *Brueelia* sp. 2<sup>M</sup>; *Philopterus* sp. 3<sup>M</sup>;  
*Ricinus subdiffusus* Nelson<sup>M</sup>  
**Expected:** *Ricinus diffusus* (Kellogg); *Ricinus fringillae* De Geer

*Spizella pallida* (Swainson),  
Clay-coloured Sparrow (CCSP)

**Recorded:** *Brueelia* sp. 3<sup>M</sup>  
**Expected:**

*Spizella breweri* Cassin,  
Brewer's Sparrow\* (BRSP)

**Recorded:** n/a  
**Expected:** *Ricinus fringillae* De Geer; *Ricinus subdiffusus* Nelson

*Spizella pusilla*,  
Field Sparrow (FISP)

**Recorded:** n/a  
**Expected:** *Machaerilaemus complexus* Malcomson; *Menacanthus chrysophaeus* (Kellogg); *Ricinus subdiffusus* Nelson

*Poocetes gramineus* (Gmelin),  
Vesper Sparrow (VESP)

**Recorded:** *Brueelia* sp. 7<sup>M</sup>  
**Expected:** *Machaerilaemus maestus* (Kellogg);  
*Ricinus fringillae* De Geer

*Chondestes grammacus* (Say),  
Lark Sparrow\* (LASP)

**Recorded:** n/a  
**Expected:** *Machaerilaemus laticorpus* (Carriker); *Brueelia angustifrons* (Carriker)

*Calamospiza melanocorys* Stejneger,  
Lark Bunting\* (LABU)

**Recorded:** n/a  
**Expected:** n/a

*Passerculus sandwichensis* (Gmelin),  
Savannah Sparrow (SAVS)

**Recorded:** *Machaerilaemus maestus* (Kellogg)<sup>M</sup>  
**Expected:** *Menacanthus chrysophaeus* (Kellogg); *Ricinus diffusus* (Kellogg)

*Ammodramus leconteii* (Audubon),  
Le Conte's Sparrow (LCSP)

**Recorded:** *Philopterus* sp. 10<sup>M</sup>  
**Expected:**

*Ammodramus bairdii* (Audubon),  
Baird's Sparrow\* (BAIS)

**Recorded:** n/a  
**Expected:** n/a

*Ammodramus savannarum* (Gmelin),  
Grasshopper Sparrow\* (GRSP)

**Recorded:** n/a  
**Expected:** *Ricinus diffusus* (Kellogg)

*Ammodramus caudacutus* Allen,  
Sharp-tailed Sparrow\* (STSP)

**Recorded:** n/a  
**Expected:** n/a

*Melospiza melodia* (Wilson),  
Song Sparrow (SOSP)

**Recorded:** n/a  
**Expected:** *Machaerilaemus maestus* (Kellogg); *Menacanthus chrysophaeus* (Kellogg); *Ricinus diffusus* (Kellogg); *Ricinus fringillae* De Geer



*Analgoidea*

We recorded 11 families of feather mites in this superfamily (Table 3). Members of the Alloptidae are associated with aquatic birds of many non-passerine orders, including loons, pelicans, sandpipers, gulls, and ducks. Males of some taxa (e.g., *Dinalloptes*) show spectacular asymmetrical modifications of the legs and body. In our study, alLOPTIDS were moderately diverse, with 10 species from five genera recorded and another five species expected to be found on the basis of the literature. Species of the Analgidae are down-inhabiting mites occurring on both passerine and non-passerine hosts. We found 26 species representing four analgid subfamilies. All members of the Analginae occur on Passeriformes, with the genus *Analges* being particularly species rich (15 species

**Table 3.** Breakdown of feather mites (Analgoidea, Pterolichoidea) recorded in the present study infesting grassland birds in Alberta and Manitoba (see Table 6 for full list, including expected species).

Superfamily	Families	Number of Genera	Number of Species
Analgoidea	Alloptidae	5	10
	Analgidae	7	26
	Avenzoariidae	7	12
	Dermoglyphidae	1	1
	Dermationidae	2	2
	Epidermoptidae	1	1
	Proctophyllodidae	8	40
	Psoroptoididae	4	6
	Pteronyssidae	3	11
	Trouessartiidae	1	10
	Xolalgidae	10	14
Pterolichoidea	Cheylabididae	1	1
	Falculiferidae	2	2
	Freyanidae	2	8
	Gabuciniidae	6	8
	Kramerellidae	3	7
	Pterolichidae	5	7
	Ptiloxenidae	2	4
	Rectijanuidae	1	1
	Syringobiidae	2	3
TOTAL	20	73	174

found in our study, several of them undescribed). The Megniniinae was the second-best-represented analgid subfamily, with five species from three genera found on the examined birds. Unlike analgines, megniniines occur on non-passerines, and we found them on rails and coots (Gruiformes: Rallidae) and Mourning Dove (Columbiformes: Columbidae). The Avenzoariidae are restricted to hosts from the Charadriiformes, including sandpipers, gulls, and terns. We found 12 species from seven genera, with an additional six species and two genera expected on the basis of the literature records.

The Dermoglyphidae, Dermationidae, and Epidermoptidae were poorly represented, with at most two species found for each of these families. Dermoglyphids are quill-dwelling mites and the other two families are composed of small-bodied, skin-dwelling species; it is possible that they were more diverse and abundant on the birds we examined, but were poorly extracted from host bodies with our method of washing, or were overlooked in the sorting process.

In contrast, members of the vane-dwelling family Proctophyllodidae were common and diverse. Proctophyllodids are almost entirely restricted to Passeriformes, although there are some records from the woodpeckers (Piciformes) and a moderate diversity from hummingbirds (Apodiformes) (Gaud and Atyeo 1996). Our proctophyllodids came only from passerines. The genus *Proctophyllodes* was particularly diverse, with 29 species observed (five of them new to science). We also collected a moderate number (seven species) of *Amerodectes*, which together with the genera *Metapterodectes* (two species found), *Nycteridocaulus* (two species), and *Tyrannidectes* (two species) represent New World radiations of proctophyllodids.

Members of the Psoroptoididae can be easily mistaken for analgids, as both of these down-dwelling groups have a similar body shape and sport extensions from the ventral sides of their anterior legs that help in clambering through the downy parts of their hosts' feathers. We found six species in four genera from both passerine and non-passerine hosts.

The Pteronyssidae were raised from a subfamily of the Avenzoariidae by Mironov (2001). They are well-sclerotized vane-dwelling mites associated with woodpeckers (Piciformes) and passerines. Six of the 11 species of pteronyssids that we found in this study were from the genus *Scutulanysus*, which is particularly diverse on swallows (Hirundinidae). The Trouessartiidae are also composed of heavily sclerotized vane-dwelling species. The genus *Trouessartia* is the most species rich in the family, and all reliable host records are from the Passeriformes. Although fewer than 100 species are currently described, the actual richness is likely to be about 700 species (Santana 1976). We found 10 species of *Trouessartia*, five of them new to science.

The last of the analgoid families, the Xolalgidae, had the highest generic richness of all feather mite families in our study with 10 genera observed; however, the number of species per genus was low, with a maximum of three (*Ingrassia*). Host range for xolalgids is broad, including members of 14 orders of birds. We found xolalgids on representatives of eight orders (Anseriformes, Charadriiformes, Ciconiiformes, Accipitriformes, Falconiformes, Gruiformes, Passeriformes, Pelecaniformes, and Suliformes).

### ***Pterolichoidea***

Pterolichooids are most diverse on non-passerine birds, with members of only a few families associated with Passeriformes (Gaud and Atyeo 1996). In our study, all pterolichooids, with the exception of a few Gabuciniidae, were collected from non-passerines (Tables 4 and 6). No family was particularly diverse, with observed genus-level richness ranging

from one to six, and species richness from one to eight. Two families were represented by one species each, the Cheylabididae (on Swainson's Hawk) and Rectijanuidae (on Wood Duck). The Freyanidae are vane-dwelling mites that occur on aquatic birds and in our study were found on numerous species of ducks and geese (six *Freyana* spp.) and also on the Double-crested Cormorant (*Michaelia* n.sp.). The Gabuciniidae was the most genus-rich pterolichoid family with six genera (eight species) collected from the birds examined. Most were from the Accipitriformes, but we found a new species of *Paragabucinia* on the Common Nighthawk (Caprimulgiformes) and *Gabucinia delibata* from the Common Raven and American Crow (Passeriformes). Two of the three genera of Kramerellidae that we observed were from owls (Strigiformes) and the third, *Pseudogabucinia*, was collected from hawks (Accipitriformes).

The most diverse family of pterolichoids is the Pterolichidae with more than 100 described genera that have codiversified with non-passerines, particularly Galliformes (>30 genera) and Psittaciformes (>20 genera). We collected only five genera and seven species, although an additional three genera are expected to occur on sandpipers and grouse in Canadian grasslands. Similarly, we found an unexpectedly low diversity of Syringobiidae: three genera with only one species each, when another four genera should be present on the charadriiform birds in grasslands, on the basis of the literature (Table 5). The low observed number may be an artifact of our washing-based collection method, as syringobiids are quill-dwelling mites that are best collected via dissection of feathers (Dabert 2003). Ptiloxenidae are morphologically similar to syringobiids but occupy the vanes of feathers. Three species in two genera were found in our study, from grebes (Podicipediformes) and sandpipers (Charadriiformes).

### Current Status—Future Needs

Since the plea of Galloway and Danks (1990) for directed collection and study of the ectoparasites in Canada, considerable effort has been made to address gaps in our knowledge about a range of ectosymbionts, including chewing lice and feather mites. The increase in known diversity of these groups resulting from this study is obvious from what we report here for birds breeding in the grassland biomes of Manitoba, Saskatchewan, and Alberta. In the synopsis of ectoparasites of birds by Wheeler and Threlfall (1989), only two species of Pterolichoidea and 14 species of Analgoidea were recorded in Canada from birds included in our study, given the nomenclature adopted at the time. None of these species had been recorded for any of the Prairie Provinces. Here we report 134 named and 38 as yet undescribed species of feather mites from Manitoba and Alberta. In addition to these, we found representatives of two genera (*Microlichus* sp. and *Xolalgoidea* sp.) that we could not place because the specimens were the wrong sex or in too poor condition to allow us to confirm species-level identification, but that may also turn out to be new to science. Wheeler and Threlfall (1989) included about 24 genera and 38 species of chewing lice recorded from grassland birds in the Prairies, most of which were the results of a study by Brown and Wilk (1944) in Alberta. Here we report 54 genera and 183 species.

Despite considerable effort to sample as many species of grassland birds as possible, we were still limited by our reliance on birds obtained through salvage efforts. It is difficult to obtain permits to collect and handle many of these species of birds, some of which are threatened, endangered, or, in the case of the Greater Prairie Chicken, extirpated. In addition, many species are at the northern limit of their range and are

not generally abundant, especially in places where people are likely to encounter dead or injured specimens that are eligible to be salvaged. Fifty-three species of birds are included here, 39 of which are passerines, for which there are no records of known species of chewing lice. Of these, we have examined at least one specimen of 17 species, but no recognized species of lice were collected, though sample sizes were generally small ( $n = 1-18$  specimens). Clearly, additional collecting effort is warranted, especially among species of passerine birds. Many species of lice and feather mites have also been recorded from birds that are known to breed in grasslands and elsewhere, but for which we have no records *specifically* in the prairie grasslands. It is possible that these ectosymbionts do not infest birds in this part of their range. It is more likely that most are present, and additional sampling effort is needed to establish their occurrence, especially when one considers that the majority of these birds are migratory and travel considerable distances to mingle over winter with members of their species that nest in locations outside of Canada.

Grasslands are under threat from many sources, including natural resource development, cultivation, overgrazing by livestock, drainage of wetlands, urbanization, and pollution of land and water by human activities (Bond and Parr 2010). Dire consequences for many species are predicted from climate change (Thomas *et al.* 2004), and considering that many grassland birds are among the most seriously affected (Herkert 1995), we must learn as much as possible about their ectosymbiont fauna in the interest of meaningful conservation efforts. These ectosymbionts are entirely dependent upon their hosts for survival, and as host populations decline, the risks of losing sustainable populations of their ectosymbionts increase (Koh *et al.* 2004). Many species of chewing lice, for example, are present at low levels of prevalence and intensity. At some point, the probability of successful transfer from one host to another in sufficient numbers to sustain a population becomes so low that the ectosymbionts may be extirpated even if their host populations do not seem direly depressed. For many species of grassland birds, it is unlikely that we shall ever fully understand even the most fundamental aspects of the host–ectosymbiont relationship. Perhaps the most we can hope for is a list of the species of ectosymbionts, such as we have begun to assemble in this chapter.

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**Table 4.** Published records, new records, and expected records for feather mites on birds breeding in grassland biomes of Alberta (A) and Manitoba (M). Alphabetical superscripts for recorded species coincide with provinces (this study); published records for expected species are listed in Proctor (2013). n/a indicates that no published information is available.

Bird Hosts		Recorded and Expected Species of Feather Mites
<b>PODICIPEDIFORMES</b>		
<b>Podicipedidae</b>		
<i>Podilymbus podiceps</i> (Linnaeus), Pied-billed Grebe (PBGR)	Recorded: <i>Ptiloxenus</i> n. sp. 1 <sup>M</sup> Expected: n/a	
<i>Podiceps grisegena</i> (Boddaert), Red-necked Grebe (RNGR)	Recorded: <i>Ptiloxenus major</i> (Mégnin & Trouessart) <sup>A,M</sup> Expected: n/a	
<i>Podiceps auritus</i> (Linnaeus), Horned Grebe (HOGR)	Recorded: <i>Ptiloxenus major</i> (Mégnin & Trouessart) <sup>M</sup> ; <i>Ptiloxenus</i> sp. <sup>A</sup> Expected: n/a	
<i>Podiceps nigricollis</i> Brehm, Black-necked Grebe (BNGR)	Recorded: <i>Ptiloxenus major</i> (Mégnin & Trouessart) <sup>M</sup> Expected: n/a	
<i>Aechmophorus occidentalis</i> (Lawrence), Western Grebe (WEGR)	Recorded: <i>Ptiloxenus</i> n. sp. 2 <sup>M</sup> ; <i>Ptiloxenus</i> sp. <sup>A</sup> Expected: n/a	
<i>Aechmophorus clarkii</i> (Lawrence), Clark's Grebe (CLGR)	Recorded: n/a Expected: n/a	
<b>PELECANIFORMES</b>		
<b>Pelecanidae</b>		
<i>Pelecanus erythrorhynchos</i> Gmelin, American White Pelican (AWPE)	Recorded: <i>Pelicanoptes onocrotali</i> Fain & Atyeo <sup>A</sup> ; <i>Scutomegninia gaudi</i> Mironov <sup>A,M</sup> ; <i>Plicatalloptes pelecani</i> (Dubinin) <sup>M</sup> ; <i>Metingrassia pelecani</i> Mironov & Galloway <sup>M</sup> Expected: <i>Parabdeliorhynchus pelecanus</i> (Dubinin)	
<b>SULIFORMES</b>		
<b>Phalacrocoracidae</b>		
<i>Phalacrocorax auritus</i> (Lesson), Double-crested Cormorant (DCCO)	Recorded: <i>Scutomegninia microfalciifera</i> Mironov <sup>A,M</sup> ; <i>Metingrassia minutidisca</i> Gaud <sup>A,M</sup> ; <i>Michaelia</i> n. sp. <sup>A,M</sup> ; <i>Dinalloptes chelionatus</i> Atyeo & Peterson <sup>A,M</sup> ; <i>Plicatalloptes subcrassipes</i> (Dubinin & Dubinna) <sup>M</sup> Expected: n/a	

## CICONIIFORMES

### Ardeidae

*Botaurus lentiginosus* (Rackett),  
American Bittern (AMIB)

*Ardea herodias* Linnaeus,  
Great Blue Heron (GBHE)

*Butorides virescens* (Linnaeus),  
Green Heron (GRHE)

*Nycticorax nycticorax* (Linnaeus),  
Black-crowned Night-Heron (BCNH)

### Threskiornithidae

*Plegadis chihi* (Vieillot),  
White-faced Ibis (WFIB)

## ANSERIFORMES

### Anatidae

*Branta canadensis* (Linnaeus),  
Canada Goose (CAGO)

*Aix sponsa* (Linnaeus),  
Wood Duck (WODU)

*Anas strepera* Linnaeus,  
Gadwall (GADW)

*Anas americana* Gmelin,  
American Wigeon (AMWI)

*Anas platyrhynchos* Linnaeus,  
Mallard (MALL)

*Anas discors* Linnaeus,  
Blue-winged Teal (BWTE)

**Recorded:** *Ardeacarus ardeae* (Canestrini)<sup>M</sup>; *Pteraloptes stellaris* (Buchholz)<sup>M</sup>  
**Expected:** n/a

**Recorded:** *Ardeacarus ardeae* (Canestrini)<sup>M</sup>  
**Expected:** n/a

**Recorded:** n/a  
**Expected:** n/a

**Recorded:** n/a  
**Expected:** *Ardeacarus ardeae* (Canestrini)

**Recorded:** n/a  
**Expected:** *Scutomegninia ibidis* (Trouessart)

**Recorded:** *Freyana brantina* Vasyukova & Mironov<sup>M</sup>; *Brephosceles cygni* Vasyukova & Mironov *aff.*<sup>M</sup>  
**Expected:** n/a

**Recorded:** *Zygochelifera beeri* Atyeo<sup>M</sup>; *Rectijana braaschi* Atyeo & Peterson *aff.*<sup>M</sup>; *Freyana dendronessae* Dubinin<sup>M</sup>;  
*Freyana* n. sp.<sup>M</sup>; *Vingrassia velata* (Mégnin)<sup>M</sup>  
**Expected:** n/a

Recorded: n/a  
Expected: n/a

**Recorded:** *Ingrassia* sp.<sup>A</sup>  
**Expected:** *Freyana anatina* (Koch); *Freyana largifolia* Mégnin & Trouessart

**Recorded:** *Alloptes* sp.<sup>A</sup>; *Freyana anatina* (Koch)<sup>M</sup>; *Freyana* sp.<sup>A</sup>; *Bdellorhynchus polymorphus* Trouessart<sup>M</sup>; *Vingrassia velata* (Mégnin)<sup>M</sup>  
**Expected:** *Brephosceles anatina* Dubinin; *Freyana largifolia* Mégnin & Trouessart

**Recorded:** *Freyana anatina* (Koch)<sup>M</sup>; *Freyana largifolia* Mégnin & Trouessart<sup>A</sup>; *Bdellorhynchus polymorphus* Trouessart<sup>M</sup>;  
*Bdellorhynchus* sp.<sup>A</sup>  
**Expected:** n/a

Bird Hosts	Recorded and Expected Species of Feather Mites
<i>Anas clypeata</i> Linnaeus, Northern Shoveler (NOSH)	<b>Recorded:</b> <i>Freyana anatina</i> (Koch) <sup>M</sup> ; <i>Ingrassia</i> sp. <sup>A</sup> <b>Expected:</b> <i>Bdellorhynchus polymorphus</i> Trouessart; <i>Freyana largifolia</i> Ménégnin & Trouessart; <i>Vingrassia velata</i> (Ménégnin); <i>Neodermatation anatum</i> (Fain)
<i>Anas acuta</i> Linnaeus, Northern Pintail (NOPI)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Bdellorhynchus polymorphus</i> Trouessart; <i>Brephosceles anatina</i> Dubinin; <i>Freyana anatina</i> (Koch); <i>Freyana largifolia</i> Ménégnin & Trouessart; <i>Vingrassia velata</i> (Ménégnin)
<i>Anas crecca</i> Linnaeus, American Green-winged Teal (AGWT)	<b>Recorded:</b> <i>Freyana anatina</i> (Koch) <sup>M</sup> <b>Expected:</b> <i>Bdellorhynchus polymorphus</i> Trouessart; <i>Brephosceles anatina</i> Dubinin; <i>Freyana largifolia</i> Ménégnin & Trouessart; <i>Vingrassia velata</i> (Ménégnin)
<i>Anas cyanoptera</i> Vieillot, Cinnamon Teal (CITE)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Bdellorhynchus polymorphus</i> Trouessart; <i>Freyana largifolia</i> Ménégnin & Trouessart
<i>Aythya valisineria</i> (Wilson), Canvasback (CANV)	<b>Recorded:</b> <i>Freyana aythinae</i> Dubinin <sup>M</sup> <b>Expected:</b> n/a
<i>Aythya americana</i> (Eyton), Redhead (REDH)	<b>Recorded:</b> <i>Freyana aythinae</i> Dubinin <sup>M</sup> <b>Expected:</b> <i>Freyana nyrocae</i> Dubinin
<i>Aythya affinis</i> (Eyton), Lesser Scaup (LESC)	<b>Recorded:</b> <i>Vingrassia velata</i> (Ménégnin) <sup>M</sup> <b>Expected:</b> <i>Freyana aythinae</i> Dubinin; <i>Freyana nyrocae</i> Dubinin
<i>Bucephala albeola</i> (Linnaeus), Bufflehead (BUFF)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Freyana bucephalae</i> Dubinin
<i>Bucephala clangula</i> (Linnaeus), Common Goldeneye (COGO)	<b>Recorded:</b> <i>Freyana bucephalae</i> Dubinin <sup>M</sup> <b>Expected:</b> <i>Bdellorhynchus polymorphus</i> Trouessart; <i>Brephosceles bucephali</i> Mironov
<i>Melanitta fusca</i> (Linnaeus), White-winged Scoter (WWSC)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Freyana oidemiae</i> Dubinin
<i>Oxyura jamaicensis</i> (Gmelin), Ruddy Duck (RUDU)	<b>Recorded:</b> <i>Bdellorhynchus oxyurae</i> Dubinin <sup>A,M</sup> <b>Expected:</b> n/a
<b>ACCIPITRIFORMES</b>	
<b>Cathartidae</b>	
<i>Cathartes aura</i> (Linnaeus), Turkey Vulture (TUVU)	<b>Recorded:</b> <i>Ancyralges cathartinus</i> Mironov & Galloway <sup>M</sup> ; <i>Cathartacarus aurae</i> Mironov & Galloway <sup>M</sup> <b>Expected:</b> n/a

**Accipitridae**

<i>Circus cyaneus</i> (Linnaeus), Northern Harrier (NOHA)	<b>Recorded:</b> <i>Aetacarus leptotrichus</i> Gaud <sup>M</sup> <b>Expected:</b> <i>Pseudogabucinia intermedia</i> (Mégnin & Trouessart)
<i>Accipiter striatus</i> Vieillot, Sharp-shinned Hawk (SSHA)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Accipiter cooperii</i> (Bonaparte), Cooper's Hawk (COHA)	<b>Recorded:</b> <i>Prooposolenidia accipitris</i> Mironov & Proctor <sup>A,M</sup> <b>Expected:</b> n/a
<i>Buteo swainsoni</i> Bonaparte, Swainson's Hawk (SWHA)	<b>Recorded:</b> <i>Hieracolicus nisi</i> (Canestrini) <sup>M</sup> ; <i>Pseudogabucinia intermedia</i> <sup>M</sup> ; <i>Hemicheylobis praecox</i> (Trouessart) <sup>M</sup> <b>Expected:</b> n/a
<i>Buteo jamaicensis</i> (Gmelin), Red-tailed Hawk (RTHA)	<b>Recorded:</b> <i>Hieracolicus nisi</i> (Canestrini) <sup>M</sup> ; <i>Pseudogabucinia intermedia</i> (Mégnin & Trouessart) <sup>M</sup> <b>Expected:</b> n/a
<i>Buteo regalis</i> (Gray), Ferruginous Hawk (FEHA)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Haliaeetus leucocephalus</i> (Linnaeus), Bald Eagle (BAEA)	<b>Recorded:</b> <i>Aetacarus phylloproctus</i> (Mégnin & Trouessart) <sup>M</sup> ; <i>Pseudallopitinus aquilinus</i> (Trouessart) <sup>A,M</sup> <b>Expected:</b> n/a
<i>Aquila chrysaetos</i> (Linnaeus), Golden Eagle (GOEA)	<b>Recorded:</b> <i>Pseudallopitinus aquilinus</i> (Trouessart) <sup>M</sup> <b>Expected:</b> n/a
<b>Pandionidae</b>	
<i>Pandion haliaetus</i> (Linnaeus), Osprey (OSPR)	<b>Recorded:</b> <i>Pandionacarus fuscus</i> (Nitsch) <sup>A,M</sup> ; <i>Analloptes buettikeri</i> Mironov <sup>A,M</sup> <b>Expected:</b> n/a
<b>FALCONIFORMES</b>	
<b>Falconidae</b>	
<i>Falco sparverius</i> Linnaeus, American Kestrel (AMKE)	<b>Recorded:</b> <i>Epoplichus minor</i> (Mégnin & Trouessart) <sup>M</sup> ; <i>Dubininia accipitrina</i> (Trouessart) <sup>M</sup> <b>Expected:</b> n/a
<i>Falco columbarius</i> Linnaeus, Merlin (MERL)	<b>Recorded:</b> <i>Epoplichus minor</i> (Mégnin & Trouessart) <sup>M</sup> ; <i>Aetacarus</i> n. sp. <sup>M</sup> <b>Expected:</b> <i>Dubininia accipitrina</i> (Trouessart)
<i>Falco mexicanus</i> Schlegel, Prairie Falcon (PRFA)	<b>Recorded:</b> n/a <b>Expected:</b> n/a

Bird Hosts	Recorded and Expected Species of Feather Mites
<b>GALLIFORMES</b>	
<b>Phasianidae</b>	
<i>Centrocercus urophasianus</i> (Bonaparte), Sage Grouse (SAGR)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Tympanuchus cupido</i> (Linnaeus), Greater Prairie Chicken (GRPC)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Tetraolichus cupido</i> Atyeo & Gaud
<i>Tympanuchus phasianellus</i> (Linnaeus), Sharp-tailed Grouse (STGR)	<b>Recorded:</b> <i>Paralges</i> sp. <sup>A</sup> <b>Expected:</b> n/a
<b>GRUIFORMES</b>	
<b>Rallidae</b>	
<i>Rallus limicola</i> Vieillot, Virginia Rail (VIRA)	<b>Recorded:</b> <i>Metanalgas appendiculatus</i> (Haller) <sup>M</sup> , <i>Grallolichus</i> n. sp. <sup>M</sup> <b>Expected:</b> <i>Analloptes megnini</i> (Trouessart); <i>Gymnalloptes pallens</i> (Trouessart & Neumann)
<i>Porzana carolina</i> (Linnaeus), Sora (SORA)	<b>Recorded:</b> <i>Grallobia</i> n. sp. <sup>M</sup> , <i>Grallobia</i> sp. <sup>A</sup> ; <i>Gymnalloptes pallens</i> (Trouessart & Neumann) <sup>A, M</sup> ; <i>Metanalgas holderi</i> Mironov & Galloway <sup>A, M</sup> ; <i>Megniniella ratcliffi</i> Mironov & Galloway <sup>A, M</sup> ; <i>Psilobrephosceles ortygometrae</i> (Canestrini) <sup>A, M</sup> ; <i>Psiloxenus</i> sp. <sup>A</sup> ; <i>Parazumpitia</i> n. sp. <sup>M</sup> <b>Expected:</b> n/a
<i>Fulica americana</i> Gmelin American Coot (AMCO)	<b>Recorded:</b> <i>Analloptes megnini</i> (Trouessart) <sup>M</sup> , <i>Analloptes</i> sp. A, <i>Gymnalloptes pallens</i> (Trouessart & Neumann) <sup>M</sup> , <i>Grallobia fulicae</i> (Trouessart) <sup>A, M</sup> ; <i>Grallolichus proctogamus</i> (Trouessart) <sup>M</sup> , <i>Megniniella fulicae</i> Gaud <sup>A, M</sup> ; <i>Tennalgas</i> n. sp. <sup>M</sup> <b>Expected:</b> n/a
<b>CHARADRIIFORMES</b>	
Charadriidae	
<i>Charadrius vociferus</i> Linnaeus Killdeer (KILL)	<b>Recorded:</b> <i>Bychovskitata vociferi</i> Mironov & Dabert <sup>M</sup> , <i>Phyllochaeta tenuiseta</i> Dabert & Atyeo <sup>M</sup> , <i>Sokoloviana kucheruki</i> Cerny <sup>A, M</sup> <b>Expected:</b> <i>Brephosceles longistriatus</i> Peterson
<i>Charadrius melodus</i> Ord Piping Plover (PIPL)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Brephosceles longistriatus</i> Peterson; <i>Bychovskitata semipalmati</i> Mironov & Dabert; <i>Phyllochaeta melodus</i> Dabert
<i>Charadrius montanus</i> Townsend Mountain Plover (MOPL)	<b>Recorded:</b> n/a <b>Expected:</b> n/a

**Recurvirostridae**

*Himantopus mexicanus* (Müller)  
Black-necked Stilt (BNST)  
*Recurvirostra americana* Gmelin  
American Avocet (AMAV)

**Recorded:** n/a  
**Expected:** *Bychovskitata subcharadrii* Dubinin; *Sokoloviana gracilis* (Mégnin & Trouessart)  
**Recorded:** n/a  
**Expected:** n/a

**Scolopaciidae**

*Gallinago delicata* (Ord)  
Wilson's Snipe (WISN)  
*Limosa fedoa* (Linnaeus)  
Marbled Godwit (MAGO)  
*Numenius americanus* Bechstein  
Long-billed Curlew  
*Bartramia longicauda* (Bechstein)  
Upland Sandpiper (UPSA)  
*Actitis macularia* (Linnaeus)  
Spotted Sandpiper (SPSA)

**Recorded:** *Ingrassia fissitarsa* (Gaud)<sup>M</sup>  
**Expected:** *Capelloptes flagellicaulus* (Trouessart & Neumann)

**Recorded:** n/a  
**Expected:** *Limosilichus fedoa* Dabert

**Recorded:** n/a  
**Expected:** *Limosilichus numeni* Vasyukova & Mironov

**Recorded:** n/a  
**Expected:** *Pomeranzevia bartramica* (Mironov & Dabert)

**Recorded:** *Ingrassia forcipata* (Haller)<sup>M</sup>; *Phyllochaeta maculariae* Daberta<sup>M</sup>  
**Expected:** *Bychovskitata macularii* Mironov & Dabert; *Pilochaeta rafalski* Dabert

*Catoptrophorus semipalmatus* (Gmelin)  
Willet (WILL)

**Recorded:** n/a  
**Expected:** *Montchadskiana tridentata* Dabert & Ehmsberger; *Syringobia chelopus* Trouessart & Neumann

**Phalaropidae**

*Phalaropus tricolor* (Vieillot)  
Wilson's Phalarope (WIPH)

**Recorded:** *Avenzoaria phalaropi* Gaud<sup>M</sup>; *Alloptes phalaropinus* Vasyukova & Mironov<sup>M</sup>  
**Expected:** n/a

**Laridae**

*Larus delawarensis* (Ord)  
Ring-billed Gull (RBGU)  
*Larus californicus* Lawrence  
California Gull (CAGU)  
*Leucophaeus pipixcan* Wagler  
Franklin's Gull (FRGU)

**Recorded:** *Alloptes oxylobus* Dubinin<sup>A,M</sup>; *Ingrassia* n. sp.<sup>M</sup>; *Paralges* n. sp.<sup>M</sup>; *Zachvatkinia larica* Mironov<sup>A,M</sup>  
**Expected:** n/a

**Recorded:** *Zachvatkinia* sp.<sup>A</sup>  
**Expected:** n/a

**Recorded:** *Alloptes oxylobus* Dubinin<sup>M</sup>; *Alloptes obtusolobus* Dubinin<sup>A</sup>; *Zachvatkinia larica* Mironov<sup>A,M</sup>; *Ingrassia* sp.<sup>A</sup>  
**Expected:** n/a

**Sternidae**

*Sterna hirundo* Linnaeus  
Common Tern (COTE)

**Recorded:** *Zachvatkinia sterna* (Canestrini & Fanzago)<sup>A,M</sup>; *Alloptes bisetatus* (Haller)<sup>M</sup>  
**Expected:** *Grenieria simplex* (Trouessart); *Thecarthra semaphora* (Trouessart); *Plutarchusia pseudocheleopus* Dubinin

Bird Hosts	Recorded and Expected Species of Feather Mites
<i>Sterna forsteri</i> Nuttall Forster's Tern (FOTE)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Grenieria simplex</i> (Trouessart)
<i>Hydroprogne caspia</i> Pallas Caspian Tern (CATE)	<b>Recorded:</b> <i>Alloptes niloticus</i> Kivganov & Mironov <sup>M</sup> ; <i>Thecarhira theca</i> (Mégnin & Trouessart) <sup>M</sup> ; <i>Zachvatkiniia caspica</i> Mironov <sup>M</sup> <b>Expected:</b> <i>Grenieria megachelata</i> Dabert & Atyeo
<i>Chlidonias niger</i> (Linnaeus) Black Tern (BLTE)	<b>Recorded:</b> <i>Zachvatkiniia chlidoniae</i> Mironov <sup>A</sup> <b>Expected:</b> <i>Alloptes bisetatus</i> (Haller); <i>Alloptes leptolobus</i> Gaud; <i>Alloptes macrochetiae</i> Dubinin; <i>Thecarhira grandis</i> Trouessart & Neumann
<b>COLUMBIFORMES</b>	
<b>Columbidae</b>	
<i>Zenaidura macroura</i> (Linnaeus) Mourning Dove (MODO)	<b>Recorded:</b> <i>Diplaegidia</i> n. sp. <sup>M</sup> ; <i>Falculifer isodontus</i> (Gaud & Barré) <sup>M</sup> ; <i>Pterophagus spilosikyus</i> Gaud & Barré <sup>M</sup> <b>Expected:</b> n/a
<b>CUCULIFORMES</b>	
<b>Cuculidae</b>	
<i>Coccyzus erythrophthalmus</i> (Wilson) Black-billed Cuckoo (BBUCU)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<b>STRIGIFORMES</b>	
<b>Strigidae</b>	
<i>Bubo virginianus</i> (Gmelin) Great Horned Owl (GHOW)	<b>Recorded:</b> <i>Petitota bubonis</i> Atyeo & Philips <sup>M</sup> ; <i>Kramerella bubonis</i> (Lonnfors) <sup>M</sup> ; <i>Pandaltura cirrata</i> (Müllet) <sup>M</sup> <b>Expected:</b> <i>Glaucalges attenuatus</i> (Buchholz)
<i>Speotyto cunicularia</i> (Molina) Burrowing Owl (BUOW)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Aegolius acadicus</i> (Gmelin) Northern Saw-whet Owl (NSOW)	<b>Recorded:</b> <i>Kramerella mrciaki</i> Cerný <sup>M</sup> ; <i>Petitota haenggi</i> Mironov <sup>M</sup> <b>Expected:</b> <i>Glaucalges attenuatus</i> (Buchholz)
<i>Asio otus</i> (Linnaeus) Long-eared Owl (LEOW)	<b>Recorded:</b> <i>Kramerella oti</i> (Lonnfors) <sup>A, M</sup> ; <i>Glaucalges attenuatus</i> (Buchholz) <sup>M</sup> ; <i>Pandaltura strigosii</i> (Buchholz) <sup>M</sup> <b>Expected:</b> n/a
<i>Asio flammeus</i> (Pontoppidan) Short-eared Owl (SEOW)	<b>Recorded:</b> <i>Kramerella flammei</i> (Lonnfors) <sup>M</sup> ; <i>Glaucalges attenuatus</i> (Buchholz) <sup>M</sup> ; <i>Pandaltura strigosii</i> (Buchholz) <sup>M</sup> <b>Expected:</b> n/a

**CAPRIMULGIFORMES**

**Caprimulgidae**

- Chordeiles minor* (Forster)  
Common Nighthawk (CONI)  
*Phalaenoptilus nuttallii* (Audubon)  
Common Poorwill (COPW)

**Recorded:** *Paragabucinia* n. sp.<sup>M</sup>; *Passeroptes* sp.<sup>A</sup>  
**Expected:** n/a

**Recorded:** n/a  
**Expected:** n/a

**APODIFORMES**

**Trochilidae**

- Archilochus colubris* (Linnaeus)  
Ruby-throated Hummingbird (RTHU)

**Recorded:** *Passeroptes* sp.<sup>A</sup>; *Microlichus* sp.<sup>A</sup>  
**Expected:** *Trochiloptes johnstoni* (Fain)

**CORACIIFORMES**

**Alcedinidae**

- Ceryle alcyon* (Linnaeus)  
Belted Kingfisher (BEKI)

**Recorded:** *Proterothrix* n. sp.<sup>M</sup>  
**Expected:** n/a

**PICIFORMES**

**Picidae**

- Picoideus pubescens* (Linnaeus)  
Downy Woodpecker (DOWO)

**Recorded:** *Neopteronysus pici* (Scopoli)<sup>M</sup>; *Pteronyssus picooides* Cerný & Schumilo<sup>A,M</sup>; *Picalgoides picimajoris* Buchholz<sup>M</sup>; *Passeroptes* sp.<sup>A</sup>  
**Expected:** n/a

- Picoideus villosus* (Linnaeus)  
Hairy Woodpecker (HAWO)

**Recorded:** *Neopteronysus pici* (Scopoli)<sup>A,M</sup>; *Pteronyssus brevipes* Berlese<sup>M</sup>; *Pteronyssus picooides* Cerný & Schumilo<sup>A,M</sup>; *Picalgoides picimajoris* Buchholz<sup>M</sup>  
**Expected:** n/a

- Colaptes auratus* (Linnaeus)  
Northern Flicker (NOFL)

**Recorded:** *Stenopteronysus proctorae* Mironov & Galloway<sup>A,M</sup>; *Picalgoides picimajoris* Buchholz<sup>aff.M</sup>; *Microlichus* sp.<sup>A</sup>; *Mexalgoides* sp.<sup>A</sup>  
**Expected:** n/a

- Sphyrapicus varius* (Linnaeus)  
Yellow-bellied Sapsucker (YBSA)

**Recorded:** *Pteronyssus sphyrapicinus* Mironov & Galloway<sup>A,M</sup>  
**Expected:** n/a



Bird Hosts	Recorded and Expected Species of Feather Mites
<b>PASSERIFORMES</b>	
<b>Tyrannidae</b>	
<i>Contopus sordidulus</i> Selater	<b>Recorded:</b> n/a
Western Wood-Pewee (WEWP)	<b>Expected:</b> n/a
<i>Empidonax alnorum</i> Brewster	<b>Recorded:</b> <i>Proctophyllodes</i> sp. <sup>A</sup>
Alder Flycatcher (ALFL)	<b>Expected:</b> n/a
<i>Empidonax traillii</i> (Audubon)	<b>Recorded:</b> n/a
Willow Flycatcher (WIFL)	<b>Expected:</b> n/a
<i>Empidonax minimus</i> (Baird & Baird)	<b>Recorded:</b> <i>Analgas</i> n. sp. 1 <sup>M</sup> , <i>Trouessartia</i> n. sp. 1 <sup>M</sup> ; <i>Proctophyllodes empidonicensis</i> Atyeo & Braasch <sup>M</sup>
Least Flycatcher (LEFL)	<b>Expected:</b> n/a
<i>Empidonax occidentalis</i> Nelson	<b>Recorded:</b> n/a
Cordilleran Flycatcher (COFL)	<b>Expected:</b> n/a
<i>Sayornis phoebe</i> (Latham)	<b>Recorded:</b> n/a
Eastern Phoebe (EAPH)	<b>Expected:</b> <i>Nycteridocaulus bilobatus</i> Atyeo; <i>Tyrannidectes banksi</i> Valim & Hemandes
<i>Sayornis saya</i> (Bonaparte)	<b>Recorded:</b> n/a
Say's Phoebe (SAPH)	<b>Expected:</b> <i>Proctophyllodes empidonicensis</i> Atyeo & Braasch
<i>Tyrannus verticalis</i> Say	<b>Recorded:</b> n/a
Western Kingbird	<b>Expected:</b> n/a
<i>Tyrannus tyrannus</i> (Linnaeus)	<b>Recorded:</b> <i>Analgas tyranni</i> Tyrrell <sup>M</sup> ; <i>Amerodectes</i> sp. <sup>A</sup> ; <i>Tyrannidectes</i> n. sp. <sup>M</sup> ; <i>Nycteridocaulus lamellus</i> Atyeo <sup>A</sup> ; <i>Trouessartia</i> n. sp. 2 <sup>M</sup> ; <i>Trouessartia</i> sp. <sup>A</sup> ; <i>Passeroptes</i> sp. <sup>A</sup>
Eastern Kingbird (EAKI)	<b>Expected:</b> n/a
<b>Alaudidae</b>	
<i>Eremophila alpestris</i> (Linnaeus)	<b>Recorded:</b> <i>Proctophyllodes microcaulus</i> Gaud <sup>M</sup> ; <i>Alaudicola bilobata</i> (Robin) <sup>M</sup> ; <i>Analgas iridentulatus</i> Haller <sup>M</sup>
Horned Lark (HOLA)	<b>Expected:</b> n/a
<b>Hirundinidae</b>	
<i>Tachycineta bicolor</i> (Vieillot)	<b>Recorded:</b> <i>Anhemialges albidus</i> (Tyrrell) <sup>M</sup> ; <i>Anhemialges</i> sp. <sup>A</sup> ; <i>Scutularmyssus tyrrelli</i> (Canestrini) <sup>A, M</sup> ; <i>Trouessartia</i> n. sp. 3 <sup>M</sup> ;
Tree Swallow (TRES)	<i>Trouessartia</i> sp. <sup>A</sup> ; <i>Xotalgoides</i> sp. <sup>A</sup>
	<b>Expected:</b> n/a

<i>Tachycineta thalassina</i> (Swainson) Violet-green Swallow (VGSW)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Progne subis</i> (Linnaeus) Purple Martin (PUMA)	<b>Recorded:</b> <i>Scutulanysus subis</i> Mironov & Galloway <sup>A, M</sup> , <i>Scutulanysus prognæ</i> Mironov & Galloway <sup>A, M</sup> , <i>Anthemialges</i> n. sp. <sup>M</sup> , <i>Trouessartia</i> n. sp. 4 <sup>M</sup> , <i>Trouessartia</i> sp. <sup>A</sup> <b>Expected:</b> n/a
<i>Stelgidopteryx serripennis</i> (Audubon) Northern Rough-winged Swallow (NRWS)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Riparia riparia</i> (Linnaeus) Bank Swallow (BANS)	<b>Recorded:</b> <i>Scutulanysus obscurus</i> (Berlese) <sup>M</sup> , <i>Trouessartia ripariae</i> Mironov <sup>A, M</sup> , <i>Trouessartia piscicauda</i> Gaud <sup>M</sup> <b>Expected:</b> <i>Pterodectes rutilus</i> Robin; <i>Scutulanysus nuntiaeversis</i> (Berlese)
<i>Hirundo rustica</i> Linnaeus Barn Swallow (BARS)	<b>Recorded:</b> <i>Scutulanysus hiruandicola</i> Mironov <sup>M</sup> , <i>Scutulanysus obscurus</i> (Berlese) <sup>M</sup> , <i>Trouessartia appendiculata</i> (Berlese) <sup>M</sup> , <i>Trouessartia microcaudata</i> Mironov <sup>M</sup> , <i>Anthemialges gaudi</i> Mironov <sup>M</sup> <b>Expected:</b> <i>Pterodectes rutilus</i> Robin; <i>Trouessartia crucifera</i> Gaud
<i>Petrochelidon pyrrhonota</i> Vieillot Cliff Swallow (CLSW)	<b>Recorded:</b> <i>Scutulanysus petrochelidonis</i> Mironov & Galloway <sup>M</sup> , <i>Scutulanysus obscurus</i> (Berlese) <sup>M</sup> , <i>Trouessartia</i> sp. 5 <sup>M</sup> <b>Expected:</b> n/a
<b>Corvidae</b>	
<i>Cyanocitta cristata</i> (Linnaeus) Blue Jay (BLJA)	<b>Recorded:</b> <i>Proctophyllodes occidentalis</i> <sup>M</sup> , <i>Proctophyllodes glandarinus</i> (Koch) aff. <sup>M</sup> , <i>Passeroptes latior</i> (Canestrini) <sup>M</sup> <b>Expected:</b> n/a
<i>Pica hudsonia</i> (Linnaeus) Black-billed Magpie (BBMA)	<b>Recorded:</b> <i>Proctophyllodes picae</i> (Koch) <sup>M</sup> , <i>Proctophyllodes</i> sp. <sup>A</sup> <b>Expected:</b> <i>Montesauria cylindrica</i> (Robin); <i>Gabucinia delibata</i> (Robin); <i>Analges corvinus</i> Mégnin ; <i>Proctophyllodes corvorum</i> Vitzthum
<i>Corvus brachyrhynchos</i> Brehm American Crow (AMCR)	<b>Recorded:</b> <i>Analges corvinus</i> Mégnin <sup>A, M</sup> , <i>Gabucinia delibata</i> (Robin) <sup>M</sup> ; <i>Trouessartia corvina</i> (Koch) <sup>M</sup> <b>Expected:</b> n/a
<i>Corvus corax</i> Linnaeus Common Raven (CORA)	<b>Recorded:</b> <i>Gabucinia delibata</i> (Robin) <sup>A, M</sup> ; <i>Proctophyllodes corvorum</i> Vitzthum <sup>A, M</sup> <b>Expected:</b> <i>Analges corvinus</i> Mégnin
<b>Paridae</b>	
<i>Poecile atricapillus</i> (Linnaeus) Black-capped Chickadee (BCCH)	<b>Recorded:</b> <i>Analges paricola</i> Chitrov & Mironov <sup>M</sup> ; <i>Sirelkoviacarus</i> sp. <sup>A</sup> ; <i>Proctophyllodes ater</i> Fritsch <sup>M</sup> <b>Expected:</b> n/a
<b>Sittidae</b>	
<i>Sitta canadensis</i> Linnaeus Red-breasted Nuthatch (RBNU)	<b>Recorded:</b> <i>Analges</i> sp. <sup>A</sup> ; <i>Proctophyllodes canadensis</i> Atyeo & Braasch <sup>A, M</sup> <b>Expected:</b> n/a

Recorded and Expected Species of Feather Mites	
<b>Bird Hosts</b>	
<b>Troglodytidae</b>	
<i>Salpinctes obsoletus</i> (Say) Rock Wren (ROWR)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Cistothorus platensis</i> (Latham) Sedge Wren (SEWR)	<b>Recorded:</b> <i>Analgus</i> n. sp. 2 <sup>M</sup> , <i>Proctophylloides</i> n. sp. 1 <sup>M</sup> <b>Expected:</b> n/a
<i>Cistothorus palustris</i> (Wilson) Marsh Wren (MAWR)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Troglodytes aedon</i> Vieillot House Wren (HOWR)	<b>Recorded:</b> <i>Analgus beaucourmii</i> Gaud <sup>M</sup> <b>Expected:</b> <i>Amerodectes troglodytis</i> (Cerný)
<b>Turdidae</b>	
<i>Sialia sialis</i> (Linnaeus) Eastern Bluebird (EABL)	<b>Recorded:</b> <i>Amerodectes sialianum</i> (Stoll) <sup>M</sup> ; <i>Proctophylloides vesca</i> Atyeo & Braasch <sup>M</sup> <b>Expected:</b> n/a
<i>Sialia currucoides</i> (Bechstein) Mountain Bluebird (MNBL)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Turdus migratorius</i> Linnaeus American Robin (AMRO)	<b>Recorded:</b> <i>Analgus magellanicus</i> Cooreman <sup>A, M</sup> ; <i>Microlichus</i> sp. <sup>A</sup> ; <i>Paralgus</i> sp. <sup>A</sup> ; <i>Proctophylloides musicus</i> Vitzthum <sup>A, M</sup> <b>Expected:</b> n/a
<b>Mimidae</b>	
<i>Dumetella carolinensis</i> (Linnaeus) Grey Catbird (GRCA)	<b>Recorded:</b> <i>Proctophylloides</i> n. sp. 2 <sup>M</sup> ; <i>Amerodectes</i> n. sp. 1 <sup>M</sup> ; <i>Proctophylloides</i> sp. <sup>A</sup> ; <i>Amerodectes</i> sp. <sup>A</sup> ; <i>Mesalgooides</i> sp. <sup>A</sup> <b>Expected:</b> n/a
<i>Mimus polyglottos</i> (Linnaeus) Northern Mockingbird (NOMO)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Oreoscoptes montanus</i> (Townsend) Sage Thrasher (SATH)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Toxostoma rufum</i> (Linnaeus) Brown Thrasher (BRTH)	<b>Recorded:</b> <i>Proctophylloides</i> n. sp. 3 <sup>M</sup> ; <i>Metapterodectes</i> n. sp. <sup>M</sup> <b>Expected:</b> n/a
<b>Motacillidae</b>	
<i>Anthus spragueii</i> (Audubon) Sprague's Pipit (SPPI)	<b>Recorded:</b> n/a <b>Expected:</b> n/a

<b>Bombycillidae</b>		
<i>Bombycilla cedrorum</i> Vieillot		
Cedar Waxwing (CEDW)		<b>Recorded:</b> <i>Analges integer</i> Giebel <sup>M</sup> ; <i>Proctophyllodes ampelidis</i> (Buchholz) <sup>M</sup> ; <i>Proctophyllodes</i> sp. <sup>A</sup> <b>Expected:</b> n/a
<b>Laniidae</b>		
<i>Lanius ludovicianus</i> Linnaeus		
Loggerhead Shrike (LOSH)		<b>Recorded:</b> <i>Analges integer</i> Giebel <sup>M</sup> ; <i>Proctophyllodes ludovicianus</i> Atyeo & Braasch <sup>M</sup> <b>Expected:</b> n/a
<b>Virionidae</b>		
<i>Vireo olivaceus</i> (Linnaeus)		
Red-eyed Vireo (REVI)		<b>Recorded:</b> <i>Analges</i> n. sp. 3 <sup>M</sup> ; <i>Analges</i> sp. <sup>A</sup> ; <i>Amerodectes</i> n. sp. 2 <sup>M</sup> <b>Expected:</b> <i>Proctophyllodes stoddardi</i> Atyeo & Braasch
<i>Vireo gilvus</i> (Vieillot)		
Warbling Vireo (WAVI)		<b>Recorded:</b> <i>Analges</i> n. sp. 3 <sup>M</sup> ; <i>Proctophyllodes quadratus</i> Atyeo & Braasch <sup>M</sup> <b>Expected:</b> n/a
<b>Parulidae</b>		
<i>Geothlypis trichas</i> (Linnaeus)		
Common Yellowthroat (COYE)		<b>Recorded:</b> <i>Amerodectes geothlypis</i> (Berla) aff. <sup>M</sup> <b>Expected:</b> n/a
<i>Icteria virens</i> (Linnaeus)		
Yellow-breasted Chat (YBCH)		<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Setophaga coronata</i> (Linnaeus)		
Yellow-rumped Warbler (YRWA)		<b>Recorded:</b> <i>Analges digitatus</i> Haller <sup>M</sup> ; <i>Proctophyllodes quadrisetosus</i> Atyeo & Braasch <sup>M</sup> <b>Expected:</b> n/a
<i>Setophaga petechia</i> (Linnaeus)		
Yellow Warbler (YEWA)		<b>Recorded:</b> <i>Trouessartia</i> sp. <sup>A</sup> <b>Expected:</b> <i>Proctophyllodes dendroicae</i> Atyeo & Braasch
<i>Setophaga ruticilla</i> (Linnaeus)		
American Redstart (AMRE)		<b>Recorded:</b> <i>Proctophyllodes</i> n. sp. 4 <sup>M</sup> <b>Expected:</b> n/a
<b>Cardinalidae</b>		
<i>Pheucticus melanocephalus</i> (Swainson)		
Black-headed Grosbeak (BHGR)		<b>Recorded:</b> n/a <b>Expected:</b> <i>Proctophyllodes pheuctici</i> Atyeo & Braasch
<i>Spiza americana</i> (Gmelin)		
Dickcissel (DICK)		<b>Recorded:</b> n/a <b>Expected:</b> <i>Proctophyllodes tricetratus</i> Atyeo & Braasch
<i>Passerina amoena</i> (Say)		
Lazuli Bunting (LAZB)		<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Passerina cyanea</i> (Linnaeus)		
Indigo Bunting (INBU)		<b>Recorded:</b> <i>Proctophyllodes polyxenus</i> Atyeo & Braasch <sup>M</sup> <b>Expected:</b> n/a

Bird Hosts	Recorded and Expected Species of Feather Mites
<b>Emberizidae</b>	
<i>Pipilo erythrophthalmus</i> (Linnaeus) Eastern Towhee (EATO)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Proctophylloides polyxenus</i> Atyeo & Braasch
<i>Pipilo maculatus</i> Swainson Spotted Towhee (SPTO)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Spizella passerina</i> (Bechstein) Chipping Sparrow (CHSP)	<b>Recorded:</b> <i>Analgus</i> n. sp. 4 <sup>M</sup> , <i>Proctophylloides polyxenus</i> Atyeo & Braasch <sup>M</sup> , <i>Sirelkoviticarus</i> n. sp. <sup>M</sup> <b>Expected:</b> n/a
<i>Spizella pallida</i> (Swainson) Clay-coloured Sparrow (CCSP)	<b>Recorded:</b> <i>Analgus</i> sp. <sup>A</sup> <b>Expected:</b> <i>Proctophylloides polyxenus</i> Atyeo & Braasch
<i>Spizella breweri</i> Cassin Brewer's Sparrow (BRSP)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Pooecetes gramineus</i> (Gmelin) Vesper Sparrow (VESP)	<b>Recorded:</b> <i>Metapterodectes muticus</i> (Banks) <sup>M</sup> <b>Expected:</b> n/a
<i>Chondestes grammacus</i> (Say) Lark Sparrow (LASP)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Proctophylloides polyxenus</i> Atyeo & Braasch
<i>Calamospiza melanocorys</i> Stejneger Lark Bunting (LABU)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Proctophylloides calamospizae</i> Atyeo & Braasch
<i>Passerculus sandwichensis</i> (Gmelin) Savannah Sparrow (SAVS)	<b>Recorded:</b> <i>Analgus</i> n. sp. 5 <sup>M</sup> , <i>Proctophylloides polyxenus</i> Atyeo & Braasch <sup>M</sup> <b>Expected:</b> n/a
<i>Ammodramus leconteii</i> (Audubon) Le Conte's Sparrow (LCSP)	<b>Recorded:</b> <i>Proctophylloides</i> sp. <sup>A</sup> <b>Expected:</b> n/a
<i>Ammodramus bairdii</i> (Audubon) Baird's Sparrow (BAIS)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<i>Ammodramus savannarum</i> (Gmelin) Grasshopper Sparrow (GRSP)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Proctophylloides polyxenus</i> Atyeo & Braasch
<i>Ammodramus caudacutus</i> Allen Sharp-tailed Sparrow (STSP)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Proctophylloides polyxenus</i> Atyeo & Braasch
<i>Melospiza melodia</i> (Wilson) Song Sparrow (SOSP)	<b>Recorded:</b> <i>Proctophylloides armatus</i> (Banks) <sup>M</sup> <b>Expected:</b> n/a

<i>Calcarius mccownii</i> (Lawrence) McCown's Longspur (MCLO)	<b>Recorded:</b> <i>Proctophyllodes plectrophenax</i> Mironov <sup>M</sup> <b>Expected:</b> n/a
<i>Calcarius ornatus</i> (Townsend) Chestnut-collared Longspur (CCLO)	<b>Recorded:</b> n/a <b>Expected:</b> n/a
<b>Icteridae</b>	
<i>Dolichonyx oryzivorus</i> (Linnaeus) Bobolink (BOBO)	<b>Recorded:</b> <i>Proctophyllodes pullizonatus</i> Atyeo & Braasch <sup>M</sup> <b>Expected:</b> n/a
<i>Xanthocephalus xanthocephalus</i> (Bonaparte) Yellow-headed Blackbird (YHBL)	<b>Recorded:</b> <i>Proctophyllodes egglestoni</i> Spory <sup>M</sup> <b>Expected:</b> n/a
<i>Agelaius phoeniceus</i> (Linnaeus) Red-winged Blackbird (RWBL)	<b>Recorded:</b> <i>Proctophyllodes egglestoni</i> Spory <sup>A,M</sup> , <i>Mesalgoides johnstoni</i> (Spory) <sup>M</sup> , <i>Mesalgoides</i> sp. <sup>A</sup> , <i>Sirelkoviacarus critesi</i> Spory <sup>M</sup> <b>Expected:</b> n/a
<i>Sturnella neglecta</i> Audubon Western Meadowlark (WEME)	<b>Recorded:</b> <i>Mesalgoides</i> n. sp. <sup>M</sup> ; <i>Proctophyllodes trisetosus</i> Ewing & Storer <sup>M</sup> <b>Expected:</b> n/a
<i>Quiscalus quiscula</i> (Linnaeus) Common Grackle (COGR)	<b>Recorded:</b> <i>Proctophyllodes egglestoni</i> Spory <sup>M</sup> , <i>Proctophyllodes mexicanus</i> Atyeo & Braasch <sup>M</sup> , <i>Mesalgoides johnstoni</i> (Spory) <sup>M</sup> , <i>Sirelkoviacarus critesi</i> Spory <sup>M</sup> <b>Expected:</b> n/a
<i>Euphagus cyanocephalus</i> (Wagler) Brewer's Blackbird (BRBL)	<b>Recorded:</b> <i>Proctophyllodes egglestoni</i> Spory <sup>A,M</sup> , <i>Mesalgoides</i> sp. <sup>A</sup> <b>Expected:</b> n/a
<i>Euphagus carolinus</i> (Müller) Rusty Blackbird (RUBL)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Proctophyllodes egglestoni</i> Spory; <i>Proctophyllodes mexicanus</i> Atyeo & Braasch
<i>Molothrus ater</i> (Boddaert) Brown-headed Cowbird (BHCO)	<b>Recorded:</b> <i>Amerodectes molothrus</i> Mironov <sup>M</sup> ; <i>Proctophyllodes</i> n. sp. 5 <sup>M</sup> ; <i>Proctophyllodes</i> sp. <sup>A</sup> ; <i>Analges</i> sp. <sup>A</sup> <b>Expected:</b> <i>Proctophyllodes egglestoni</i> Spory
<i>Icterus galbula</i> (Linnaeus) Baltimore Oriole (BAOR)	<b>Recorded:</b> <i>Proctophyllodes icteri</i> Atyeo & Braasch <sup>M</sup> , <i>Proctophyllodes</i> sp. <sup>A</sup> ; <i>Amerodectes</i> n. sp. 3 <sup>M</sup> ; <i>Amerodectes</i> sp. <sup>A</sup> ; <i>Analges</i> sp. <sup>A</sup> <b>Expected:</b> n/a
<i>Icterus bullockii</i> (Swainson) Bullock's Oriole (BUOR)	<b>Recorded:</b> n/a <b>Expected:</b> <i>Proctophyllodes icteri</i> Atyeo & Braasch
<b>Fringillidae</b>	
<i>Spinus tristis</i> (Linnaeus) American Goldfinch (AMGO)	<b>Recorded:</b> <i>Proctophyllodes spini</i> Atyeo & Braasch <sup>A,M</sup> , <i>Analges passerinus</i> (Linnaeus) <sup>M</sup> , <i>Sirelkoviacarus</i> sp. <sup>A</sup> <b>Expected:</b> n/a
<i>Carpodacus mexicanus</i> (Müller) House Finch (HOFI)	<b>Recorded:</b> <i>Analges</i> n. sp. 6 <sup>M</sup> <b>Expected:</b> <i>Proctophyllodes vegetans</i> Trouessart

**Table 5.** List of taxa of chewing lice (Insecta: Phthiraptera) known or expected (\*) from native birds breeding in grasslands in Manitoba, Saskatchewan, and Alberta. Some species of lice are known to infest a number of species of hosts included in this study; \*\* indicates a species of louse expected to occur but not collected or recorded from any hosts in grasslands in Manitoba, Saskatchewan, or Alberta. Taxa that may be undescribed or that cannot be identified to species in this study are indicated as “sp.”

## AMBLYCERA

### Laemobothriidae

- Laemobothrion (Eulaemobothrion) atrum* (Nitzsch, 1818) – AMCO  
*Laemobothrion (Eulaemobothrion) simile* Kellogg, 1869\*\* – EAGR  
*Laemobothrion (Laemobothrion) glutinans* Nitzsch [In Giebel], 1861 – TUVU  
*Laemobothrion (Laemobothrion) maximum* (Scopoli, 1763) – RTHA, SWHA, NOHA\*, COHA\*, OSPR\*, GOEA\*, FEHA\*  
*Laemobothrion (Laemobothrion) tinnunculi* (Linnaeus, 1758) – PRFA, MERL\*, AMKE\*  
*Laemobothrion (Laemobothrion) vulturis* (Fabricius, 1775)\*\* – BAEA, GOEA

### Menoponidae

- Actornithophilus hoplopteri* (Mjöberg, 1910) – KILL  
*Actornithophilus lacustris* Clay, 1962 – WILL  
*Actornithophilus limosae* (Kellogg, 1908) – MAGO  
*Actornithophilus mexicanus* (Emerson, 1953)\*\* – BNST  
*Actornithophilus ochraceus* (Nitzsch, 1818) – PIPL\*, MOPL\*  
*Actornithophilus patellatus* (Piaget, 1890)\*\* – LBCU  
*Actornithophilus piceus lari* (Packard, 1870) – FRGU, RBGU, CAGU\*  
*Actornithophilus piceus piceus* (Denny, 1842) – COTE, CATE\*, FOTE\*  
*Actornithophilus stictus* (Kellogg & Paine, 1911)\*\* – WISN  
*Actornithophilus umbrinus* (Burmeister, 1838) – WIPH, SPSA\*  
*Actornithophilus uniseriatus* (Piaget, 1880) – AMAV  
*Amyrsidea perdicis* (Denny, 1842)\*\* – GRPC, STGR  
*Austromenopon aegialitidis* (Durrant, 1906) – KILL, PIPL\*  
*Austromenopon atrofulvum* (Piaget, 1880) – BLTE, CATE, COTE\*, FOTE\*  
*Austromenopon durisetosum* (Blagoveshtchensky, 1948) – WISN  
*Austromenopon himantopi* Timmermann, 1954\*\* – BNST  
*Austromenopon limosae* Timmermann, 1954 – MAGO  
*Austromenopon micrandrum* (Nitzsch [In Giebel], 1866) – AMAV  
*Austromenopon sachtlebeni* Timmermann, 1954 – WILL  
*Austromenopon transversum* (Denny, 1842) – FRGU, RBGU, CAGU\*  
*Bonomiella columbae* Emerson, 1957 – MODO  
*Bonomiella zenaidae* Cicchino & González-Acuña, 2012\*\* – MODO  
*Ciconiphilus butoridiphagus* Carriker, 1964\* – GRHE  
*Ciconiphilus cygni* Price & Beer, 1965\*\* – COGO  
*Ciconiphilus decimfasciatus* (Boisduval & Lacordaire, 1835) – BCNH, GBHE  
*Ciconiphilus pectiniventris* (Harrison, 1916) – CAGO  
*Colpocephalum brachysomum* Kellogg & Chapman, 1902 – GHOW, SEOW\*  
*Colpocephalum flavescens* (De Haan, 1829) – BAEA, GOEA  
*Colpocephalum impressum* Rudow, 1866\*\* – GOEA  
*Colpocephalum kelloggi* Osborn, 1902 – TUVU  
*Colpocephalum nanum* Piaget, 1890 – COHA, RTHA, SSHA  
*Colpocephalum napiforme* Rudow, 1869\*\* – OSPR, RTHA  
*Colpocephalum pectinatum* Osborn, 1902\*\* – BUOW  
*Colpocephalum subzeraphae* Tendeiro, 1988 – AMKE, MERL  
*Colpocephalum turbinatum* Denny, 1842 – BAEA, RTHA, SWHA, NOHA\*, OSPR\*, PRFA\*  
*Colpocephalum unciferum* Kellogg, 1896 – AWPE  
*Colpocephalum zeraphae* Anseri, 1955 – PRFA  
*Cuculiphilus alternatus* (Osborn, 1902) – TUVU  
*Eidmanniella pellucida* (Rudow, 1869) – DCCO  
*Hohorstiella paladinella* Hill & Tuff, 1978 – MODO  
*Holomenopon acutae* Price, 1971\*\* – NOPI

- Holomenopon bucephalae* Price, 1971\*\* – BUFF, COGO  
*Holomenopon clauseni* Price, 1971 – BWTE, WODU, BUFF\*  
*Holomenopon clypeilargum* Eichler, 1943 – BWTE, AGWT, WODU, AMWI\*, NOSH\*, NOPI\*, CITE\*, CANV\*  
*Holomenopon leucoxanthum* (Burmeister, 1838) – CAGO, AGWT, MALL, REDH, LESC, WODU, CANV, RUDU, AMWI\*, GADW\*, NOSH\*, NOPI\*, CITE\*, BUFF\*  
*Holomenopon loomisii* (Kellogg, 1896)\*\* – WWSC  
*Holomenopon maxbeieri* Eichler, 1954 – MALL  
*Holomenopon setigerum* (Blagoveshtchensky, 1948) – NOSH, NOPI\*, AGWT\*, CITE\*  
*Kurodaia acadicae* Price & Beer, 1963 – NSWO  
*Kurodaia flammei* Price & Beer, 1963\*\* – SEOW  
*Kurodaia fulvofasciata* (Piaget, 1880) – BAEA, RTHA, SWHA, NOHA\*, SWHA\*  
*Kurodaia haliaeeti* (Denny, 1842) – OSPR  
*Kurodaia magna* Emerson, 1960 – GHOW  
*Machaerilaemus americanus* (Ewing, 1930) – PUMA  
*Machaerilaemus clayae* (Balát, 1966)\*\* – BANS  
*Machaerilaemus complexus* Malcomson, 1937\*\* – FISP  
*Machaerilaemus cyanocittae* Price, Hellenthal & Dalgleish, 2002 – BLJA  
*Machaerilaemus laticorpus* (Carriker, 1903) – RUBL, RWBL, YHBB, LASP\*  
*Machaerilaemus maestus* (Kellogg & Chapman, 1899) – SAVS, SOSP\*, VESP\*, EATO\*, BRTH\*  
*Machaerilaemus malleus* (Burmeister, 1838) – BARS, CLSW  
*Menacanthus aedonidis* Price, 1977 – HOWR  
*Menacanthus alaudae* (Schrank, 1776) – AMGO, WEME\*, HOLA\*, HOFI\*  
*Menacanthus aurocapillus* Carriker, 1958 – OVEN  
*Menacanthus camelinus* (Nitzsch [In Giebel], 1874)\*\* – LOSH  
*Menacanthus chrysophaeus* (Kellogg, 1896)\*\* – SOSP, FISP  
*Menacanthus curuccae* (Schrank, 1776)\*\* – REVI  
*Menacanthus dendroicae* Price, 1977 – YRWA  
*Menacanthus eurysternus* (Burmeister, 1838) – AMRO, COGR, BAOR, BLJA, BBMA, NOFL, DOWO\*, NOMO\*, BRTH\*, AMRE\*, RWBL\*, BHCb\*  
*Menacanthus geothlypis* Price, 1977\*\* – COYE  
*Menacanthus gonophaeus* (Burmeister, 1838) – CORA  
*Menacanthus obsoleti* Price, 1977\*\* – ROWR  
*Menacanthus pici* (Denny, 1842) – DOWO, HAWO, NOFL, YBSA  
*Menacanthus quiscali* Price, 1977\*\* – COGR, BHCO, RUBL  
*Menacanthus sturnellae* Price, 1977 – WEME, CEDW\*  
*Menacanthus tenuifrons* (Blagoveshtchensky, 1940)\*\* – MAWR, SEWR  
*Menacanthus tyranni* Price, 1977 – EAKI, WEKI  
*Myrsidea aquilonia* Clay, 1968 – RUBL  
*Myrsidea conspicua* (Kellogg & Chapman, 1902)\*\* – HOFI  
*Myrsidea dissimilis* (Kellogg, 1896) – PUMA  
*Myrsidea emersoni* Clay, 1966 – AMRO  
*Myrsidea fuscomarginata* (Osborn, 1896) – BHCO, COGR, RWBL\*  
*Myrsidea interrupta* (Osborn, 1896) – AMCR  
*Myrsidea latifrons* (Carriker [ & Schull], 1910) – BANS  
*Myrsidea melanorum* (Kellogg, 1896)\*\* – EATO  
*Myrsidea ridulosa* (Kellogg & Chapman, 1899)\*\* – YEWA  
*Myrsidea rustica* (Giebel, 1874) – BARS  
*Myrsidea vinlandica* Klockenhoff & Schirmers, 1976 – CORA  
*Myrsidea* sp. – TRES  
*Myrsidea* sp. – AMRE  
*Nosopon lucidum* (Rudow, 1869) – AMKE, MERL, PRFA, COHA, NOHA, RTHA, SSHA\*  
*Piagetella incomposita* (Kellogg & Chapman, 1899) – DCCO  
*Piagetella peralis* (Leidy, 1878) – AWPE  
*Pseudomenopon dolium* (Rudow, 1869) – WEGR, HOGH\*, BNHR\*  
*Pseudomenopon pilosum* (Scopoli, 1763) – AMCO  
*Pseudomenopon scopulacorne* (Denny, 1842) – SORA, VIRA  
*Trinoton anserinum* (Fabricius [J.C.], 1805) – CAGO  
*Trinoton querquedulae* (Linnaeus, 1758) – BWTE, AGWT, GADW, MALL, NOPI, CANV, REDH, WWSC, WODU, RUDU\*, CITE\*



**Ricinidae**

- Ricinus arcuatus* (Kellogg & Mann, 1912) – EAKI  
*Ricinus australis* (Kellogg, 1896)\*\* – LAZB, INBU  
*Ricinus calcarii* Nelson, 1972\*\* – CCLO  
*Ricinus dalgleishi* Nelson, 1972 – COYE, CEDW\*  
*Ricinus dendroicae* Nelson, 1972\*\* – YEWA, YRWA  
*Ricinus diffusus* (Kellogg, 1896)\*\* – CHSP, SAVS, GRSP, LCSP, SOSP\*  
*Ricinus elongatus* (Olfers, 1816) – AMRO, BOWA  
*Ricinus fringillae* De Geer, 1778 – BCCH, BANS\*, EATO\*, CHSP\*, BRSP\*, VESP\*, SOSP  
*Ricinus lineatus* (Osborn, 1896) – RTHU\*\*  
*Ricinus marginatus* (Children, 1836) – EAKI, EAPH, LEFL, WEWP\*, WIFL\*, WEKI\*  
*Ricinus microcephalus* (Kellogg, 1896)\*\* – HOFI  
*Ricinus serratus* (Durrant, 1906)\*\* – HOLA  
*Ricinus sittae* Nelson, 1972\*\* – RBNU  
*Ricinus subdiffusus* Nelson, 1972 – CHSP, BRSP\*, FISP\*  
*Ricinus subhastatus* (Durrant, 1906)\*\* – EATO  
*Ricinus sucinaceus* (Kellogg, 1896)\*\* – WIFL, SAPH  
*Ricinus vireoensis* Nelson, 1972 – REVI  
*Trochilocetes* sp. – RTHU

**ISCHNOCERA****Philopteridae**

- Acidoproctus moschatae* (Linnaeus, 1758) – CANV, REDH, LESC\*  
*Alcedoffula alcyonae* Carriker, 1959 – BEKI  
*Anaticola anseris* (Linnaeus, 1758) – CAGO  
*Anaticola clangulae* (Fabricius [O.], 1780) – BUFF, COGO  
*Anaticola crassicornis* (Scopoli, 1763) – BWTE, AGWT, GADW, MALL, NOSH, NOPI, WODU, RUDU, CITE\*  
*Anaticola mergiserrati* (De Geer, 1778) – COME, CANV, REDH, WWSC  
*Anatoecus dentatus* (Scopoli, 1763) – BWTE, AGWT, AMWI, CAGO, COGO, GADW, MALL, REDH, WODU, RUDU, CITE\*, BUFF\*  
*Anatoecus icterodes* (Nitzsch, 1818) – BWTE, AGWT, CAGO, COGO, GADW, MALL, BUFF, REDH, WODU, RUDU, CITE\* (This species is synonymized with *I. dentatus* by Grossi *et al.* In press)  
*Anatoecus penicillatus* Kéler, 1960 – CAGO  
*Aquanirmus colymbinus* (Scopoli, 1763) – HOGH  
*Aquanirmus occidentalis* Edwards, 1965 – WEGH  
*Aquanirmus podilymbus* Edwards, 1965 – PBGR  
*Ardeicola botauri* (Osborn, 1896) – AMBI  
*Ardeicola cruscula* Carriker, 1960 – GBHE  
*Brueelia americana* Cicchino & Castro, 1996\*\* – BHCO  
*Brueelia angustifrons* (Carriker, 1902)\*\* – LASP  
*Brueelia biocellata* (Piaget, 1880) – BBMA, CORA  
*Brueelia brunneinucha* Cicchino, 1983 – GRCA, NOMO\*  
*Brueelia cedrorum* (Piaget, 1880) – CEDW  
*Brueelia clayae* Ansari, 1956 – BLJA  
*Brueelia domestica* (Kellogg & Chapman, 1899) – BARS  
*Brueelia dorsale* Williams, 1983\*\* – BRTH  
*Brueelia emersoni* Cicchino & Castro, 1996 – RUBL  
*Brueelia iliaci* (Denny, 1842) – AMRO  
*Brueelia interposita* (Kellogg, 1899)\*\* – YEWA  
*Brueelia longa* (Kellogg, 1896) – CLSW  
*Brueelia longifrons* Carriker, 1956 – BCCH  
*Brueelia ornatissima* (Giebel, 1874) – BHCO, COGR, RWBL, BOBO\*  
*Brueelia parabolocybe* (Carriker, 1903) – EAKI  
*Brueelia pseudopicturata* Cicchino, 1986 – WEME  
*Brueelia rotundata* (Osborn, 1896) – AMCR  
*Brueelia rotundifrons* Cicchino, 1981\*\* – SATH  
*Brueelia straminea* (Denny, 1842) – DOWO, NOFL\*, YBSA\*  
*Brueelia subis* (Carriker, 1963) – PUMA  
*Brueelia tenuis* (Burmeister, 1838) – BANS  
*Brueelia xanthocephali* (Osborn, 1896) – YHBB  
*Brueelia* sp. 1 – BAOR

*Brueelia* sp. 2 – CHSP  
*Brueelia* sp. 3 – CCSP  
*Brueelia* sp. 4 – HOFI  
*Brueelia* sp. 5 – INBU  
*Brueelia* sp. 6 – TRES  
*Brueelia* sp. 7 – VESP  
*Brueelia* sp. 8 – COYE  
*Carduiceps clayae* Timmermann, 1954 – MAGO  
*Cirrophthirius testudinarius* (Children, 1836) – AMAV  
*Columbicola baculoides* (Paine, 1914) – MODO  
*Columbicola macrourae* (Wilson, 1941) – MODO  
*Craspedorrhynchus americanus* Emerson, 1960 – RTHA  
*Craspedorrhynchus aquilinus* (Denny, 1842) – GOEA  
*Craspedorrhynchus halioti* (Osborn, 1896) – BAEA  
*Craspedorrhynchus subhaematopus* Emerson, 1960 – COHA  
*Craspedorrhynchus* sp. 1 – MERL  
*Craspedorrhynchus* sp. 2 – PRFA  
*Craspedorrhynchus* sp. 3 – SSHA  
*Craspedorrhynchus* sp. 4 – SWHA  
*Cuculicola erythrophthalmus* Emerson, 1964 – BBCU  
*Cuculoecus coccygii* (Osborn, 1896) – BBCU  
*Cummingsiella ambigua* (Burmeister, 1838)\*\* – WISN  
*Degeeriella aquilarum* Eichler, 1943\*\* – GOEA  
*Degeeriella carruthi* Emerson, 1953 – AMKE  
*Degeeriella discocephalus* (Burmeister, 1838) – BAEA, GOEA  
*Degeeriella fulva* (Giebel, 1874) – RTHA, GOEA\*  
*Degeeriella nisis* (Giebel, 1866) – SSHA  
*Degeeriella regalis* (Giebel, 1866) – SWHA  
*Degeeriella rufa* (Burmeister, 1838) – MERL, PRFA  
*Degeeriella vagans* (Giebel, 1874) – COHA  
*Falcolipeurus marginalis* (Osborn, 1902) – TUVU  
*Falcolipeurus suturalis* (Rudow, 1869)\*\* – GOEA  
*Fulicoffula americana* Emerson, 1960 – SORA  
*Fulicoffula comstocki* (Kellogg & Chapman, 1902)\*\* – VIRA  
*Fulicoffula distincta* Emerson, 1960 – SORA  
*Fulicoffula longipila* (Kellogg, 1896) – AMCO  
*Goniodes centroceri* Simon, 1938\*\* – SAGR  
*Goniodes cupido* Rudow, 1870\*\* – GRPC  
*Goniodes nebraskensis* Carriker, 1945 – STGR  
*Incidifrons monachus* (Kellogg & Paine, 1911)\*\* – VIRA  
*Incidifrons transpositus* (Kellogg, 1896) – AMCO  
*Lagopoecus gibsoni* Hopkins, 1947 – SAGR\*, STGR (possible err. det.)  
*Lagopoecus perplexus* (Kellogg & Chapman, 1899)\*\* – STGR  
*Lunaceps clayae* Timmermann, 1954 – MAGO  
*Multicola macrocephalus* (Kellogg, 1896) – CONI  
*Ornithobius gontioleurus* Denny, 1842 – CAGO  
*Pectinopygus farallonii* (Kellogg, 1896) – DCCO  
*Pectinopygus tordoffi* Elbel & Emerson, 1956 – AWPE  
*Penenirmus albiventris* (Scopoli, 1763)\*\* – HOWR  
*Penenirmus auritus* (Scopoli, 1763) – DOWO, HAWO, YBSA  
*Penenirmus jungens* (Kellogg, 1896) – NOFL  
*Penenirmus quadripustulatus* (Kellogg & Mann, 1912)\*\* – EATO  
*Philoaterus agelaii* (Osborn, 1896) – BHCO, RWBL  
*Philoaterus coarctatus* (Scopoli, 1763) – LOSH  
*Philoaterus corvi* (Linnaeus, 1758) – CORA  
*Philoaterus crassipes* (Burmeister, 1838) – BLJA  
*Philoaterus domesticus* (Kellogg, 1896) – PUMA  
*Philoaterus major* (Kellogg, 1896) – TRES, CLSW\*  
*Philoaterus microsomaticus* Tandan, 1955 – BARS, BANS\*  
*Philoaterus osborni* Edwards, 1952 – AMCR, CORA\*

- Philopterus picae* (Denny, 1842) – BBMA  
*Philopterus quisqualis* (Osborn, 1896) – COGR  
*Philopterus sialii* (Osborn, 1896) – EABL  
*Philopterus tropicalis* Carriker, 1956\*\* – NRWS  
*Philopterus* sp. 1 – BCCH  
*Philopterus* sp. 2 – CEDW  
*Philopterus* sp. 3 – CHSP  
*Philopterus* sp. 4 – EAKI  
*Philopterus* sp. 5 – EAPH  
*Philopterus* sp. 6 – INBU  
*Philopterus* sp. 7 – REVI  
*Philopterus* sp. 8 – YHBB  
*Philopterus* sp. 9 – YRWA  
*Philopterus* sp. 10 – LCSP  
*Philopterus* sp. 11 – AMGO  
*Philopterus* sp. 12 – BAOR  
*Physconelloides zenauidurae* (McGregor, 1917) – MODO  
*Picicola foedus* (Kellogg & Chapman, 1899) – EAPH, EAKI, WEKI, SAPH\*  
*Picicola orpheus* (Osborn, 1896) – GRCA  
*Picicola porisma* Dalgleish, 1969 – NOFL  
*Picicola snodgrassi* (Kellogg, 1896) – DOWO, HAWO\*  
*Quadriceps assimilis* (Piaget, 1890)\*\* – MNPL  
*Quadriceps boeophilus* (Kellogg, 1896) – KILL  
*Quadriceps carrikeri* Hopkins & Timmermann, 1954 – WILL  
*Quadriceps caspius* (Giebel, 1874) – CATE  
*Quadriceps fimbriatus* (Giebel, 1866) – WIPH  
*Quadriceps hemichrous* (Nitzsch [In Giebel], 1866)\*\* – BNST  
*Quadriceps macrocephalus* (Waterston, 1914)\*\* – PIPL  
*Quadriceps phaeonotus* (Nitzsch [In Giebel], 1866) – BLTE  
*Quadriceps punctatus lingulatus* (Waterston, 1914) – FRGU  
*Quadriceps punctatus regressus* Timmermann, 1952\*\* – CATE  
*Quadriceps punctatus sublingulatus* Timmermann, 1952 – RBGU  
*Quadriceps sellatus* (Burmeister, 1838) – COTE  
*Quadriceps semifissus* (Nitzsch [In Giebel], 1866) – AMAV, BNST\*  
*Quadriceps zephyra* (Timmermann, 1954)\*\* – AMAV  
*Quadriceps* sp. – FOTE  
*Rallicola advenus* (Kellogg, 1896) – AMCO  
*Rallicola kelloggi* Emerson, 1957 – VIRA  
*Rallicola mystax* (Giebel, 1874) – SORA  
*Rallicola subporzanae* Emerson, 1957 – SORA  
*Rhynonirmus scolopacis* (Denny, 1842) – WISN  
*Rotundiceps cordatus* (Osborn, 1896) – MAGO  
*Saemundssonina conica conica* (Denny, 1842)\*\* – KILL  
*Saemundssonina kratochvili* Balát, 1950\*\* – WISN  
*Saemundssonina lari* (Fabricius [O.], 1780) – FRGU, RBGU, CAGU\*  
*Saemundssonina laticaudata* (Rudow, 1869) – CATE  
*Saemundssonina lobaticeps* (Giebel, 1874) – BLTE  
*Saemundssonina parvigenitalis* Ward, 1955\*\* – FOTE  
*Saemundssonina platygaster platygaster* (Denny, 1842)\*\* – PIPL  
*Saemundssonina sterna* (Linnaeus, 1758) – COTE  
*Saemundssonina tricolor* Carriker, 1956\*\* – WIPH  
*Saemundssonina* sp. 1 – WILL  
*Saemundssonina* sp. 2 – MAGO  
*Strigiphilus acadicus* Emerson & Price, 1973 – NSWO  
*Strigiphilus barbatus* (Osborn, 1902) – LEOW  
*Strigiphilus cursor* (Burmeister, 1838) – SEOW  
*Strigiphilus oculatus* (Rudow, 1870) – GHOW  
*Strigiphilus speotyti* (Osborn, 1896) – BUOW  
*Strigiphilus syrni* (Packard, 1873) – GHOW  
*Sturnidoecus simplex* (Kellogg, 1896) – AMRO

**Table 6.** List of feather mite taxa (Acari: Astigmatina: Analgoidea, Pterolichoidea) from grassland-breeding native birds in Canada. Both found and expected taxa are listed; species marked with an asterisk (\*) after the date of description are expected species from Table 3. “n. sp.” indicates species that appear to be new to science. “aff.” means that mites are slightly different from typical individuals or descriptions of corresponding species, but not enough to consider them as separate species. “unplaced” indicates that the specimens found were not the correct age/sex, or were too damaged, for species-level identification. Asterisks after host abbreviations indicate that these bird species are expected to host a particular mite species, on the basis of the literature, but that these associations were not recorded in our study.

### **Superfamily Analgoidea**

#### **Alloptidae**

*Alloptes bisetatus* (Haller, 1882) – COTE  
*Alloptes leptolobus* Gaud, 1976\* – BLTE  
*Alloptes macrochetæ* Dubinin, 1951\* – BLTE  
*Alloptes niloticus* Kivganov & Mironov, 1992 – CATE  
*Alloptes obtusolobus* Dubinin, 1951 – FRGU  
*Alloptes oxylobus* Dubinin, 1951 – RBGU, FRGU  
*Alloptes phalaropinus* Vasyukova & Mironov, 1991 – WIPH  
*Alloptes* sp. (unplaced) – MALL  
*Brephosceles anatina* Dubinin, 1951\* – MALL, NOPI, AGWT  
*Brephosceles bucephali* Mironov, 1985\* – COGO  
*Brephosceles cygni* Vasyukova & Mironov, 1986 *aff.* – CAGO  
*Brephosceles longistriatus* Peterson, 1971\* – KILL, PIPL  
*Dinalloptes chelionatus* Atyeo, & Peterson, 1966 – DCCO  
*Plicatalloptes pelecani* (Dubinin, 1954) – AWPE  
*Plicatalloptes subcrassipes* (Dubinin & Dubinina, 1954) – DCCO  
*Psilobrephosceles ortymogetrae* (Canestrini, 1878) – SORA

#### **Analgidae**

##### **Analginae**

*Analges beaucournui* Gaud, 1973 – HOWR  
*Analges corvinus* Mégnin, 1877 – BBMA\*, AMCR, CORA\*  
*Analges digitatus* Haller, 1882 – YWRA  
*Analges integer* Giebel, 1871 – CEDW, LOSH  
*Analges magellanicus* Cooreman, 1953 – AMRO  
*Analges paricola* Chirov & Mironov, 1983 – BCCH  
*Analges passerinus* (Linnaeus, 1758) – AMGO  
*Analges tridentulatus* Haller, 1882 – HOLA  
*Analges tyranni* Tyrrell, 1882 – EAKI  
*Analges* n. spp. 1-6 – LEFL(1), REVI(2), WAVI(3), CHSP(4), SAVS(5), HOFI(6)  
*Analges* spp. (unplaced) – RBNU, REVI, CCSP, BHCO, BAOR  
*Anhemialges albidus* (Tyrrell, 1882) – TRES  
*Anhemialges gaudi* Mironov, 2009 – BARS  
*Anhemialges* n. sp. – PUMA  
*Anhemialges* sp. (unplaced) – TRES

##### **Anomalginae**

*Strelkoviacarus critesi* Spory, 1965 – RWBL, COGR  
*Strelkoviacarus* n. sp. – CHSP  
*Strelkoviacarus* spp. (unplaced) – BCCH, AMGO

##### **Ancyralginae**

*Ancyralges cathartinus* Mironov & Galloway, 2003 – TUVU

##### **Megniniinae**

*Diplaegidia* n. sp. – MODO  
*Megniniella fulicae* Gaud, 1958 – AMCO  
*Megniniella ratcliffi* Mironov & Galloway, 2002 – SORA  
*Metanalges holderi* Mironov & Galloway, 2002 – SORA  
*Metanalges appendiculatus* (Haller, 1882) – VIRA

**Avenzoariidae****Avenzoariinae**

*Avenzoaria phalaropi* Gaud, 1972 – WIPH

*Bychovskiata macularii* Mironov & Dabert, 1997\* – SPSA

*Bychovskiata semipalmati* Mironov & Dabert, 1995\* – PIPL

*Bychovskiata subcharadrii* Dubinin, 1951\* – BNST

*Bychovskiata vociferi* Mironov & Dabert, 1997 – KILL

*Capelloptes flagellicaulus* (Trouessart & Neumann, 1888)\* – WISN

*Pomeranzevia bartramica* (Mironov & Dabert, 1995)\* – UPSA

**Bonnetellinae**

*Bdellorhynchus polymorphus* Trouessart, 1885 – MALL, BWTE, NOSH\*, NOPI\*, AGWT\*, CITE\*, COGO\*

*Bdellorhynchus oxyurae* Dubinin, 1956 – RUDU

*Bdellorhynchus* sp. (unplaced) – BWTE

*Pandionacarus fuscus* (Nitzsch, 1818) – OSPR

*Scutomegninia gaudi* Mironov, 2000 – AWPE

*Scutomegninia ibidis* (Trouessart, 1885)\* – WFIB

*Scutomegninia microfalcifera* Mironov, 1990 – DCCO

*Zachvatkinia caspica* Mironov, 1989 – CATE

*Zachvatkinia chlidoniae* Mironov, 1989 – BLTE

*Zachvatkinia larica* Mironov, 1989 – RBGU, FRGU

*Zachvatkinia sterna* (Canestrini & Fanzago, 1876) – COTE

*Zachvatkinia* sp. (unplaced) – CAGU

*Zygochelifer beeri* Atyeo, 1984 – WODU

**Dermoglyphidae**

*Paralges* n. sp. – RBGU

*Paralges* sp. (unplaced) – STGR, AMRO

**Dermationidae**

*Neodermaton anatum* (Fain, 1964)\* – NOSH

*Passeroptes latior* (Canestrini, 1894) – BLJA

*Passeroptes* spp. (unplaced) – CONI, RTHU, DOWO, EAKI

*Pelecanoptes onocrotali* Fain & Atyeo, 1975 – AWPE

*Trochiloptes johnstoni* (Fain, 1965)\* – RTHU

**Epidermoptidae**

*Microlichus* spp. (unplaced) – RTHU, NOFL, AMRO

**Proctophyllodidae****Proctophyllodinae**

*Nycteridocaulus bilobatus* Atyeo, 1966\* – EAPH

*Nycteridocaulus lamellus* Atyeo, 1966 – EAKI

*Proctophyllodes ampelidis* (Buchholz, 1869) – CEDW

*Proctophyllodes armatus* (Banks, 1909) – SOSP

*Proctophyllodes ateri* Fritsch, 1961 – BCCH

*Proctophyllodes calamospizae* Atyeo & Braasch, 1966\* – LABU

*Proctophyllodes canadensis* Atyeo & Braasch, 1966 – RBNU

*Proctophyllodes corvorum* Vitzthum, 1922 – BBMA\*, CORA

*Proctophyllodes dendroicae* Atyeo & Braasch, 1966\* – YEWA

*Proctophyllodes eglestoni* Spory, 1965 – YHBL, RWBL, COGR, BRBL, RUBL\*, BHCO\*

*Proctophyllodes empidonis* Atyeo & Braasch, 1966 – LEFL, SAPH\*

*Proctophyllodes glandarinus* (Koch, 1841) *aff.* – BLJA

*Proctophyllodes icteri* Atyeo & Braasch, 1966 – BAOR, BUOR

*Proctophyllodes ludovicanus* Atyeo & Braasch, 1966 – LOSH

*Proctophyllodes mexicanus* Atyeo & Braasch, 1966 – COGR, RUBL\*

*Proctophyllodes microcaulus* Gaud, 1957 – HOLA

*Proctophyllodes musicus* Vitzthum, 1922 – AMRO  
*Proctophyllodes occidentalis* Atyeo & Braasch, 1966 – BLJA  
*Proctophyllodes pheuctici* Atyeo & Braasch, 1966\* – BHGR  
*Proctophyllodes picae* (Koch, 1840) – BBMA  
*Proctophyllodes plectrophenax* Mironov, 2012 – MCLO  
*Proctophyllodes polyxenus* Atyeo & Braasch, 1966 – INBU, EATO\*, CHSP, CCSP\*, LASP\*, SAVS, GRSP\*, STSP\*  
*Proctophyllodes pullizonatus* Atyeo & Braasch, 1966 – BOBO  
*Proctophyllodes quadratus* Atyeo & Braasch, 1966 – WAVI  
*Proctophyllodes quadrisetosus* Atyeo & Braasch, 1966 – YRWA  
*Proctophyllodes spini* Atyeo & Braasch, 1966 – AMGO  
*Proctophyllodes stoddardi* Atyeo & Braasch, 1966\* – REVI\*  
*Proctophyllodes tricetratus* Atyeo & Braasch, 1966\* – DICK  
*Proctophyllodes trisetosus* Ewing & Storer, 1915 – WEME  
*Proctophyllodes vegetans* Trouessart, 1899\* – HOFI  
*Proctophyllodes vesca* Atyeo & Braasch, 1966 – EABL  
*Proctophyllodes* n. spp. 1-5 – SEWR(1), GRCA(2), BRTH(3), AMRE(4), BHCO(5)  
*Proctophyllodes* spp. (unplaced) – ALFL, BBMA, GRCA, CEDW, LCSP, BHCO, BAOR

#### **Pterodectinae**

*Alaudicola bilobata* (Robin, 1877) – HOLA  
*Amerodectes molothrus* Mironov, 2008 – BHCO  
*Amerodectes sialiarum* (Stoll, 1893) – EABL  
*Amerodectes troglodytis* (Cerný, 1974)\* – HOWR  
*Amerodectes geothlypis* (Berla, 1973) *aff.* – COYE  
*Amerodectes* n. spp. 1-3 – GRCA(1), REVI(2), BAOR(3)  
*Amerodectes* spp. (unplaced) – EAKI, GRCA, BAOR  
*Metapterodectes muticus* (Banks, 1909) – VESP  
*Metapterodectes* n. sp. – BRTH  
*Montesauria cylindrica* (Robin, 1877)\* – BBMA  
*Proterothrix* n. sp. – BEKI  
*Pterodectes rutilus* Robin, 1877\* – BARS  
*Tyrannidectes banksi* Hernandes & Valim, 2009\* – EAPH  
*Tyrannidectes* n. sp. – EAKI

#### **Psoroptoididae**

*Mesalgoides johnstoni* (Spory, 1965) – RWBL, COGR  
*Mesalgoides* n. sp. – WEME  
*Mesalgoides* spp. (unplaced) – NOFL, GRCA, RWBL, BRBL  
*Pandalura cirrata* (Müller, 1860) – GHOW  
*Pandalura strigisoti* (Buchholz, 1869) – LEOW, SEOW  
*Picalgoides picimajoris* (Buchholz, 1869) – DOWO, HAWO, NOFL  
*Temnalges* n. sp. – AMCO

#### **Pteronyssidae**

*Neopteronysus pici* (Scopoli, 1763) – DOWO, HAWO  
*Pteronyssus brevipes* Berlese, 1885 – HAWO  
*Pteronyssus picoides* Cerný & Schumilo, 1973 – DOWO, HAWO  
*Pteronyssus sphyrapicus* Mironov & Galloway, 2006 – YBSA  
*Scutulanysus hirundicola* Mironov, 1985 – BARS  
*Scutulanysus nuntiaeveris* (Berlese, 1884)\* – BANS  
*Scutulanysus obscurus* (Berlese, 1884) – BANS, BARS, CLSW  
*Scutulanysus petrochelidonis* Mironov & Galloway, 2006 – CLSW  
*Scutulanysus prognei* Mironov & Galloway, 2006 – PUMA  
*Scutulanysus subis* Mironov & Galloway, 2006 – PUMA  
*Scutulanysus tyrrelli* (Canestrini, 1899) – TRES  
*Stenopteronysus proctorae* Mironov & Galloway, 2006 – NOFL

**Trouessartiidae**

- Trouessartia appendiculata* (Berlese, 1886) – BARS  
*Trouessartia corvina* (Koch, 1841) – AMCO  
*Trouessartia crucifera* Gaud, 1957\* – BARS  
*Trouessartia microcaudata* Mironov, 1983 – BARS  
*Trouessartia piscicauda* Gaud, 1957 – BANS  
*Trouessartia ripariae* Mironov, 1983 – BANS  
*Trouessartia* n. spp. 1-5 – LEFL(1), EAKI(2), TRES(3), PUMA(4), CLSW(5)  
*Trouessartia* spp. (unplaced) – EAKI, TRES, PUMA, YEWA

**Xolalgidae****Ingrassiinae**

- Analloptes buettikeri* Mironov, 1997 – OSPR  
*Analloptes megnini* (Trouessart, 1885) – VIRA\*, AMCO  
*Analloptes* sp. (unplaced) – AMCO  
*Dubininia accipitrina* (Trouessart, 1885) – AMKE, MERL\*  
*Glaucalges attenuatus* (Buchholz, 1869) – GHOW\*, NSOW\*, LEOW, SEOW  
*Gymnaloptes pallens* (Trouessart & Neumann, 1888) – VIRA\*, SORA, AMCO  
*Ingrassia fissitarsa* (Gaud, 1958) – WISN  
*Ingrassia forcipata* (Haller, 1882) – SPSA  
*Ingrassia* n. sp. – RGPU  
*Ingrassia* spp. (unplaced) – AMWI, NOSH, FRGU  
*Metingrassia pelecani* Mironov & Galloway, 2002 – AWPE  
*Metingrassia minutidisca* Gaud, 1973 – DCCO  
*Pteraloptes stellaris* (Buchholz, 1869) – AMBI  
*Vingrassia velata* (Mégnin, 1877) – WODU, MALL, NOSH\*, NOPI, AGWT, LESC

**Xolalginae**

- Xolalgoides* sp. – TRES

**Zumptiinae**

- Parazumptia* n. sp. – SORA

**Superfamily Pterolichoidea****Cheylabididae**

- Hemicheylabis praecox* (Trouessart, 1885) – SWHA

**Falculiferidae**

- Falculifer isodontus* Gaud & Barré, 1992 – MODO  
*Pterophagus spilosikyus* Gaud & Barré, 1992 – MODO

**Freyanidae**

- Freyana anatina* (Koch, 1844) – AMWI\*, MALL, BWTE, NOSH, NOPI, AGWT  
*Freyana aythinae* Dubinin, 1853 – CANV, REDH, LESC\*  
*Freyana brantina* Vasyukova & Mironov, 1991 – CAGO  
*Freyana bucephalae* Dubinin, 1950 – BUFF\*, COGO  
*Freyana dendronessae* Dubinin, 1950 – WODU  
*Freyana largifolia* Mégnin & Trouessart, 1884 – AMWI\*, MALL\*, BWTE, NOSH\*, NOPI\*, AGWT\*, CITE\*  
*Freyana nyrocae* Dubinin, 1950\* – REDH, LESC  
*Freyana oidemiae* Dubinin, 1950\* – WWSC  
*Freyana* n. sp. – WODU  
*Freyana* sp. (unplaced) – MALL  
*Michaelia* n. sp. – DCCO

**Gabuciniidae**

- Aetacarus leptotrichus* Gaud, 1983 – NOHA  
*Aetacarus phylloproctus* (Mégnin & Trouessart, 1884) – BAEA

*Aetacarus* n. sp. – MERL

*Cathartacarus aurae* Mironov & Galloway, 2003 – TUVU

*Gabucinia delibata* (Robin, 1877) – BBMA\*, AMCR, CORA

*Hieracolicthus nisi* (Canestrini, 1878) – SWHA, RTHA

*Paragabucinia* n. sp. – CONI

*Proaposenidia accipitris* Mironov & Proctor, 2007 – COHA

#### **Kramerellidae**

*Kramerella bubonis* (Lonnfors, 1937) – GHOW

*Kramerella mrciaki* Cerný, 1973 – NSOW

*Kramerella oti* (Lonnfors, 1937) – LEOW

*Kramerella flammei* (Lonnfors, 1937) – SEOW

*Parabdellorhynchus pelecanus* (Dubinin, 1954)\* – AWPE

*Petitota bubonis* Atyeo & Philips, 1984 – GHOW

*Petitota haenggi* Mironov, 1997 – NSOW

*Pseudogabucinia intermedia* (Méglin & Trouessart, 1884) – NOHA\*, SWHA, RTHA

#### **Pterolichidae**

##### **Ardeacarinae**

*Ardeacarus ardeae* (Canestrini, 1978) – AMBI, GBHE, BCNH\*

##### **Pterolichinae**

*Epoplichus minor* (Méglin & Trouessart, 1884) – AMKE, MERL

*Grallobia fulcae* (Trouessart, 1885) – AMCO

*Grallobia* n. sp. – SORA

*Grallobia* sp. (unplaced) – SORA

*Grallolichus proctogamus* (Trouessart, 1885) – AMCO

*Grallolichus* n. sp. – VIRA

*Montchadskiana tridentata* Dabert & Ehmsberger, 1999\* – WILL

*Pilochaeta rafalski* Dabert, 1997\* – SPSA

*Pseudaloptinus aquilinus* (Trouessart, 1884) – BAEA, GOEA

*Tetraolichus cupido* Atyeo & Gaud, 1992\* – GRPC

#### **Ptiloxenidae**

*Ptiloxenus major* (Méglin & Trouessart, 1884) – RNGR, HOGH, BNGR

*Ptiloxenus* n. spp. 1-2 – PBGR(1), WEBR(2)

*Ptiloxenus* spp. (unplaced) – HOBR, WEGH, SORA

*Sokoloviana gracilis* (Méglin & Trouessart, 1884)\* – BNST

*Sokoloviana kucheruki* Cerný, 1974 – KILL

#### **Rectijanuidae**

*Rectijanua braaschi* Atyeo & Peterson, 1976 *aff.* – WODU

#### **Syringobiidae**

*Grenieria simplex* (Trouessart, 1886)\* – COTE, FOTE

*Grenieria megachelata* Dabert & Atyeo, 1997\* – CATE

*Limosilichus fedoa* Dabert, 2003\* – MAGO

*Limosilichus numeni* Vasyukova & Mironov, 1986\* – LBCU

*Phyllochaeta maculariae* Dabert, 2003 – SPSA

*Phyllochaeta melodus* Dabert, 2003\* – PIPL

*Phyllocheta tenuiseta* Dabert & Atyeo, 1993 – KILL

*Plutarchusia pseudochelepus* Dubinin, 1956\* – COTE

*Syringobia chelepus* Trouessart & Neumann, 1888\* – WILL

*Thecarthra grandis* (Trouessart & Neumann, 1888)\* – BLTE

*Thecarthra semaphora* (Trouessart, 1886)\* – COTE

*Thecarthra theca* (Méglin & Trouessart, 1884) – CATE



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## Chapter 6

# Springtails (Hexapoda: Collembola) of the Prairie Grasslands of Canada

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**Abstract.** Collembola, also known as “springtails”, are common components of many soil systems, including grasslands. The published studies from Canadian grasslands that explore soil microarthropod communities suggest that both the diversity and densities of Collembola are low compared with those in other habitats (e.g., forest systems) and other fauna groups (e.g., Acari). Very few studies, however, document and describe Canadian grassland Collembola at the species level, and all major grassland areas of Canada are undersampled for Collembola. For grasslands outside the Prairies Ecozone, no record of sampling was found for Collembola in southern Ontario tallgrass systems, nor has there been a concerted effort of collection in bunchgrass/sagebrush habitats of British Columbia. Despite the paucity of direct information from Canada, studies from the mid-central United States and elsewhere provide the basis for a potential species-level checklist. In particular, species from the following families are expected to dominate species diversity in Canadian grasslands: Isotomidae, Entomobryidae, Hypogastruridae, and Sminthuridae. The dearth of species-level knowledge is due to the lack of taxonomic expertise for the Collembola in Canada.

**Résumé.** Les collemboles sont présents dans de nombreux systèmes de sols, y compris ceux des prairies. Les études publiées portant sur les prairies canadiennes qui se penchent sur les communautés de microarthropodes terricoles donnent à conclure que la densité et la diversité des collemboles présents dans ces communautés sont faibles comparativement à celles observées dans d'autres habitats (ex : sols forestiers) ou à celles caractérisant d'autres groupes fauniques (ex : acariens). Cependant, rares sont les études qui examinent et décrivent les espèces de collemboles des prairies canadiennes, et aucune des principales zones de prairies du Canada n'a fait l'objet d'échantillonnages exhaustifs des collemboles. À l'extérieur de l'écozone des prairies, il semble que les collemboles n'aient fait l'objet d'aucun travail d'échantillonnage dans les écosystèmes à herbes hautes du sud de l'Ontario, ni d'aucun effort concerté de collecte dans les peuplements de graminées cespiteuses ou d'arboises de la Colombie-Britannique. Malgré la rareté des informations directes provenant du Canada, les études réalisées dans le centre des États-Unis et ailleurs fournissent le point de départ d'une possible liste des espèces. En particulier, on s'attend à ce que les espèces appartenant aux familles suivantes occupent une place dominante dans les prairies canadiennes : isotomidés, entomobryidés, hypogastruridés et sminthuridés. Le manque de connaissances sur les espèces de collemboles découle de l'absence d'experts de ce groupe au Canada.

### Introduction

Collembola, also known as “springtails,” are small (0.5–3 mm), wingless, hexapodous arthropods. The common name springtail is derived from a ventral appendage of many species called the furcula, which is used in predator defence (Hopkin 1997). The diagnostic feature of collembolans, however, is the presence of a tubular colophore used primarily in maintaining moisture balance (Hopkin 1997). Collembola, previously considered within

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the class Insecta (Apterygota: Collembola), are now considered as a sister clade to the Insecta within the subphylum Hexapoda (Entognatha: Collembola). Controversy on this placement and the monophyly of Hexapoda (Nardi *et al.* 2003; Meusemann *et al.* 2010) continued for many years, when inconsistencies arose depending on whether analyses were based on morphology, mitochondrial DNA sequences, or nuclear genes. However, a subsequent analysis has firmly placed Collembola within the Hexapoda and the hexapods as a monophyletic group (Timmermans *et al.* 2008). As such, Collembola are considered basal hexapods, yet the status of Entognatha as a distinct clade remains uncertain (Meusemann *et al.* 2010). As the Collembola occur in two distinct body forms, elongate and globular, morphological taxonomy within the group led to the previous distinction of two orders, Arthropleona and Symphypleona (Christiansen and Bellinger 1980), whereas modern taxonomy now recognizes four orders: Poduromorpha, Entomobryomorpha, Symphypleona, and Neelipleona (Deharveng 2004).

Collembola are common components of many soil systems (Petersen and Luxton 1982; Behan-Pelletier 2003). Feeding habits, based on both gut enzyme analysis (Berg *et al.* 2004) and stable isotope ratios (Chahartaghi *et al.* 2005), suggest that most Collembola species fall within a continuum from phycophages/herbivores to primary and secondary decomposers. Many species display “r-selection” characteristic life history traits (i.e., fast, semelparous reproduction and short lifespan), which allows them to respond quickly to environmental change. The primary abiotic factors affecting collembolan density and diversity are moisture and soil acidity (Hopkin 1997). Collembola play an important, albeit mostly indirect, role in decomposition through their interactions with the microbial community (Visser 1985).

Despite recent discussion on placement and classifications within the Collembola (Xiong *et al.* 2008), species-level taxonomy for the group is relatively well-known (Behan-Pelletier and Bisset 1992). There are approximately 7,850 known species worldwide (Janssens 2007), with approximately 700 species described from North America (about 80% of estimated diversity); the known number of species in Canada is 412, whereas the estimated number of Canadian Collembola is roughly 520 species (Behan-Pelletier 2003).

### Collembola of Canadian Grassland Ecosystems

Few Canadian studies document and describe grassland Collembola communities, and only two studies describe the biodiversity of grassland Collembola and document species-level data. Aitchison (1979) found 16 species of winter-active Collembola in a tallgrass Manitoba prairie, where *Isotoma manitobae* was the most abundant species. This study illustrates how poorly Collembola are known in Canada because the dominant species was previously undescribed. Berg and Pawluk (1984), found 10 Collembola species across seven prairie and agricultural vegetative covers in central Alberta, eight of which were found in native fescue grassland sites. In general, grassland areas have only low-to-moderate diversity (Petersen and Luxton 1982); thus, richness values presented in the aforementioned studies (16 and 10) may be typical of Canadian grassland Collembola diversity. However, species richness reported by Aitchison (1979) is likely an underrepresentation of total Collembola diversity, as sampling was performed in winter when abundances were low, and the collection method used was pitfall traps, which could preclude endogeic (burrowing) species.

Collembola densities are better known than richness estimates, both in grasslands and in general. Densities of Collembola typically range from 100 to 670,000 individuals/

m<sup>2</sup> (Petersen and Luxton 1982) worldwide, with the highest densities associated with moist, organic forest soils. Grasslands typically have low-to-moderate densities, which are influenced by factors such as soil moisture and soil organic matter (Petersen and Luxton 1982; Ferguson 2001). For instance, in grassland sites of northeastern Illinois and southwestern Michigan, Brand and Dunn (1998) recorded densities of 104–500 individuals/m<sup>2</sup> in native grasslands, and 27–361 individuals/m<sup>2</sup> in restored grasslands. In a study of the relationships among roots, mycorrhizal fungi, and Collembola in a native grassland near Regina, Saskatchewan (50°28'N; 104°22'W), Steinaker and Wilson (2008) used an *in situ* below-ground “rhizotron” camera to look at collembolan density. They found that densities were greater in forest than in grassland but varied little among horizons within the grassland sites (~250 individuals/m<sup>2</sup>). This contradicts the results of most vertical distribution studies, which show that densities of Collembola tend to be greatest in the top few centimetres of soil in grassland systems (Berg and Pawluk 1984), in association with greater soil moisture and organic matter at the soil surface. Other factors driving Collembola density in grassland systems include plant species richness (Salamon *et al.* 2004; Sabais *et al.* 2011) and disturbance regimes (e.g., grazing; Dombos 2001; Clapperton *et al.* 2002). Collembola densities also change seasonally, whereby abundance peaks in summer and secondarily in the fall, but remains low in the spring (Berg and Pawluk 1984; Steinaker and Wilson 2008) and winter (Aitchison 1979).

#### ***Notable Canadian Grassland Collembola Studies***

- Aitchison (1979) found 16 species of Collembola in aspen parkland and tallgrass prairie near Fort Whyte, Manitoba (49°49'N; 97°13'W).
- Berg and Pawluk (1984) found 10 Collembola species across seven different vegetative covers, including fescue grasslands near Breton, Alberta (53°07'N; 114°28'W); eight species were collected from the fescue sites.
- Ferguson (2001) studied collembolan densities in different habitat types along a grassland-to-forest gradient near Saskatoon, Saskatchewan (52°10'N; 106°41'W), and found that abundances did not differ among habitat types, but were significantly positively correlated with soil humidity.
- Clapperton *et al.* (2002) summarized the changes in abundance and diversity under different grazing regimes of an Alberta fescue prairie (50°11'N; 113°53'W). They found that grazing reduced the soil moisture and increased the temperature and bulk density of the soil, and that Collembola were more abundant in the reduced grazing plots.
- Steinaker and Wilson (2008) used an *in situ* below-ground rhizotron camera to look at collembolan density in a native grassland near Regina, Saskatchewan (50°28'N; 104°22'W). They found that densities were greater in forest than in grassland but varied little among horizons within the grassland sites.

#### **Estimated Collembola Diversity in Canadian Grasslands**

Most studies of microarthropods in Canadian grassland systems do not present a list of species for Collembola. Skidmore (1995) presents a checklist of the known species of Collembola for Canada and Alaska, which includes 52 species recorded from the Prairie Provinces of Alberta and Saskatchewan. Not all of these species would have been from grassland habitats, and not all grasslands in Canada are included in this list. However, this is



the only checklist available to initiate a list of Collembola species for Canadian grasslands. Therefore, presented here is a possible species list for Canadian grassland Collembola that is based primarily on the work of Skidmore (1995), cross-referenced with species recorded from the northern United States (e.g., Northfield Minnesota prairie (Jensen *et al.* 1973); tallgrass prairie in southwestern Michigan and northeastern Illinois (Brand and Dunn 1998)); and a single reference for *Willemia arida* in dry grasslands in the southern British Columbia interior (Cannings and Scudder 2005) (Table 1).

The most comprehensive study of grassland Collembola to date in North America was by Brand and Dunn (1998), who explored the diversity and abundance of Collembola in native and restored tallgrass prairie in southwestern Michigan and northeastern Illinois. Brand and Dunn (1998) found 27 species in native grasslands, with the highest diversity being 26 species found at a single location. These 27 species of Collembola are also likely found in southern Manitoba or Ontario grasslands. In their study, Brand and Dunn (1998) concluded that soil moisture was the most important factor affecting richness and abundance on grassland sites, and they considered it to be the driving factor separating differences between native and restored sites, with the highest soil humidity occurring under native prairie. The most commonly encountered species by Brand and Dunn (1998) were *Hypogastrura boletivora*, *Isotoma viridis*, and *Lepidocyrtus pallidus*. There is anecdotal evidence for the dominance of isotomids, entomobryids, lepidocyrtins, hypogastrurids, and sminthurids in grasslands. In addition, grassland Collembola noted from Europe and the United Kingdom (e.g., *Tullbergia krausbaueri*, *Folsomia quadrioculata*, *Isotoma viridis*; Butcher *et al.* 1971) are similar to species observed in grassland studies of North America (Jensen *et al.* 1973; Aitchison 1979; Skidmore 1995; Brand and Dunn 1998), suggesting that these species may be common components of grassland habitats.

### Ecology of Collembola in Grassland Systems

Jonas *et al.* (2007) used an experimental mesocosm system and  $\delta C^{13}$  stable isotope analysis to determine that Collembola feed on both arbuscular mycorrhizal fungi and saprophytic fungi in grassland habitats. Ladygina *et al.* (2008) used phospholipid fatty acid and isotope analyses to demonstrate that Collembolan species may actively switch diets in grassland soil food webs when other Collembola species are present. Yet despite the documented microbial feeding of Collembola and their assumed role in decomposition and nutrient cycling, Hunt *et al.* (1987) estimated that Collembola play only a small role in the detrital food web of prairie systems because of low population abundances, consumption rates, predation rates, and waste production compared with other more dominant soil fauna groups, such as predaceous and fungivorous mites and nematodes.

### Biogeographical Aspects

Biogeographical information is also sparse for grassland Collembola. There is some information on geographical distributions of Collembolan species provided in the taxonomic identification keys of Christiansen and Bellinger (1980). In Canada, the primary collection of Collembola is housed at the Canadian National Collection of Insects, Arachnids and Nematodes in Ottawa, which contains 35 type specimens and approximately 2,000 slides of identified and 500 slides of unidentified specimens (Behan-Pelletier 2003). However, most specimens in the collection are from arctic, subarctic, and mixed forest habitats, with prairie habitats and grassland locations poorly represented.

**Table 1.** Checklist of Collembola likely present in Canadian grasslands, based on species occurrences in grasslands in the United States. *Species checklist available at:* <http://dx.doi.org/10.5886/xd2b2ssg>

Family	Genus	Species/ Authority	References
Hypogastruridae	<i>Hypogastrura</i>	<i>christianseni</i> Yosii, 1960	Skidmore (1995)
		<i>nivicola</i> (Fitch, 1847)	Skidmore (1995)
		<i>ripperi</i> Gilsin 1952	D. Johnson (pers. obs.)
	<i>Ceratophysella</i> ( <i>Hypogastrura</i> )	<i>boletivora</i> Lippert & Butler, 1976	Brand and Dunn (1998); Skidmore (1995)
	<i>Ceratophysella</i>	<i>armata</i> (Nicolet, 1841)	Aitchison (1979)
	<i>Willemia</i>	<i>arida</i> Fjellberg, 1991	Skidmore (1995); Cannings and Scudder (2005)
		<i>denisi</i> Mills, 1932	Skidmore (1995)
	<i>Xenylla</i>	<i>humicola</i> (Fabricius, 1780)	Skidmore (1995)
<i>grisea</i> Axelson, 1900		Brand and Dunn (1998)	
Odontellidae	<i>Pseudochorutes</i>	<i>aureofasciatus</i> Harvey, 1898	Skidmore (1995)
		sp.	Aitchison (1979)
	<i>Neanura</i>	<i>muscorum</i> (Templeton, 1835)	Skidmore (1995); Aitchison (1979); Brand and Dunn (1998); Berg and Pawluk (1984)
Onychiuridae	<i>Onychiurus</i>	<i>absoloni</i> (Boener, 1901)	Skidmore (1995)
		<i>subtenuis</i> Folsom, 1917	Aitchison (1979)
		sp.	Brand and Dunn (1998)
	<i>Tullbergia</i>	<i>krasbaueri</i> Borner, 1901	Skidmore (1995); Butcher <i>et al.</i> (1971)
		<i>iowensis</i> Mills, 1932	Skidmore (1995)
		<i>granulata</i> Mills, 1934	Brand and Dunn (1998)
		<i>macrochaeta</i> (Rusek, 1976)	Skidmore (1995)
		<i>mala</i> Christiansen and Bellinger, 1980	Skidmore (1995)
sp.	Berg and Pawluk (1984); Hunt <i>et al.</i> (1987)		
Isotomidae	<i>Folsomides</i>	<i>americanus</i> Denis, 1931	Berg and Pawluk (1984); Skidmore (1995)
		<i>Folsomia</i>	<i>elongata</i> (MacGillivray, 1896)
		<i>finetaria</i> (Linnaeus, 1758)	Skidmore (1995)
		<i>nivalis</i> (Packard, 1873)	Skidmore (1995)
		<i>quadrioculata</i> (Tullberg, 1871)	Skidmore (1995); Butcher <i>et al.</i> (1971)
		sp.	Berg and Pawluk (1984)
	<i>Isotoma</i>	<i>ekmani</i> Fjellberg, 1977	Skidmore (1995)
		<i>notabilis</i> Schäffer, 1896	Skidmore (1995)
		<i>violacea</i> Tullberg, 1876	Skidmore (1995); Aitchison (1979)
		<i>viridis</i> Bourlet, 1839	Skidmore (1995); Aitchison (1979); Brand and Dunn (1998); Jensen <i>et al.</i> (1973); Butcher <i>et al.</i> (1971)
<i>nigrifrons</i> Folsom, 1937		Aitchison (1979)	

Family	Genus	Species/ Authority	References
		<i>blufusata</i> Fjellberg, 1978	Aitchison (1979)
		<i>manitobae</i> Fjellberg, 1978	Aitchison (1979)
		spp.	Brand and Dunn (1998); Hunt <i>et al.</i> (1987)
	<i>Isotomurus</i>	<i>palustris</i> (Muller, 1776)	Aitchison (1979)
	<i>Isotomiella</i>	<i>minor</i> (Schäffer 1896)	Skidmore (1995); Aitchison (1979)
Entomobryidae	<i>Entomobrya</i>	<i>bicolor</i> Guthrie, 1903	Jensen <i>et al.</i> (1973)
		<i>comparata</i> Folsom, 1919	Skidmore (1995)
		<i>confusa</i> Christiansen, 1958	Skidmore (1995)
		<i>gisini</i> Christiansen, 1958	Skidmore (1995); Aitchison (1979)
		<i>griseoolivata</i> (Packard, 1873)	Skidmore (1995)
		<i>guthriei</i> Mills, 1931	Skidmore (1995)
		<i>nivalis</i> (Linnæus, 1758)	Skidmore (1995); Aitchison (1979)
		<i>purpurascens</i> Packard, 1873	Skidmore (1995); Brand and Dunn (1998)
		spp.	Hunt <i>et al.</i> (1987); Aitchison (1979)
		<i>quadrilineata</i> Büker, 1939	Brand and Dunn (1998)
	<i>Lepidocyrtus</i>	<i>cinereus</i> Folsom, 1924	Skidmore (1995); Berg and Pawluk (1984)
		<i>cyaneus</i> Tullberg, 1871	Aitchison (1979); Jensen <i>et al.</i> (1973)
		<i>pallidus</i> Reuter, 1892	Brand and Dunn (1998)
		<i>paradoxus</i> Uzel, 1890	Brand and Dunn (1998)
		<i>violaceus</i> (Lubbock, 1873)	Brand and Dunn (1998)
		sp.	Hunt <i>et al.</i> (1987)
	<i>Orchesella</i>	<i>ainsliei</i> Folsom, 1924	Jensen <i>et al.</i> (1973); Aitchison (1979)
		<i>hexfasciata</i> Harvey, 1951	Brand and Dunn (1998)
		<i>cincta (vaga)</i> Linnaeus, 1758	Aitchison (1979)
	<i>Pseudosinella</i>	<i>octopunctata</i> Boerner, 1901	Skidmore (1995)
		<i>rolfsi</i> Mills, 1932	Brand and Dunn (1998)
	<i>Willowsia</i>	<i>buskii</i> (Lubbock, 1869)	Skidmore (1995)
Tomoceridae	<i>Tomocerus</i>	<i>flavescens</i> (Tullberg, 1871)	Skidmore (1995); Aitchison (1979); Brand and Dunn (1998); Jensen <i>et al.</i> (1973)
		<i>vulgaris</i> (Tullberg, 1871)	Skidmore (1995)
Arrhopalitidae	<i>Arrhopalites</i>	<i>amarus</i> Christiansen, 1966	Brand and Dunn (1998)
		<i>caecus</i> (Tullberg, 1871)	Skidmore (1995)
		<i>pygmaeus</i> (Wankel, 1861)	Skidmore (1995)
Sminthuridae	<i>Sminthurus</i>	<i>mencenbergae</i> Snider, 1983	Skidmore (1995)
		<i>pumilis</i> Krausbauer, 1898	Brand and Dunn (1998)
		<i>henshawi</i> (Folsom 1896)	Brand and Dunn (1998)
		spp.	Brand and Dunn (1998); Hunt <i>et al.</i> (1987)
Bourletiellidae	<i>Bourletiella</i>	sp.	Brand and Dunn (1998)

## Research Priorities

All major grassland areas of Canada are undersampled for Collembola. Sampling is not expected to reveal many new species of Collembola (Behan-Pelletier and Bissett 1992), but rather, given the rarity of information from these habitats, sampling will serve as a baseline for biodiversity monitoring and as a record to gauge biodiversity loss associated with grassland habitat loss. To my knowledge, there is no recorded sampling of Collembola in southern Ontario tallgrass/savannah, of which an estimated 3% of the original habitat remains (Rodger 1998). Further, it appears that no concerted effort has been made to collect Collembola in the bunchgrass/sagebrush habitat of British Columbia. Given the importance of this group as a bioindicator of soil ecosystem health, there is currently a need to increase capacity for taxonomic expertise of Collembola in Canada, as well as to collect in these under-represented habitats.

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## Chapter 7

# Stoneflies (Plecoptera) of the Canadian Prairie Provinces

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**Abstract.** Most Plecoptera (stonefly) species require cool, well-oxygenated water and are therefore not as well represented in prairie grassland habitats as they are in steep mountain streams or forested habitats. One hundred thirty-one species of Plecoptera have been recorded from the Prairie Provinces of Alberta, Saskatchewan, and Manitoba, including 61 that occur in or border aquatic habitats in the Prairies Ecozone. Alberta has the highest stonefly diversity because of its proximity to the mountains (108 species, 104 of which occur in the mountains), and the diversity in Saskatchewan is similar to that of Manitoba at 44 and 46 species, respectively. Only 2 of the 61 Prairies Ecozone species (*Perlesta dakota* and *Pteronarcys pictetii*) are restricted to this ecozone in Canada, and most of the species that occur in the Prairies Ecozone also occur in the Boreal Shield and Boreal Plains ecozones (40 species) and/or in the Montane Cordillera Ecozone (42 species). A list of species collected for each province and ecozone is provided, with references and probable refugial origins. Information on stonefly ecology, taxonomic works, zoogeography, and importance as monitoring tools pertinent to the region is also presented.

**Résumé.** La plupart des espèces de plécoptères (perles) ont besoin d'eau fraîche et bien oxygénée et ne sont donc pas aussi présentes dans les habitats des prairies qu'elles ne le sont dans les cours d'eau des habitats de montagne ou de forêt. On a recensé 131 espèces de plécoptères dans les provinces des prairies — Alberta, Saskatchewan et Manitoba —, y compris 61 vivant à l'intérieur ou à la périphérie d'habitats aquatiques de l'écozone des prairies. L'Alberta présente la plus grande diversité de plécoptères à cause de la proximité des Rocheuses (108 espèces, dont 104 se trouvent en montagne), tandis que la Saskatchewan et le Manitoba présentent des diversités semblables (44 et 46 espèces respectivement). Seules 2 des 61 espèces de l'écozone des prairies (*Perlesta dakota* et *Pteronarcys pictetii*) sont exclusives à cette écozone au Canada, la plupart des espèces observées dans l'écozone des prairies se trouvant également dans les écozones du bouclier boréal et des plaines boréales (40 espèces) ou dans l'écozone de la cordillère alpestre (42 espèces). Une liste des espèces prélevées dans chaque province et dans chaque écozone est fournie, accompagnée de références et d'informations sur les refuges d'où elles sont probablement issues. On présente enfin des informations sur l'écologie des plécoptères, les études taxonomiques réalisées sur ces insectes, leur zoogéographie et leur importance en tant qu'outils de surveillance pertinents pour la région.

## Introduction

Stoneflies (Plecoptera) (Fig. 1) spend most of their life cycles as aquatic larvae before emerging from the water as terrestrial adults. The majority of stoneflies require well-oxygenated water and are found in clean, cool, fast-flowing streams and rivers (Hynes 1976; Stewart and Harper 1996; Stewart and Stark 2002, 2008), although a few species are also known from cold boreal and alpine lakes (Harper 1979; Donald and Anderson 1980; Dossall and Lehmkuhl 1987). This restricts most Canadian species to areas such as the

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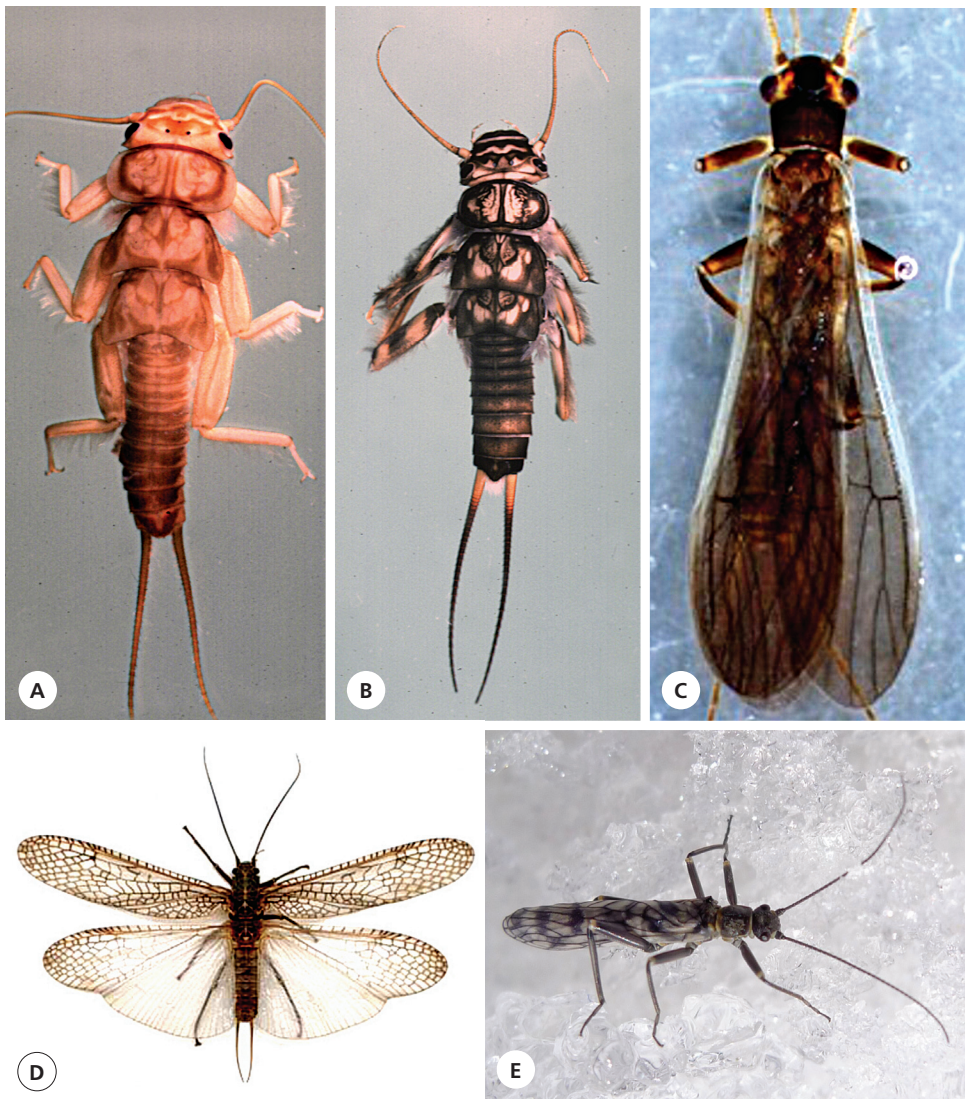
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western mountains and forested areas of the east and north (Harper 1979; Miyazaki and Lehmkuhl 2011). In the grassland portions of the Prairie Provinces (Mixed Grassland and Moist Mixed Grassland ecoregions; Shorthouse 2010), cool and well-oxygenated habitats (at least in summer) are relatively rare and few species have adapted to warm, slow-moving prairie waters; thus, stonefly diversity is comparatively low (Harper 1979; Dossdall and Lehmkuhl 1987; Miyazaki and Lehmkuhl 2011). Adults are poor fliers (Stewart and Stark 2002), and so the prairie landscape effectively acts as a dispersal barrier between eastern and western species.



**Fig. 1.** Examples of Plecoptera from the Canadian Prairie Provinces. A, *Acroneuria abnormis* nymph, B, *Claassenia sabulosa* nymph, C, *Perlesta dakota* adult, D, *Pteronarcys dorsata* adult, E, Winter stonefly adult on snow. All photos by L. Dossdall except for C, *Perlesta*, which is by Dale Parker.

Relatively little recent research has focused specifically on the Plecoptera of the Canadian Prairie Provinces. Early workers who contributed to the knowledge of the western Canadian fauna included Banks (1907), Neave (1929, 1933, 1934), and Ricker (1943, 1944, 1946). Ricker listed only 23 species from the Canadian Prairies and adjacent parkland (Ricker 1946) and an additional 11 species from the northern Prairie Provinces (Ricker 1944) on the basis of his collections and specimens from the Canadian National Collection. Ricker continued to work on the Canadian fauna for several years and made several important contributions to the knowledge of western Canadian stoneflies (e.g., Ricker 1952, 1964; Ricker *et al.* 1968; Ross and Ricker 1971; Stewart and Ricker 1997).

Regional taxonomic treatments with information on species from the Canadian Prairie Provinces followed (e.g., see list in Table 1), but no further attempts were made to provide a systematic list for this region until 1979, with the publication of “Stoneflies (Plecoptera) of Saskatchewan” (Dosdall and Lehmkuhl 1979). That work increased the number of known Saskatchewan species from 11 to 41 (with two additions listed in Dosdall 1992), largely due to extensive new collecting in all areas of the province. Twenty-five of these species were found in the Prairies Ecozone (as defined in Shorthouse 2010), though eight of these were restricted to the Cypress Hills. Subsequently, Flannagan and Flannagan (1982) listed 38 species of stoneflies and their postglacial distributions from Manitoba, and they identified 21 species that were present in the Prairies Ecozone. Burton (1984) reported 44 species in Manitoba from a combination of historical records and new collecting, with 22 from Prairies Ecozone streams and rivers. There is no equivalent comprehensive published treatment of the Alberta stoneflies except at the generic level (Clifford 1991), and so it

**Table 1.** References that provide identification keys relevant to stoneflies from the Canadian Prairies.

Family	Reference
All	Needham and Claassen 1925; Baumann <i>et al.</i> 1977; Stewart and Oswood 2006; Stewart and Stark 2008.
Capniidae	Nebeker and Gaufin 1965 ( <i>Capnia columbiana</i> complex); Harper and Hynes 1971 <i>b</i> ; Nelson and Baumann 1987 ( <i>Capnura</i> ); Nelson and Baumann 1989 ( <i>Capnia</i> ); Stark and Baumann 2004 ( <i>Paracapnia</i> ); Zenger and Baumann 2004 ( <i>Isocapnia</i> ).
Nemouridae	Harper and Hynes 1971 <i>d</i> ; Baumann 1975; Baumann and Kondratieff 2010 ( <i>Lednia</i> ).
Leuctridae	Harper and Hynes 1971 <i>a</i> ; Stark and Kyzar 2001 ( <i>Paraleuctra</i> ); Baumann and Stark 2009 ( <i>Paraleuctra alta</i> ).
Taeniopterygidae	Harper and Hynes 1971 <i>c</i> ; Fullington and Stewart 1980 ( <i>Taeniopteryx</i> ); Stanger and Baumann 1993 ( <i>Taenionema</i> ); Stewart 2000.
Chloroperlidae	Fiance 1977; Surdick 1985; Alexander and Stewart 1999 ( <i>Suwallia</i> ); Surdick 2004.
Peltoperlidae	Stark 2000.
Perlidae	Stark and Gaufin 1976 ( <i>Acroneuria</i> ); Peckarsky 1979 ( <i>Acroneuria</i> ); Stark and Szczytko 1981 ( <i>Paragnetina</i> ); Stark 1989 ( <i>Perlesta placida</i> complex); DeWalt <i>et al.</i> 2001 ( <i>Perlesta</i> ); Kondratieff and Baumann 1999 ( <i>Perlesta</i> ); Stark 2004.
Perlodidae	Szczytko and Stewart 1979 ( <i>Isoperla</i> ); Kondratieff 2004; Sandberg and Stewart 2005 ( <i>Isogenoides</i> ).
Pteronarcyidae	Nelson 2000.

is difficult to draw comparisons with the wide range of ecoregions and habitats found in the province. Information on the Alberta prairie fauna must be gleaned from regional taxonomic and ecological studies (e.g., Radford and Hartland-Rowe 1971; Donald and Anderson 1977, 1980; Barton 1980; Donald 1980; Donald and Mutch 1980; and see Table 1). For example, Donald and Anderson (1977) reported 74 species in the Waterton River drainage extending from the subalpine headwater zone in the Rocky Mountains to the grasslands of the Prairies Ecozone near Lethbridge, and Donald and Mutch (1980) found 59 species in their study of the Bow River. In both studies, the highest diversity was found in the mountain streams, with a sharp decline in diversity into the Prairies Ecozone.

Overall, the taxonomy of stoneflies has improved dramatically during the last 25 years. A well-illustrated larval key to the North American genera was published in 1988 and updated in 2002 (Stewart and Stark 2002), and a generic key to the North American larvae and adults can be found in Stewart and Stark (2008) with an accompanying thorough list of ecological and taxonomic references. More recently, several attempts have been made to bring together distributional and taxonomic information on the stonefly species in North America (Stark *et al.* 1986, 1998), including an updated searchable database for global nomenclature and distribution (DeWalt *et al.* 2013). Although these latter resources allow a researcher to construct a list of the stoneflies from each jurisdiction fairly quickly, information on specific habitats or localities is much more difficult to obtain. The goal of this chapter is to provide an update to the Plecoptera species recorded from the three Prairie Provinces of Canada, with special reference to the Prairies Ecozone, through a review of the existing literature.

## Ecology

Stonefly larvae fill a number of important niches in aquatic systems since they include herbivore/detrivores (algae/biofilm scrapers, shredders of leaves and other organic particles, or collectors of fine material that has been deposited on the substrate) and predators (Stewart and Stark 2002). Some groups are dominated by members that feed mainly on one food source or another (e.g., many Pteronarcyidae, Nemouridae, and Capniidae are shredders; some Taeniopterygidae, Leuctridae, and Peltoperlidae are collectors or scrapers; and most Perlidae, Perlodidae, and Chloroperlidae are predators). However, some species are omnivorous or show ontogenic shifts throughout their lives (e.g., several predatory species shift from herbivory/detrivory to carnivory as they grow; Stewart and Stark 2002). Stewart and Stark (2002) therefore caution against applying functional feeding group classifications (e.g., Merritt *et al.* 2008) too broadly and assuming that all species within a family or genus show the same feeding habits throughout their life cycles. Knowledge of feeding habits do, however, help to determine the habitats in which stoneflies are found. The large Pteronarcyidae and Peltoperlidae are usually found in leaf packs, Leuctridae usually inhabit sandy or gravel substrates where they feed on fine organic detritus, and other families may be found over a range of habitats from erosional to depositional sites (Stewart and Stark 2008). The adults of a number of families feed on algae, lichens, pollen, and young leaves and buds of the vegetation adjacent to the larval habitat (Stewart and Stark 2008).

Many plecopterans have specific environmental requirements with respect to stream or river size, substrate type, water temperature, and flow rate (Stewart and Stark 2002, 2008). A major habitat determinant for many species is their requirement for high oxygen levels, and oxygen concentrations in the water correlate with environmental variables such

as water current, water temperature, and biological oxygen demand (Cole 1994). High water currents mix atmospheric oxygen into the water, and so swiftly moving streams are frequently well oxygenated. However, as water temperature increases, its ability to hold oxygen decreases; therefore, oxygen levels are usually low in warm streams. Bacterial decomposition of organic material also uses oxygen; as a result, high nutrient inputs (frequently associated with agricultural runoff) that result in algal blooms and subsequent decay of the organic material also cause declines in oxygen (Cole 1994). Therefore, stoneflies are usually restricted to cool, clean streams. Within these types of streams, however, their specific microhabitats depend on both their feeding habits and their ability to withstand water currents; leaf-shredders are usually found in leaf packs, whereas fine detritus collectors are found in depositional areas, either within the substrate or in slower current. Predators may be found over a range of habitats. These requirements result in characteristic longitudinal faunal changes from headwaters to large rivers (Stewart and Stark 2002). For example, Plecoptera species composition changed and their diversity declined from the cool alpine and subalpine reaches to the warm prairies in the Waterton and Bow rivers (Alberta) (Donald and Anderson 1977; Donald and Mutch 1980). Similar patterns are found where cool boreal streams drain into prairie streams (Dosdall and Lehmkuhl 1979). Stoneflies in relatively warm locations may seek out cooler spring-fed sections of streams to develop throughout the year (Stewart and Stark 2002), and several of the “grasslands” sites (within the Mixed Grassland or Moist Mixed Grassland ecoregions) with stoneflies are from spring brooks originating in hilly outcrop areas (Dosdall and Lehmkuhl 1979; Burton 1984).

Life cycles of North American stoneflies are highly variable, both within genus and even within species, depending on habitat conditions. Life cycles vary from requiring one year (univoltine) to requiring two or more years (semivoltine), with some species in the north possibly requiring three to four years (Stewart and Stark 2002). In some cases, a larval or egg diapause allows species to withstand harsh conditions (such as drying or high summer temperatures) during the life cycle. Life cycles and developmental timing therefore vary from fixed in some species to temperature-dependent in others. Stewart and Stark (2008) suggest that many species with restricted ranges have determinate (fixed) life cycle patterns, whereas those that are more widespread may be more affected by water temperature. Once larval development is complete, final-instar larvae move onto rocks or structures toward shore to emerge, with most North American species emerging between late winter and mid-summer and a few emerging in late summer or fall (Stewart and Stark 2002). The families Taeniopterygidae and Capniidae (the “winter stoneflies”) avoid warm summer temperatures by growing (as larvae) during the fall and winter and emerging in early spring as the ice begins to break up (Fig. 1E) (Dosdall 1976; Flannagan 1978; Flannagan and Cobb 1983). Many species spend the warm summer months in egg or larval diapause or in the hyporheic zone (deep in the substrate) (Harper and Hynes 1970; Stanford and Gaufin 1974; Dosdall 1976). These adaptations, along with choosing cool microhabitats such as spring outflows, likely allow these species to inhabit the prairie regions that would otherwise be too warm for them.

### Postglacial Dispersal and Distributions

In North America, Plecoptera diversity is relatively high to the east (where there is hilly terrain and broadleaf forest) and west (in the western mountains), but declines sharply in the Great Plains (including the Prairies Ecozone in Canada) (Ricker 1964; Dosdall and

Lehmkuhl 1979; Flannagan and Flannagan 1982). Adult Plecoptera are generally weak fliers, usually dispersing along drainage networks and only short distances overland (Ricker 1964; Stewart and Stark 2008). However, some evidence of long-distance dispersal has been found in *Pteronarcys californica* in western North America (Kauwe *et al.* 2004). Present stonefly distribution patterns relate to the changes in postglacial drainage patterns (see below) that provided direct connections with glacial refugia and allowed the stoneflies to disperse widely as the glaciers retreated. However, stonefly distribution patterns in the Canadian Prairie Provinces have changed little since deglaciation because of the limited number of suitable habitats (cool streams and rivers) and the long distances between habitats acting as effective barriers for further dispersal within and through the region (Lehmkuhl 1980; Flannagan and Flannagan 1982).

The Wisconsinan glaciation (100,000 to 17,000 years before present (bp)) destroyed much of the flora and fauna of Canada, with the exception of a few isolated refugia (Matthews 1979). In the north, parts of Yukon and Alaska (Beringia) were ice free, and smaller unglaciated areas may have existed on Banks Island, along the Anderson and Mackenzie rivers, in northern portions of Ellesmere and Baffin islands, and in “Pearyland” (Northern Greenland) (Matthews 1979). The Queen Charlotte Islands (Haida Gwaii) on the west coast and parts of the mouth of the St. Lawrence River and the Maritimes, Newfoundland, and Magdalen Islands on the east coast were likely unglaciated (Matthews 1979). The Cypress Hills of Saskatchewan and Alberta and a small area along the Saskatchewan–Montana border were likely also ice free and could have served as refugia (Christiansen 1979; Matthews 1979). Although these areas were apparently ice free, there is no direct evidence that, other than Beringia, they acted as refugia for stoneflies. However, three areas to the south clearly acted as glacial refugia during this period: the temperate southeast from the east coast of North America west to the Appalachians and Mississippi River, the central Great Plains region between the Mississippi and the western montane region, and the Pacific mountain refugium in the southwest United States (Scudder 1978; Matthews 1979). As the glaciers began to retreat to the north, some of the flora and fauna that inhabited these refugia colonized the newly unglaciated areas. Thus, much of the flora and fauna of Canada, including the Plecoptera now inhabiting the prairie region, have southern origins (Ricker 1964; Stewart *et al.* 1973; Lehmkuhl 1980).

As the ice sheet retreated between 17,000 and 10,000 years bp (Christiansen 1979), lakes and rivers formed and drained in different directions (Christiansen 1979; Pielou 2008), creating water linkages that significantly affected stonefly distributions (Dosdall and Lehmkuhl 1979; Flannagan and Flannagan 1982). During the initial phases, the ice retreated upslope, which allowed meltwater to flow away from the glacier face in southern Alberta, Saskatchewan, and Manitoba directly into the Missouri/Mississippi River system (Christiansen 1979), establishing a connection with the Central Great Plains refugium. As the ice retreated farther northeast, it retreated downslope and dammed the natural flow direction (Christiansen 1979; Pielou 2008), causing a number of meltwater lakes, including Lake Agassiz, to develop. The various lakes were connected by spillways and glacial streams, forming a continuous aquatic connection along the foot of the glacier from the mountains to eastern Canada (Christiansen 1979). This provided connections to the region with the refugia of eastern Canada and the southeastern United States, as well as with that of the western mountains. After the ice receded, water continued to flow eastward from the mountains into Lake Agassiz, strengthening the west–east connection. Periods of glacial advance followed by retreats severed and re-established the links with the Missouri/Mississippi drainage and the eastern refugia (Flannagan and Flannagan 1982).

A late advance also established a corridor between Lake Agassiz and the Mackenzie River system (Christiansen 1979), thus connecting Beringia with the prairies. About 8,000 years bp, the ice retreated enough to open a corridor to Hudson Bay that drained Lake Agassiz (Flannagan and Flannagan 1982), establishing the present-day drainages.

### Present-day Stonefly Patterns in the Canadian Prairie Provinces

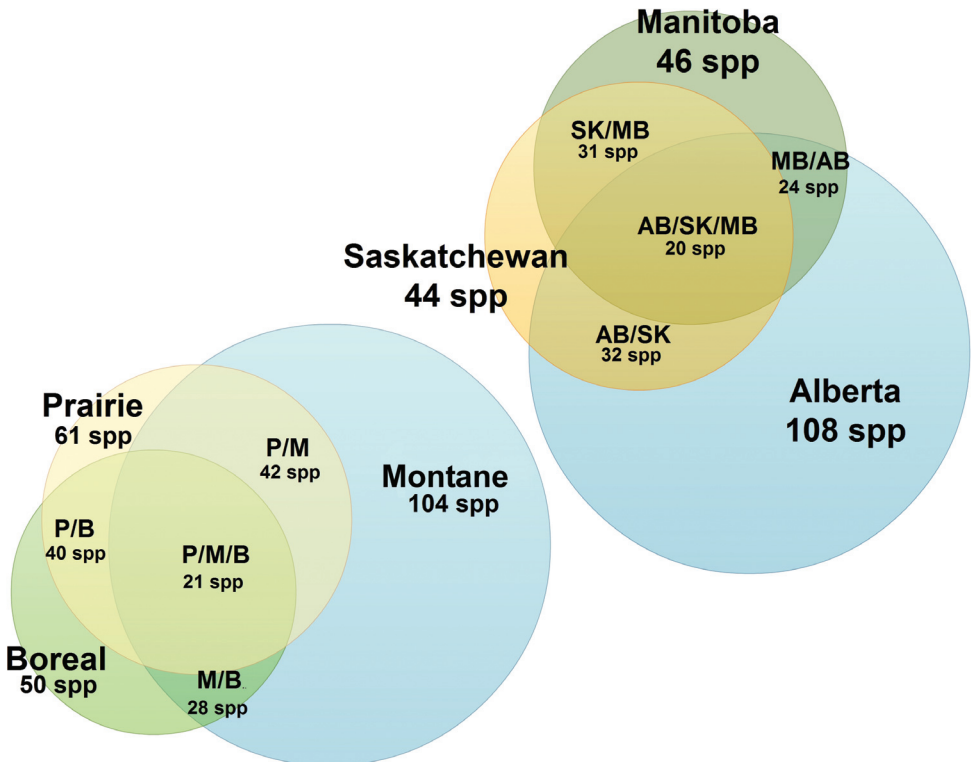
One hundred thirty-one Plecoptera species are known from Alberta, Saskatchewan, and Manitoba (Table 2); this represents nearly 20% of the approximately 675 known North American species and about half of the approximately 255 Canadian species (DeWalt *et al.* 2013). The species are listed in Table 3, along with information about distributions in North America and the Prairie Provinces, probable postglacial colonization routes, and locality notes. Nine families are recognized in the Nearctic, and all are represented in the Prairie Provinces (Tables 2 and 3). Four of the families are in the superfamily Nemouroidea Newman 1853 (Group Euholognatha): Capniidae (26 species in nine genera), Leuctridae (nine species in six genera), Nemouridae (19 species in 10 genera), and Taeniopterygidae (seven species in five genera) (Table 2). The Group Systellognatha is represented by two superfamilies: Pteronarcyzoidea Newman 1853 and Perloidea Latreille 1802. Pteronarcyzoidea includes Pteronarcyidae (five species in two genera) and Peltoperlidae

**Table 2.** Numbers of genera and species in each stonefly family reported from the Prairie Provinces.

	Prairie Provinces		Alberta		Saskatchewan		Manitoba	
	Genera	spp.	Genera	spp.	Genera	spp.	Genera	spp.
<b>Superfamily Group Euholognatha</b>								
<b>Nemouroidea</b>								
Capniidae	9	26	6	21	4	9	5	9
Leuctridae	6	9	5	8	2	2	1	1
Nemouridae	10	19	9	17	6	6	5	7
Taeniopterygidae	5	7	4	6	2	2	3	4
<b>Superfamily Group Systellognatha</b>								
<b>Perloidea</b>								
Chloroperlidae	9	22	9	22	3	4	2	2
Perlidae	8	10	5	5	5	6	7	8
Perlodidae	9	31	9	23	4	13	4	13
<b>Pteronarcyzoidea</b>								
Peltoperlidae	1	2	1	2	0	0	0	0
Pteronarcyidae	2	5	2	4	2	2	1	2
<b>Totals</b>	<b>59</b>	<b>131</b>	<b>50</b>	<b>108</b>	<b>28</b>	<b>44</b>	<b>28</b>	<b>46</b>

(two species in one genus). Perloidea includes Chloroperlidae (22 species in nine genera), Perlidae (10 species in eight genera), and Perlodidae (31 species in nine genera) (Table 2). The stonefly fauna of the Prairie Provinces overwhelmingly consists of members with generally western distributions (based on the distribution classifications of Stark *et al.* 1998; see Table 3 for definitions). This pattern was evident for all families except for Perlidae, which has a number of widespread species spread over several geographical areas. Eighty-three species have western distributions, 26 species are midwestern, and 27 are in the northwest (note that there is some overlap since some species are found in more than one geographical area). Only 21 species in the three Prairie Provinces also occur in the east, and nine also occur in the northeast.

Species patterns can be assessed for both ecological regions and political jurisdictions, and each type of assessment provides useful information. For example, species-at-risk programs under provincial jurisdiction require information about patterns within each province, but conservation efforts require ecological information that is not limited by political boundaries. Of the 131 Prairie Province stonefly species reported in Table 3, only 61 are known from the Prairies Ecozone (Table 3, Fig. 2), including the Fescue Grassland, Mixed Grassland, and Moist Mixed Grassland ecoregions and the Cypress Upland and Aspen Parkland ecoregions. Many of these species are found in the downstream portions of rivers that originated in the mountains, or have dispersed across the northern boreal forest where



**Fig. 2.** Number of Plecoptera species and degree of species overlap for each province and habitat zone. Size of circles is proportional to the number of species. AB = Alberta; MB = Manitoba; SK = Saskatchewan; P = Prairies Ecozone; M = Montane Cordilleran Ecozone; B = Boreal, including the Boreal Plains and Boreal Shield ecozones.

cool rivers, streams, and lakes provide numerous suitable habitats. A substantial proportion of the total (104 species) has been reported in mountain streams and lakes in the Montane Cordillera Ecozone, and 55 of these have been reported only in these habitats (Fig. 2). It is therefore not surprising that the majority of the prairie species have affinities to the western mountains; nearly 70% (42 species) of the 61 species found in the Prairies Ecozone were also found in the mountain streams. There is also considerable overlap between the prairie and the boreal faunas, with 50 species occurring in boreal streams in Alberta, Saskatchewan, and Manitoba; 40 of these also extend into rivers that flow into the Prairies (or 66% of the total prairie species). More than half (28 species) of the “boreal” species also occur in mountain streams, and 21 species occur in all three of the zones (Fig. 2).

Provincially, the three Prairie Provinces show very different patterns. Alberta has the richest stonefly fauna, with 108 species, reflecting the large number of species found in the mountain streams and lakes (Table 2, Fig. 2). Forty-six of the Alberta species are found in the Prairies Ecozone (most of them in the grasslands sections of rivers such as the Bow or Waterton or in the Cypress Hills; Table 3). Saskatchewan and Manitoba have similar numbers of stonefly species, both for total numbers (44 and 46 species, respectively) and for numbers found within grassland habitats of the Prairies Ecozone (36 and 38 species, respectively), sharing about two-thirds of their species (Fig. 2). Only 30% of the Alberta species are also found in Saskatchewan and 22% of the Alberta species are found in Manitoba (Fig. 2).

### Origins of the Prairie Stonefly Fauna

The strong affinity shown by the prairie grasslands Plecoptera to the boreal cordillera mountain fauna is due to the close proximity of the Alberta prairies to the mountains and foothills, the early postglacial drainage patterns, and the present-day direct drainage links (i.e., mainly the Saskatchewan River system; Flannagan and Flannagan 1982). This is particularly pronounced in Alberta, where 87% (40 of 46 species) of species in grassland habitats (including both the Moist Mixed Grassland and Mixed Grassland ecoregions) are also in the mountains (with the remaining six grasslands species also found in boreal streams). The overall mountain influence on the prairies fauna declines eastward. Close to 70% of species in grassland ecoregions in Saskatchewan are also found in the mountains (25 of 36 species, 18 of which are also in boreal streams), and only 45% of grassland ecoregions species in Manitoba are also found in the mountains (17 of 38 species, 15 of these also in boreal streams) (Table 3). Therefore, although the majority of the Prairies Ecozone species (36) are believed to have originated in the southwestern refugia (Ricker 1964; Dossdall and Lehmkuhl 1979; Flannagan and Flannagan 1982), other refugia also contributed to the Plecoptera of the Canadian Prairies. Three species are believed to have colonized from the Southern Great Plains refugium (SC in Table 3) and 21 from the east and southeastern refugia (SE in Table 3). Only one species, *Isoperla decolorata*, has reached the edge of the prairies in Saskatchewan from the Beringia refugium (B in Table 3). There appears to be no evidence at present for truly endemic species that may have survived the Ice Age in the Cypress Hills refugium. The Plecoptera fauna of the prairies is therefore entirely the result of immigration from glacial refugia (Lehmkuhl 1980).

When considered at the provincial level, the patterns also vary with distance from the mountains. The Plecoptera fauna of Alberta is dominated by species from the southwestern and western mountains (95 of 108 total species, 40 of 46 prairie species; Table 3). Two Alberta species, *Acronuria abnormis* and *Isoperla longiseta*, were reported (Dossdall



and Lehmkuhl 1979) to have colonized the Prairie Provinces from the south via rivers in the Central Plains refugium rather than through forested streams in the east (though *A. abnormis* is also widespread in the east and may be eastern in origin), but of these, only *I. longiseta* has been reported in the Alberta Prairies Ecozone. Seven species have reached Alberta from the eastern refugia, presumably via northern connections through the Boreal Shield and Boreal Plains ecozones. All seven of these species are also in boreal streams in Alberta (Barton 1980), and only *Taeniopteryx nivalis* is also found in the Prairies Ecozone (Table 3). Four Alberta species likely originated in the Beringia refugium (Table 3), but no species are known to have reached the Alberta prairies from Beringia.

Dossdall and Lehmkuhl (1979) and Dossdall (1992) summarized the postglacial stonefly colonization patterns in Saskatchewan. Twenty-three of the 44 species (25 of 36 of the prairie grasslands species) colonized the province from the southwest (Table 3), and eight of these species (*Isocapnia missouri*, *Utacapnia trava*, *Podmosta delicatula*, *Paraleuctra vershina*, *Suwallia lineosa*, *Hesperoperla pacifica*, *Isoperla quinquepunctata*, and *Skwala americana*) are restricted (or nearly so) to the Cypress Hills of southeastern Alberta and southwestern Saskatchewan. Except for *Isoperla quinquepunctata* (found in the South Saskatchewan River, as *I. patricia*), these species have not yet colonized the prairie rivers and streams immediately surrounding the Cypress Hills. A number of montane species dispersed north and east into the boreal regions of Saskatchewan (Table 3). Four of these, *Capnia gracilaria*, *Capnia vernalis*, *Zapada cinctipes*, and *Claassenia sabulosa*, subsequently moved south into the prairies from the boreal forest. The first two are also known from the Cypress Hills, but not from the surrounding prairies, and it is likely that the origins of the prairie populations for these species are from the boreal forest rather than the Cypress Hills population. Thirteen species have colonized Saskatchewan from the east/southeast, and four of these, *Pteronarcys dorsata*, *Shipsa rotunda*, *Isoperla marlynia*, and *Taeniopteryx nivalis*, have dispersed from the eastern refugia into the Saskatchewan prairies. Five species are believed to have colonized Saskatchewan from Beringia, but *Isoperla decolorata* is the only species from Beringia that inhabits the prairies, and it does so only in Saskatchewan. Three species, *Isoperla longiseta*, *Isoperla bilineata*, and *Acroneuria abnormis*, likely moved into Saskatchewan from the south via the Southern Great Plains refugium, moving northward just after the glacier started receding and when the Saskatchewan River was connected with the Missouri drainage. Both *I. bilineata* and *A. abnormis* are also widespread in the east (DeWalt *et al.* 2013), and so postglacial recolonization patterns should be confirmed through further study.

Flannagan and Flannagan (1982) and Burton (1984) summarized postglacial movements of stoneflies in Manitoba. In contrast to that of the western provinces, the Manitoba fauna is dominated by stonefly species colonizing from southeastern refugia (24 of 46 species; 24 of 38 prairie species; Table 3), reflecting the importance of glacial Lake Agassiz, the predominant aquatic glacial feature in Manitoba. Fourteen species have reached Manitoba from the western refugia, and of these, *Capnia confusa*, *C. gracilaria*, *Megaleuctra stigmata*, *Zapada cinctipes*, *Isogenoides elongata*, and *Malenka californica* have reached the Manitoba prairies. It is likely that they moved through boreal forest aquatic connections and then southward into the Manitoba prairies. Five species have colonized Manitoba from Beringia, and all five are restricted to northern and boreal parts of the province (Table 3). Three species of the Manitoba Prairies (*A. abnormis*, *I. bilineata*, and *I. longiseta*) are thought to have survived the Ice Age in the eastern or Great Plains refugia and moved northward as rivers changed with the glacial retreat (Dossdall and Lehmkuhl 1979; Flannagan and Flannagan 1982).

### Role in Environmental Monitoring

Plecoptera are generally intolerant to pollutants (Surdick and Gaufin 1978; Stewart and Stark 2002), making the stoneflies useful tools in the study of environmental impacts. Exposure to contaminants or organic enrichment have caused structural deformities (Donald 1980) or reductions in species diversity and abundance (e.g., Donald and Mutch 1980; Dossdall and Lehmkuhl 1989a, 1989b) in Plecoptera in prairie streams. Impoundments have also caused downstream reductions in the plecopteran fauna by altering water temperature regimes, nutrient sources, and flow rates (Donald and Mutch 1980).

The main river systems of the prairies have been subjected to intense pollution through city sewage, industrial discharges, agricultural contaminants, pest control, and regulation for irrigation purposes, hydroelectric generation, or flood control (Rosenberg *et al.* 2005; Schindler and Donahue 2006). These developments have undoubtedly had an impact on the abundance and diversity of the plecopteran fauna and may have caused localized extinctions of some species. For example, DeWalt *et al.* (2005) noted dramatic declines in many Plecoptera species in Illinois, which they attributed to habitat disruption, mainly from agriculture and urban development. They compared stonefly records (published and from museum specimens) before and after 1950, noting two extinctions and 20 extirpations of a total of 77 species. The greatest impacts were on large and long-lived predatory perlids and perlodids and in large rivers in prairie habitats. Fochetti and de Figueroa (2006) suggest that in Europe, the Plecoptera are one of the most endangered groups in running waters, again due to habitat alteration from human activities. The narrow ecological requirements of stoneflies and their relatively poor dispersal abilities mean that they do not tolerate these changes. Therefore, conservation efforts that could improve and maintain the abundance and diversity of prairie Plecoptera, especially at the local stream level, include riparian (streamside) protection and livestock fencing to reduce erosion and manure runoff into water bodies. Current efforts in all three Prairie Provinces to enact wastewater guidelines and control nutrient inputs could also help enhance the habitat for the prairie stonefly fauna. However, climate change and increased anthropogenic development are expected to continue altering temperatures, water volumes, and nutrient loads in western Canadian streams (Schindler and Donahue 2006; and see Rosenberg *et al.* 2005 for specific data on silt loads, water chemistry, contaminants, and water volumes for different sections of the major western Canadian prairie rivers).

Assessing the long-term effects of habitat alterations in these aquatic habitats is difficult because with few exceptions (e.g., the long-term studies on the Saskatchewan River system in Saskatchewan, summarized in Miyazaki and Lehmkuhl 2011), long-term records do not exist anywhere in the Prairie Provinces. It would be useful to repeat the province-wide surveys that were carried out during the 1970s (Dossdall and Lehmkuhl 1979) and 1980s (Burton 1984) to determine whether the stonefly fauna has changed over the past three decades. Such surveys would not answer questions about faunal changes that have occurred since European settlement of the prairies, but could identify current species extirpations or species at risk. These surveys would be especially useful for the large river predatory species, which have declined in other prairie regions (e.g., DeWalt *et al.* 2005). In addition, surveys should be conducted on spring-brook habitats that are critical for much of the Canadian prairie stonefly fauna. Stoneflies are well-known indicators of clean and unpolluted waters, but without ongoing surveys and baseline assessments, their utility in monitoring both long-term changes and short-term remediation efforts, for example, are limited. Such assessments are urgently needed.

**Table 3.** Plecoptera recorded from the Canadian Prairie Provinces. Common names and distribution summaries are from Stark *et al.*<sup>29</sup> **Key: Distribution summaries:** NE = NW/KY northward; MW = OH/IN/IL/IO/WI/MI and Great Plains states; SE = SC/NC/TN south and west to LA and eastern TX; E = wider eastern, including NE and SE; NW = northern California northward (along mountains); SW = extreme southern CA, eastward to NM, AZ, west TX; W = wider western, including NW and SW; M: Mexico. **Origins:** B = Beringia origins; SW = southwestern and montane origins; SC = Southern Great Plains origin; SE = southeastern origins. **Ecozone:** Includes species that have been recorded from aquatic habitats in the ecozone in Canada; p = prairies (referring to the Prairies Ecozone, including Cypress Hills and streams within the Aspen Parkland Ecozone); m = montane; b = boreal zone in Canada, but may also include other forested streams in the east. The North American distribution information is from DeWalt *et al.*<sup>6</sup> except as noted. Numbers in the distribution columns refer to the reference footnotes for specific records. *Species checklist available at:* <http://dx.doi.org/10.5886/gagds797>

Species, Common Name	Distr.	Orig.	North American Distribution and Notes	Prairie Provinces Distribution			
				AB	SK	MB	Zone
<b>Capniidae</b>							
<i>Allocapnia granulata</i> (Claassen 1924). Common snowfly.	E, MW	SE	CAN: MB, ON, PQ, USA: AL, AR, DC, IA, IL, IN, KS, KY, LA, MD, MI, MN, MO, MS, NJ, NY, OH, OK, PA, TN, TX, VA, WI, WV. <b>Remarks:</b> Red River tributaries in prairies zone <sup>6,3</sup> and boreal streams bordering the prairies <sup>3,16</sup> in southern Manitoba; in small cobble bottom streams in Iowa <sup>16</sup> .	-	-	3, 6, 13, 14, 16	p, b
<i>Bolshecapnia milami</i> (Nebeker and Gauflin 1967). Glacier snowfly.	NW	SW?	CAN: AB, BC, USA: CO, ID, MT, NM. <b>Remarks:</b> Mountain streams <sup>30</sup> , including the mountain zone in Waterton <sup>8</sup> and Bow River drainages <sup>9</sup> .	6, 8, 9, 30	-	-	m
<i>Bolshecapnia sasquatchi</i> (Ricker 1965). Sasquatch snowfly.	NW	SW?	CAN: AB <sup>30</sup> , BC, USA: WA. <b>Remarks:</b> Northwestern Nearctic <sup>30</sup> .	30	-	-	m
<i>Bolshecapnia spenceri</i> (Ricker 1965). Ice snowfly.	NW	SW?	CAN: AB, BC, USA: MT. <b>Remarks:</b> Near high mountain lakes <sup>30</sup>	6, 30	-	-	m
<i>Capnia cheama</i> Ricker 1965. Cheama snowfly.	NW	SW?	CAN: AB, BC, YK, USA: MT. <b>Remarks:</b> Northwestern Nearctic and Rocky Mountains <sup>30</sup> ; Bow River in Alberta <sup>9</sup> .	6, 9, 30	-	-	m
<i>Capnia coloradensis</i> Claassen 1937. Colorado snowfly.	W	SW	CAN: BC, MB, SK, YK, USA: AK, CO, ID, MT, NM, WY. <b>Remarks:</b> Western mountains <sup>30</sup> and boreal zone in Saskatchewan <sup>10</sup> and Manitoba <sup>3</sup> .	-	6, 10	3, 6, 14	m, b
<i>Capnia confusa</i> Claassen 1936. Widespread snowfly.	W	SW	CAN: AB, BC, MB, NT, SK, YK, USA: AK, CA, CO, ID, MT, NM, SD, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , Waterton <sup>8</sup> , Kanaskis <sup>35</sup> , and Bow River <sup>9</sup> drainages (from the montane to grasslands zones) in Alberta, boreal zone in Saskatchewan <sup>10</sup> and Manitoba <sup>3,14,17</sup> , and Prairies Ecozone in Manitoba (Stoney Creek, Minnedosa) <sup>3</sup> .	6, 8, 9, 25, 30	6, 10	3, 6, 14, 17	p, m, b

<i>Capnia gracilaria</i> Claassen 1924. Slender snowfly.	W	SW	CAN: AB, BC, MB, SK, YK. USA: CA, CO, ID, MT, NM, NV, OR, SD, UT, WA, WY. MEX: Baja California. <b>Remarks:</b> Western mountains <sup>30</sup> ; Waterton drainage in Alberta and Cypress Hills in Saskatchewan <sup>10</sup> and springs in the Prairies Ecozone in Alberta (Big Hill Springs, northwest of Calgary) <sup>21</sup> and Saskatchewan (near Saskatoon) <sup>22</sup> ; southern boreal (Duck Mountain) <sup>3,14</sup> ; and prairie <sup>18,24</sup> streams in Manitoba. This species was described from Aweme Manitoba <sup>18,24</sup> and Ricker described it as a cordilleran species which has spread over most of the prairies <sup>36</sup> .	6, 8, 10, 12	3, 6, 14, 16, 18, 24, 26	p, m, b
<i>Capnia nana</i> Claassen 1924. Dwarf snowfly.	W	SW?	CAN: AB, BC, YK. USA: AK, CO, ID, MT, OR, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in Waterton River drainage, Alberta <sup>8</sup> .	6, 8, 30	-	m
<i>Capnia nearctica</i> Banks 1918. Nearctic snowfly.	NE, NW	B	CAN: BC, MB, NT, NU, ON, SK <sup>11</sup> , YK. USA: AK. <b>Remarks:</b> Northern transcontinental <sup>30</sup> , boreal habitats near Lake Athabasca <sup>11</sup> , and at Churchill, Manitoba <sup>3</sup> .	-	11	b
<i>Capnia petila</i> Jewett 1954. Thin snowfly.	W	SW?	CAN: AB, BC, YK. USA: ID, MT, OR, UT, WY. <b>Remarks:</b> Central to northern Rocky Mountains <sup>30</sup> ; mountain zone in Waterton River drainage, Alberta <sup>8</sup> .	6, 8, 30	-	m
<i>Capnia sextuberculata</i> Jewett 1954. Six-knobbed snowfly.	W	SW?	CAN: AB, BC. USA: MT, OR, WA. <b>Remarks:</b> Central to northern Rocky Mountains <sup>30</sup> .	6, 30	-	m
<i>Capnia vernalis</i> Newport 1848. Vernal snowfly.	E, W	SW	CAN: AB, BC, LB, MB, NB, NF, NT, NU, ON, PQ, SK. USA: AK, CO, ID, MI, MN, MT, NM, NV, UT, WI, WY. <b>Remarks:</b> Northern transcontinental and south along Rockies <sup>30</sup> ; into the grassland zone in southern Alberta <sup>8,26</sup> ; in the northern boreal in Manitoba <sup>3</sup> and Saskatchewan <sup>10</sup> . Described by Ricker as an eastern species which has spread west <sup>26</sup> (there are also old records (1918 and 1940) from the Saskatchewan River at Saskatoon <sup>20</sup> ).	6, 8, 9, 26, 30	6, 10, 20	p, m, b
<i>Capnura manitoba</i> (Claassen 1924). Manitoba snowfly.	NE, MW	SE	CAN: MB, NB, ON, PQ. USA: CT, MA, ME, MI, NY, VT, WI. <b>Remarks:</b> An eastern species reported from small streams near Aweme in southwestern Manitoba <sup>3,26</sup> .	-	3, 6, 23, 16, 26	p, b
<i>Eucapnopsis brevicauda</i> (Claassen 1924). Short-tailed snowfly.	W	SW	CAN: AB, BC, YK. USA: AK, AZ, CA, CO, ID, MT, NM, NV, OR, SD, UT, WA, WY. <b>Remarks:</b> Northwestern mountains <sup>25,30</sup> ; grassland to mountain zones in both the Waterton <sup>8</sup> and Bow River <sup>9</sup> drainages in southern Alberta.	6, 8, 9, 25, 30	-	p, m
<i>Isocapnia agassizii</i> Ricker 1943. Agassiz snowfly.	NW	SW?	CAN: AB, BC, YK. USA: AK, OR, WA. <b>Remarks:</b> Northwestern Nearctic <sup>30</sup> .	6, 30	-	m
<i>Isocapnia crinita</i> (Needham and Claassen 1925). Hooked snowfly.	W	SW	CAN: AB, SK, YK. USA: AK, CO, ID, MT, NM, UT, WY. <b>Remarks:</b> Rocky Mountains and western Nearctic <sup>30</sup> ; montane species occurring in Cypress Hills <sup>10</sup> .	6, 10, 30	6, 10	p, m

Species, Common Name	Distr.	Orig.	North American Distribution and Notes	Prairie Provinces Distribution				
				AB	SK	MB	Zone	
<i>Isocapnia grandis</i> (Banks 1907). Giant snowfly.	W	SW?	CAN: AB, BC, YK. USA: AK, CA, ID, MT, OR, UT, WA, WY. <b>Remarks:</b> Western Nearctic, extending southward along the mountains <sup>30</sup> ; Kananaskis area in Alberta Rockies <sup>25</sup> .	6, 25, 30	-	-	m	
<i>Isocapnia hyalita</i> Ricker 1959. Hyalite snowfly.	W	SW?	CAN: AB. USA: CO, ID, MT, OR, UT, WY. <b>Remarks:</b> Range limited to Rocky Mountains from Utah to Alberta <sup>31</sup> .	6, 31	-	-	m	
<i>Isocapnia integra</i> Hanson 1943. Alberta snowfly.	W, NW	SW	CAN: AB, BC, SK, YK. USA: AK, ID, MT, SD, WY. <b>Remarks:</b> Northern Rocky Mountains <sup>30</sup> ; in Alberta, found in the mountain zone in Waterton River drainage <sup>8</sup> and the grasslands to the mountains in the Bow River <sup>7,9</sup> ; Cypress hills in Saskatchewan (as <i>I. missouri</i> <sup>10</sup> ).	6, 7, 8, 9, 10, 30	10	-	p, m	
<i>Isocapnia vedderensis</i> (Ricker 1943). Vedder snowfly.	W	SW?	CAN: AB, BC, YK. USA: AK, CA, CO, ID, MT, NM, UT, WA. <b>Remarks:</b> Rocky Mountains <sup>30</sup> ; in the mountain zone in the Bow River drainage <sup>9</sup> .	6, 9, 30	-	-	m	
<i>Mesocapnia oenone</i> (Neave 1929). Wine snowfly.	NW	SW?	CAN: AB, BC, YK. USA: AK, MT, OR, WA. <b>Remarks:</b> Northwestern mountains <sup>30</sup> ; mountain zone in the Kananaskis <sup>25</sup> , Waterton <sup>8</sup> and Bow River <sup>9</sup> drainages, Alberta.	6, 8, 9, 25, 30	-	-	m	
<i>Paracapnia angulata</i> Hanson 1961. Angulate snowfly.	E, MW, W	SE?	CAN: LB, MB, NB, PQ, ON, SK. USA: AR, CO, CT, DE, IL, KY, MA, MD, ME, MI, MO, NC, NH, NJ, NY, OH, OK, PA, SD, TN, VA, WI, WV, WY. <b>Remarks:</b> Cold streams, e.g., spring-fed streams or cold lake outlets; boreal in Saskatchewan (including sites around Lake Athabasca) <sup>10,11</sup> , and Manitoba <sup>3,14</sup> .	-	6, 10, 11	3, 6, 14	b	
<i>Utacpnia columbiana</i> (Claassen 1924). Columbian snowfly.	NW	SW	CAN: AB, BC, NT, YK. USA: AK, CA, MT, OR. <b>Remarks:</b> Northwestern Nearctic <sup>30</sup> ; from grassland to mountain zones in Waterton <sup>8</sup> and Bow River <sup>9</sup> drainages, Alberta.	6, 7, 8, 9, 30	-	-	p, m	
<i>Utacpnia distincta</i> (Frison 1937). Distinctive snowfly.	W	SW?	CAN: AB. USA: ID, MT, WY. <b>Remarks:</b> collected by Ricker near Lake Louise, Alberta <sup>2</sup> .	6, 22, 28	-	-	m	
<i>Utacpnia trava</i> (Nebeker and Gaufin 1965). Yellowstone snowfly.	W	SW	CAN: AB, BC, MB, SK. USA: ID, MT. <b>Remarks:</b> Western mountains <sup>30</sup> ; grassland to mountain zones along the Bow River <sup>9</sup> , Alberta; present in the Cypress Hills <sup>10</sup> and also boreal in Saskatchewan <sup>10</sup> and Manitoba <sup>3,14</sup> .	6, 9, 10, 30	6, 10	3, 6, 14	p, m, b	
<b>Leuctridae</b>								
<i>Despaxia augusta</i> (Banks 1907). Autumn needletfly.	W	SW?	CAN: AB <sup>8,30</sup> , BC. USA: AK, CA, ID, MT, OR, WA. <b>Remarks:</b> Northwestern North America <sup>30</sup> ; mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	8, 30	-	-	m	

<i>Leuctra ferruginea</i> (Walker 1852). Eastern needletly.	E, MW	SE	CAN: NB, NF, NS, ON, PQ, SK. USA: AL, CT, DE, FL, KY, LA, MA, MD, ME, MI, MN, MS, NC, NJ, NY, OH, PA, SC, TN, VA, WI, WV. <b>Remarks:</b> Reaches western extent in SK boreal zone <sup>10</sup> .	-	6, 10	-	b
<i>Megalactra stigmata</i> (Banks 1900). Giant needletly.	NW	SW	CAN: AB, BC, MB. USA: MT, WA. <b>Remarks:</b> Northern Rockies and east to MB <sup>30</sup> , and reported (as <i>M. spectabilis</i> ) in the mountain zone in the Waterton River drainage, Alberta <sup>8</sup> . It was described from Winnipeg (as <i>Nemoura stigmata</i> ) <sup>3,6</sup> , but is generally found in springfed streams in the northwest, so its occurrence in MB was questioned (as a possible labeling error) by Ricker <sup>26</sup> and Burton <sup>3</sup> .	6, 8, 30	-	3, 6, 16	p, m
<i>Paralactra alta</i> Baumann and Stark 2009. Alberta needletly.	W	SW?	CAN: AB. <b>Remarks:</b> Only recorded so far from a Malaise trap sample, collected near Hinton in northwestern Alberta foothills <sup>5</sup> .	5, 6	-	-	m
<i>Paralactra forcipata</i> (Frison 1937). Bullshorn needletly.	W	SW?	CAN: AB, BC, YK <sup>30</sup> . USA: AK, CA, ID, MT, OR, WA. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Kananaskis and Waterton River drainages, Alberta <sup>8,25</sup> .	6, 8, 25, 30	-	-	m
<i>Paralactra occidentalis</i> (Banks 1907). Western needletly.	W	SW?	CAN: AB, BC, YK. USA: AK, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Waterton <sup>8</sup> , Kananaskis <sup>25</sup> , and Bow River <sup>9</sup> drainages, Alberta.	6, 8, 9, 25, 30	-	-	m
<i>Paralactra vershina</i> Gaufin and Ricker 1974. Summit needletly.	W	SW	CAN: AB, BC, SK. USA: AK, CA, CO, ID, MT, NM, NV, OR, SD, UT, WA, WY. <b>Remarks:</b> Western mountains and east to great plains <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>8</sup> and Cypress Hills <sup>10</sup> .	6, 8, 10, 30	6, 10	-	p, m
<i>Perlomyia utahensis</i> Needham and Claassen 1925. Utah needletly.	W	SW?	CAN: AB, BC, YK <sup>30</sup> . USA: CA, CO, MT, NM, OR, UT, WA, WY. <b>Remarks:</b> Western mountains, commonly associated with springs <sup>30</sup> , mountain zone in the Waterton and Kananaskis River drainages, Alberta <sup>8,25</sup> .	6, 8, 25, 30	-	-	m
<i>Pomoleuctra purcelliana</i> (Neave 1924). Purcell needletly.	W	SW?	CAN: AB, BC, YK <sup>30</sup> . USA: ID, MT, OR, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	6, 8, 30	-	-	m
<b>Nemouridae</b>							
<i>Amphinemura banksi</i> Baumann and Gaufin 1972. Rockies forestfly.	W	SW?	CAN: AB <sup>8,21,30</sup> . USA: AZ, CO, ID, MT, NM, SD, UT, WY. <b>Remarks:</b> Rocky Mountains <sup>30</sup> , mountain zone in the Waterton River drainage <sup>8</sup> and Cypress Hills, Alberta <sup>21</sup> .	8, 21, 30	-	-	p, m
<i>Amphinemura palmeni</i> (Koponen 1917) (no common name, but the common name for <i>A. linda</i> was lovely forestfly).	E, MW	SE	CAN: AB, BC, LB, MB, NT, ON, PQ, SK, YK. USA: AK, IA, MI, PA, SD, WI. <b>Remarks:</b> (as <i>A. linda</i> ) across northern North America and central Rocky Mountains, in small and medium sized streams <sup>30</sup> ; widespread boreal species across Alberta <sup>2</sup> , Saskatchewan <sup>10,11</sup> , and Manitoba <sup>3,17</sup> , and in streams bordering the prairies in Saskatchewan <sup>20</sup> ; reported in large springbrook habitat in Iowa and South Dakota <sup>18</sup> .	2, 6, 30	6, 10, 11, 20	3, 6, 17	p, m, b
<i>Lednia tumana</i> (Ricker 1952). Meltwater forestfly.	W	SW?	CAN: AB. USA: MT, WY. <b>Remarks:</b> Northern Rocky Mountains <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>4,8</sup> .	4, 6, 8, 30	-	-	m

Species, Common Name	Distr.	Orig.	North American Distribution and Notes	Prairie Provinces Distribution			
				AB	SK	MB	Zone
<i>Malenka californica</i> (Claassen 1923). California forestfly.	W	SW?	CAN: AB, BC, MB, SK. USA: CA, CO, ID, MT, NM, NV, OR, UT, WA, WY. <b>Remarks:</b> Northwestern mountains in low elevation or montane springs or streams <sup>30</sup> ; mountain zone in the Waterton <sup>8</sup> and Bow River <sup>8</sup> drainages, as well as Big Hill Springs (northwest of Calgary) in Alberta <sup>21</sup> . Reported in the northern boreal <sup>10</sup> and bordering the prairies <sup>20</sup> in Saskatchewan; and in both the boreal (Duck Mountain Park) <sup>3,17</sup> and prairie (Stoney Creek near Minnedosa) zones in Manitoba <sup>3</sup> .	6, 8, 9, 21, 30	6, 10, 20	3, 6, 17	p, m, b
<i>Malenka flexura</i> (Claassen 1923). Twisted forestfly.	W	SW?	CAN: AB, BC, ID, MT, NM, OR, WA, WY. <b>Remarks:</b> Northwestern mountains in low elevation or montane springs or streams <sup>30</sup> ; mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	6, 8, 30	-	-	m
<i>Nemoura arctica</i> Esben-Petersen 1910. Arctic forestfly.	NE, NW	B	CAN: AB, BC, MB, NT, NU, PQ. USA: AK, SD, WY. <b>Remarks:</b> Holarctic; northern or montane <sup>30</sup> ; northern boreal in Alberta <sup>2</sup> , and Manitoba <sup>3,27</sup> .	2, 6, 30	-	3, 6, 27	m, b
<i>Nemoura rickerti</i> Jewett 1971. Nearctic forestfly.	NW	B	CAN: MB, SK, NT <sup>30</sup> , YK <sup>30</sup> . USA: AK. <b>Remarks:</b> Far northwestern <sup>30</sup> ; northern boreal <sup>10</sup> in Saskatchewan.	-	6, 10	6	m, b
<i>Nemoura trispinosa</i> Claassen 1923. Three-spined forestfly.	NE, MW	SE?	CAN: LB, MB, NB, NS, ON, PE, PQ. USA: IA, IL, ME, MI, NY, OH, PA, SD, WI, WY. <b>Remarks:</b> Labrador west to Manitoba and south to Illinois <sup>28</sup> ; restricted to springbrooks in Iowa <sup>18</sup> and in the Black Hills of South Dakota <sup>19</sup> .	-	-	6, 28	p, b
<i>Podmosta decepta</i> (Frison 1942). Least forestfly.	W	SW?	CAN: AB, BC, YK <sup>30</sup> . USA: AK, CO, ID, MT, OR, UT, WA, WY. <b>Remarks:</b> Western mountains in small, high elevation creeks <sup>30</sup> ; mountain zone in the Waterton River, Alberta <sup>8</sup> .	6, 8, 30	-	-	m
<i>Podmosta delicatula</i> (Claassen 1923). Delicate forestfly.	W	SW	CAN: AB, BC, SK, YK. USA: AK, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY. <b>Remarks:</b> Intermountain areas in small, high elevation creeks <sup>30</sup> ; mountain zone in the Waterton River drainage, Alberta <sup>8</sup> ; Cypress Hills <sup>10</sup> .	6, 8, 10, 30	6, 10	-	p, m
<i>Prostioia besametsa</i> (Ricker 1952). Banded forestfly.	W	SW?	CAN: AB, BC, NT <sup>30</sup> , YK <sup>30</sup> . USA: AK <sup>30</sup> , CA, CO, ID, MT, NM, NV, OR, SD, UT, WA, WY. <b>Remarks:</b> Western mountains extending eastward, in lowland streams and rivers, usually in leaf packs <sup>30</sup> ; mountain zone in the Waterton <sup>8</sup> , Kananaskis <sup>25</sup> , and Bow River <sup>9</sup> drainages, Alberta.	6, 8, 9, 25, 30	-	-	m, b
<i>Shipsa rotunda</i> (Claassen 1923). Intrepid forestfly.	E, NW	SE	CAN: AB, NB, MB, NT, NU <sup>30</sup> , ON, PQ, SK. USA: AK, AL, AR, IA, IL, MD, ME, MI, MN, MS, NY, SC, VA, WI. <b>Remarks:</b> Widespread in the east and across Canada <sup>30</sup> ; northern boreal streams in Alberta <sup>2</sup> , and Saskatchewan <sup>10,11</sup> and the North Saskatchewan River in Saskatchewan <sup>10,20</sup> ; northern boreal and in forested streams bordering the prairies in Manitoba <sup>3</sup> , reported as uncommon in Iowa where it was in medium to large rivers <sup>18</sup> .	2, 6, 30	6, 10, 11, 20	3, 6	p, b

<i>Soyedina potteri</i> (Baumann and Gaufin 1971). Rocky Mountain forestfly.	NW	SW?	<b>CAN:</b> AB <sup>8,30</sup> , <b>USA:</b> ID, MT. <b>Remarks:</b> Northern Rocky Mountains <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	8, 30	-	-	m	
<i>Visoka cataractae</i> (Neave 1933). Cataract forestfly.	W	SW?	<b>CAN:</b> AB, BC. <b>USA:</b> AK, CA, ID, MT, OR, WA. <b>Remarks:</b> Western mountains in small cold torrential streams <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	6, 8, 30	-	-	m	
<i>Zapada cinctipes</i> (Banks 1897). Common forestfly.	W	SW	<b>CAN:</b> AB, BC, MB, NT, SK, YK. <b>USA:</b> AK, CA, CO, ID, MT, NM, NV, SD, UT, WA, WY. <b>Remarks:</b> Western North America from mountains to great plains and found over a wide temperature range <sup>30</sup> ; mountain zone in the Kananaskis <sup>25</sup> and Waterton River drainages <sup>8</sup> , and upper grasslands to mountains along the Bow River <sup>6</sup> ; northern boreal in Alberta <sup>2</sup> and Saskatchewan <sup>10,11</sup> ; Cypress Hills <sup>10,26</sup> ; prairies to the southern boreal in Manitoba <sup>3,17</sup> . Ricker <sup>26</sup> described it as a cordilleran species now spread over most of the prairies.	6, 8, 9, 10, 25, 26, 30	6, 10, 11	3, 6, 17, 26	p, m, b	
<i>Zapada columbiana</i> (Claassen 1923). Columbian forestfly.	W	SW?	<b>CAN:</b> AB, BC, NT <sup>30</sup> , YK <sup>30</sup> . <b>USA:</b> AK, CA, ID, MT, OR, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Waterton <sup>8</sup> , Kananaskis <sup>25</sup> , and Bow River <sup>6</sup> drainages and Cypress Hills <sup>21</sup> in Alberta.	6, 8, 9, 21, 25, 30	-	-	p, m	
<i>Zapada frigida</i> (Claassen 1923). Frigid forestfly.	W	SW?	<b>CAN:</b> AB <sup>8,30</sup> , BC, YK <sup>30</sup> . <b>USA:</b> AK <sup>30</sup> , CA, CO, ID, MT, NM, NV, OR, UT, WA. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in Waterton River drainage, Alberta <sup>8</sup> .	8, 30	-	-	m	
<i>Zapada haysi</i> (Ricker 1952). Intermountain stonefly.	W	SW?	<b>CAN:</b> AB <sup>8,30</sup> , BC, YK <sup>30</sup> . <b>USA:</b> AK <sup>30</sup> , CA, CO, ID, MT, NM, NV, OR, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in Waterton River drainage, Alberta <sup>8</sup> .	8, 30	-	-	m	
<i>Zapada oregonensis</i> (Claassen 1923). Oregon forestfly.	W	SW?	<b>CAN:</b> AB, BC, YK, NT. <b>USA:</b> AK, CA, CO, ID, MT, NM, NV, OR, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> ; Emerged in April/May in Kananaskis area streams in Alberta <sup>25</sup> .	6, 25, 30	-	-	m	
<b>Taeniopterygidae</b>								
<i>Doddsia occidentalis</i> (Banks 1900). Western willowfly.	W	SW?	<b>CAN:</b> AB <sup>8,9,30</sup> , BC. <b>USA:</b> AK, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Waterton <sup>8</sup> and Bow River <sup>6</sup> drainages, Alberta.	8, 9, 30	-	-	m	
<i>Oemopteryx fosketti</i> (Ricker 1965). Saskatoon willowfly.	W	SW	<b>CAN:</b> AB, MB, SK. <b>USA:</b> CO, MT, ND, UT. <b>Remarks:</b> Western North America <sup>30</sup> ; northern boreal in Alberta <sup>2</sup> and Manitoba <sup>3</sup> , and in the Saskatchewan River in Saskatchewan <sup>10,20</sup> (the type locality is the South Saskatchewan River <sup>6,9</sup> ).	2, 6, 26, 30	6, 10, 20, 26	3, 6	p, b	
<i>Strophopteryx fasciata</i> (Burmeister 1839). Mottled willowfly.	E, MW	SE?	<b>CAN:</b> MB, ON, PQ. <b>USA:</b> AL, AR, CT, DE, IA, IL, IN, KS, KY, ME, MI, MN, MO, MS, NC, ND, OH, OK, PA, SC, VA, WI, WV. <b>Remarks:</b> Southern boreal streams that border the Prairies Ecozone in Manitoba <sup>3</sup> , and in medium sized streams with abundant cobble in Iowa <sup>6</sup> .	-	-	3, 6	p, b	



Species, Common Name	Distr.	Orig.	North American Distribution and Notes				Prairie Provinces Distribution			
			AB	SK	MB	Zone				
<i>Taenionema pacificum</i> (Banks 1900). Pacific willowfly.	W	SW	CAN: AB, BC, YK. USA: AK, AZ, CA, CO, ID, MT, NM, OR, UT, WA, WY. <b>Remarks:</b> Western North America <sup>30</sup> , grasslands to the mountain zone in Waterton River <sup>8</sup> and Bow River <sup>9</sup> drainages, Alberta.				6, 8, 9, 30	-	-	p, m
<i>Taenionema pallidum</i> (Banks 1902). Common willowfly.	W	SW?	CAN: AB, BC, YK. USA: AK, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY. <b>Remarks:</b> Western North America <sup>30</sup> , (as <i>T. nigripennis</i> ) mountain zone in the Waterton <sup>8</sup> and Kananaskis <sup>25</sup> River drainages, Alberta.				6, 8, 25, 30	-	-	m
<i>Taeniopteryx nivalis</i> (Fitch 1847). Boreal willowfly.	E, MW, W	SE	CAN: AB, MB, ON, PQ, SK. USA: CA, CT, DE, IA, ID, IL, IN, ME, MI, MN, NY, OH, OR, PA, UT, WI, WA. <b>Remarks:</b> Northern North America <sup>30</sup> , boreal <sup>2</sup> and prairie habitats in Alberta <sup>2,9</sup> , Saskatchewan <sup>10,20</sup> and Manitoba <sup>3,13</sup> . It is common in small clean streams in Iowa <sup>18</sup> .				2, 6, 9, 30	6, 10, 20	3, 6, 13	p, b
<i>Taeniopteryx parvula</i> Banks 1918. Hooked willowfly.	E, MW, W	SE	CAN: AB, MB, ON, PQ, USA: AR, CO, CT, GA, IL, IN, KY, ME, MI, MN, MO, MS, NM, NJ, NY, OH, PA, SC, TN, VA, WI, WV, WY. <b>Remarks:</b> Eastern North America, extending west from New Mexico and northward into Alberta <sup>30</sup> ; boreal zone in northeastern Alberta <sup>2</sup> ; Red River tributaries <sup>3,13</sup> and southern boreal streams in Manitoba <sup>2</sup> .				2, 6, 30	3, 6, 16, 13	3, 6, 16, 13	p, b
<b>Chloroperlidae</b>										
<i>Alloperla delicata</i> Frison 1935. Delicate sallfly.	W	SW?	CAN: AB, BC. USA: AK <sup>30</sup> , CA, ID, MT, OR, WA. <b>Remarks:</b> Western mountains <sup>30</sup> , Kananaskis area streams <sup>25</sup> .				6, 25, 30	-	-	m
<i>Alloperla medveda</i> Ricker 1952. Beartooth sallfly.	W	SW?	CAN: AB, BC, YK. USA: ID, MT, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , found in the mountain zone in the Waterton River drainage in southern Alberta <sup>8</sup> .				6, 8, 30	-	-	m
<i>Alloperla serrata</i> Needham and Claassen 1925. Sawtooth sallfly.	W	SW?	CAN: AB, BC, YK. USA: AK, ID, MT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> ; mountain zone in the Waterton River drainage, Alberta <sup>5</sup> .				6, 5, 30	-	-	m
<i>Alloperla severa</i> (Hagen 1861). Western sallfly.	W	SW	CAN: AB, BC, NT, YK. USA: AK, ID, MT. <b>Remarks:</b> Western mountains <sup>30</sup> , grasslands to mountain zones in Waterton River <sup>5</sup> , Kananaskis <sup>25</sup> and Bow River <sup>9</sup> drainages, Alberta.				6, 5, 9, 30	-	-	p, m
<i>Haplloperla brevis</i> (Banks 1895). Least sallfly.	E, MW	SE	CAN: AB, BC, MB, NB, NS, NT, ON, PE, PQ, SK. USA: AL, AR, CT, DE, FL, GA, IL, IN, KY, MA, MD, ME, MI, MN, MO, MS, NC, NH, NJ, NY, OH, OK, PA, SC, TN, VA, VT, WI, WV. <b>Remarks:</b> Widespread in the east, with localized populations in the NW <sup>30</sup> , including northern boreal streams <sup>2,10,11</sup> , Saskatchewan River <sup>12,20</sup> and Cypress Hills <sup>10</sup> in Saskatchewan; boreal (Duck Mountains to Hudson Bay) and prairie (Aweme, Treesbank) sites in Manitoba <sup>3,17,26</sup> .				2, 6, 30	6, 10, 11, 20	3, 6, 15, 16, 17, 26	p, m, b
<i>Kathroperla perdita</i> Banks 1920. Longhead sallfly.	W	SW?	CAN: AB, BC, YK <sup>30</sup> . USA: AK, CA, ID, MT, NV, OR, WA. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Waterton <sup>5</sup> and Kananaskis <sup>25</sup> River drainage, Alberta.				6, 5, 25, 30	-	-	m

<i>Paraperla frontalis</i> (Banks 1902). Hypohectic saliffy.	W	SW	CAN: AB, BC, YK. USA: AK, CA, CO, ID, MT, NM, OR, SD, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , montane zone of Waterton <sup>5</sup> and Kanamaskis <sup>25</sup> River drainages and extending from montane to grasslands along the Bow River <sup>9</sup> .	6, 5, 9, 25, 30	-	-	p, m
<i>Paraperla wilsoni</i> Ricker 1965. Chilliwack saliffy.	NW	SW?	CAN: AB, BC, YK. USA: CA, ID, MT, OR, WA. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>5</sup> .	6, 5, 30	-	-	m
<i>Plumaperla diversa</i> (Frison 1935). Margined saliffy.	W	SW?	CAN: AB, BC, YK. USA: AK, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Waterton River (as <i>Triznaka diversa</i> ) <sup>8</sup> , Kanamaskis (as <i>Alloperla diversa</i> ) <sup>25</sup> and Bow River <sup>9</sup> drainages, Alberta.	6, 8, 9, 25, 30	-	-	m
<i>Sawallia autumnna</i> (Hoppe 1938). Autumn saliffy.	W	SW?	CAN: AB, BC, YK. USA: AK <sup>30</sup> , CA, CO, ID, MT, OR, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> .	6, 30	-	-	m
<i>Sawallia dubia</i> (Frison 1935). Pale saliffy.	W	SW?	CAN: AB, BC, YK. USA: AK, CA, CO, ID, MT, OR, UT, WA, WY. <b>Remarks:</b> Northwestern mountains <sup>30</sup> .	6, 30	-	-	m
<i>Sawallia forcipata</i> (Neave 1929). Forceps saliffy.	NW	SW?	CAN: AB, BC, YK. USA: AK, MT, WA. <b>Remarks:</b> Northwestern mountains <sup>30</sup> , mountain zone in the Waterton (as <i>Neaviperla forcipata</i> ) <sup>8</sup> , Kanamaskis <sup>25</sup> , and Bow River <sup>1,9</sup> drainages, Alberta.	6, 8, 9, 25, 30	-	-	m
<i>Sawallia lineosa</i> (Banks 1918). Lined saliffy.	W	SW	CAN: AB, BC, SK, YK. USA: AK, CO, ID, MT, OR, SD, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , found in Banff National Park <sup>1</sup> and mountain zone in the Waterton River drainage, southern Alberta <sup>8</sup> , as well as in the Cypress Hills <sup>10</sup> .	1, 6, 8, 10, 30	6, 10	-	p, m
<i>Sawallia pallidula</i> (Banks 1904). Yellow saliffy.	W	SW	CAN: AB, BC, MB, SK <sup>12</sup> . USA: AK, AZ, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY. <b>Remarks:</b> Western, extending into SW Canada <sup>30</sup> , prairie to mountain zones in Waterton <sup>8</sup> , Kanamaskis <sup>25</sup> , and Bow River <sup>9</sup> drainages, Alberta; southern boreal in Saskatchewan <sup>12</sup> , and in cool spring-fed streams in the Duck Mt. region of Manitoba <sup>17</sup> . Note: Stewart and Oswood <sup>30</sup> indicate that records of this species in western Canada north of southern Alberta may refer to <i>S. starki</i> .	6, 7, 8, 9, 25, 30	12	6, 17	p, m, b
<i>Sawallia starki</i> Alexander and Stewart 1999. Gallatin saliffy.	NW	SW?	CAN: AB, BC, NT <sup>30</sup> . YK <sup>10</sup> . USA: AK, CA, CO, ID, MT, NM, OR, WA, WY. <b>Remarks:</b> Central and northern Rocky Mountains and Coast Mountains <sup>30</sup> , collected near Banff in Alberta <sup>1</sup> .	1, 6, 30	-	-	m
<i>Sweltsa albertensis</i> (Needham and Claassen 1925). Alberta saliffy.	NW	SW?	CAN: AB, BC. USA: CO, ID, MT, WY. <b>Remarks:</b> Northern Rocky Mountains <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	6, 8, 30	-	-	m
<i>Sweltsa borealis</i> (Banks 1895). Boreal saliffy.	W	SW?	CAN: AB, BC, YK. USA: AK, CA, CO, ID, MT, NM, NV, OR, SD, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Waterton <sup>8</sup> and Kanamaskis <sup>25</sup> River drainages, Alberta.	6, 8, 25, 30	-	-	m

Species, Common Name	Distr.	Orig.	North American Distribution and Notes	Prairie Provinces Distribution			
				AB	SK	MB	Zone
<i>Sweltsa coloradensis</i> (Banks 1898). Colorado salfly.	W	SW	CAN: AB, BC, YK. USA: AK, AZ, CA, CO, ID, MT, NM, NV, OR, SD, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , grasslands to mountain zones in Waterton <sup>8</sup> , Kananaskis <sup>25</sup> , and Bow River <sup>9</sup> drainages, Alberta.	6, 8, 9, 25, 30	-	-	p, m
<i>Sweltsa fidelis</i> (Banks 1920). Mountain salfly.	W	SW?	CAN: AB, BC, YK. USA: AK, CA, CO, ID, MT, NV, OR, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	6, 8, 30	-	-	m
<i>Sweltsa revelstoka</i> (Jewett 1955). Canadian salfly.	NW	SW?	CAN: AB, BC. USA: AK, MT, OR, WA, WY. <b>Remarks:</b> Northwestern mountains <sup>30</sup> , mountain zone in the Waterton <sup>8</sup> , Kananaskis <sup>25</sup> , and Bow River <sup>9</sup> drainages, Alberta.	6, 8, 9, 25, 30	-	-	m
<i>Triznaka signata</i> (Banks 1895). Striped salfly.	W	SW	CAN: AB, BC, SK, YK. USA: AK, CO, ID, MT, NM, OR, SD, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , grasslands to mountain zones in Waterton <sup>8,26</sup> and Bow River <sup>9</sup> drainages, Alberta; through the northern boreal zone to Saskatchewan <sup>10</sup> .	6, 7, 8, 9, 10, 26, 30	6, 10	-	p, m, b
<i>Utaperla sopladora</i> Ricker 1952. Black salfly.	W	B	CAN: AB, BC, YK. USA: AK, ID, MT, NV, UT, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	6, 8, 30	-	-	m
<b>Peltoperlidae</b>							
<i>Yoraperla brevis</i> (Banks 1907). Least roachfly.	W	SW?	CAN: AB, BC. USA: ID, MT, OR, WY. <b>Remarks:</b> Northern Rocky Mountains <sup>30</sup> .	6, 30	-	-	m
<i>Yoraperla mariana</i> (Ricker, 1943). Brown roachfly.	NW	SW?	CAN: AB <sup>8,30</sup> , BC. USA: OR, WA. <b>Remarks:</b> Mountains of the Pacific Northwest <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	8, 30	-	-	m
<b>Perlidae</b>							
<i>Acroneuria abnormis</i> (Newman 1838). Common stone (Fig. 1A).	E, MW, W	SC or SE?	CAN: AB, MB, NB, NF, ON, PQ, SK. USA: AL, CO, CT, DE, FL, GA, IA, IL, IN, KS, KY, LA, MA, MD, ME, MI, MN, MS, MT, NC, ND, NE, NM, NY, OH, PA, SC, SD, TN, UT, VA, WI, WY. <b>Remarks:</b> Eastern North America extending across the plains and into the Rocky Mountains <sup>30</sup> , boreal zone in Alberta <sup>2</sup> ; Saskatchewan River in Saskatchewan <sup>10,30</sup> , widespread in southern Manitoba, including prairie streams and the southern boreal zone <sup>2,26</sup> . It is reported in a wide range of streams in Iowa, where it is apparently tolerant of mild pollution <sup>16</sup> .	2, 6, 30	6, 10, 20	3, 6, 26	p, b, m
<i>Acroneuria carolinensis</i> (Banks 1905). Carolina stone.	E	SE?	CAN: MB, ON, PQ. USA: AL, CT, GA, KY, MA, MD, ME, MS, NC, NH, NJ, NY, OH, PA, SC, TN, VA, WV. <b>Remarks:</b> reported from Churchill in the north to the Souris River in the southwest of Manitoba <sup>3</sup> .	-	-	3, 6	p, b
<i>Acroneuria lycorias</i> (Newman 1839). Boreal stone.	E, MW	SE	CAN: MB, NB, NS, ON, PQ, SK. USA: CT, FL, KY, IA, ME, MI, MN, NC, ND, NJ, NY, OH, PA, TN, VA, WI, WV. <b>Remarks:</b> Widespread eastern species extending to boreal Alberta <sup>2</sup> and Saskatchewan (from Lake Athabasca <sup>11</sup> to streams along the edge of the prairie, where nymphs were often collected under rocks in rapids) <sup>10</sup> , boreal habitats east of Lake Winnipeg in Manitoba, and prairies zone at Winnipeg and Aweme <sup>2,6</sup> . It is reported from small cobble bottom creeks and upper parts of large rivers in Iowa <sup>18</sup> .	-	2, 6, 10, 11	3, 6, 15, 16, 26	p, b

<i>Attaneuria ruralis</i> (Hagen 1861). Giant stone.	E, MW	SE	CAN: MB, USA: AL, AR, DC, FL, GA, IA, IL, IN, KS, MD, MI, MN, MO, MS, NC, NE, NY, OH, PA, SC, TN, VA, WI. <b>Remarks:</b> Collected around Aweme in the Prairies Ecozone in Manitoba <sup>3,26</sup> , under stones in larger streams and lakes and ponds <sup>26</sup> , and is reported from large slow rivers with woody debris in Iowa <sup>18</sup> .	-	-	3, 6, 16, 26	p, b
<i>Calineuria californica</i> (Banks 1905). Western stone.	W	SW?	CAN: AB, BC, USA: CA, ID, MT, OR, WA. <b>Remarks:</b> Western mountains <sup>30</sup> .	6, 30	-	-	m
<i>Claassenia sabulosa</i> (Banks 1900). Shortwing stone (Fig. 1B).	W	SW	CAN: AB, BC, MB, NT, NU <sup>30</sup> , ON, PQ, SK, YK. USA: AZ, CA, CO, ID, MT, NM, OR, SD, UT, WA, WY. <b>Remarks:</b> Northern and western NA <sup>30</sup> ; across the boreal zone in Alberta <sup>2</sup> Saskatchewan <sup>10,11</sup> and Manitoba <sup>3</sup> ; prairie to the mountain zone along the Bow River, Alberta <sup>9</sup> and Prairies Ecozone (Lemsford Ferry on the South Saskatchewan River) in Saskatchewan <sup>20</sup> .	2, 6, 9, 30	6, 10, 11, 20	3, 6	p, m, b
<i>Doroneuria theodora</i> (Needham and Claassen 1922). Montana stone.	W	SW?	CAN: AB, BC, USA: ID, MT, WY. <b>Remarks:</b> Northern Rocky Mountains <sup>30</sup> ; mountain zone in the Waterton <sup>8</sup> and Bow River <sup>9</sup> drainages, Alberta.	6, 8, 9, 30	-	-	m
<i>Hesperoperla pacifica</i> (Banks 1900). Golden stone.	W	SW	CAN: AB, BC, SK, YK. USA: AK, AZ, CA, CO, ID, MT, NM, NV, OR, SD, UT, WA, WY. <b>Remarks:</b> Widespread in western NA <sup>30</sup> ; prairie to the mountain zone in the Waterton River <sup>8</sup> and Bow River <sup>9</sup> drainages, Alberta; Cypress Hills in Saskatchewan <sup>10</sup> .	6, 8, 9, 10, 30	6, 10	-	p, m
<i>Paragnetina media</i> (Walker 1852). Embossed stone.	E, MW	SE	CAN: MB, NB, ON, PQ, SK. USA: AR, CT, DE, IA, IL, IN, KY, MD, ME, MI, MN, MO, NH, NY, OH, PA, VA, WI, WV. <b>Remarks:</b> Northern boreal region in Saskatchewan <sup>10</sup> and boreal and prairie rivers in Manitoba <sup>3,26</sup> ; cool shaded streams in Iowa <sup>18</sup> .	-	6, 10, 15	6, 26	p, b
<i>Perlesta</i> sp. ( <i>placidia</i> complex)	E, MW, W	SE	<b>Remarks:</b> Specimens from this species complex have been collected from the Torch River (in Saskatchewan Aspen Parkland Ecoregion), Assiniboine River (southern prairie) and edges of the boreal zone in Saskatchewan <sup>10,12,20</sup> , and in a number of prairie rivers in southwest Manitoba <sup>3</sup> . It was recorded as <i>Perlesta placida</i> in a number of accounts <sup>3,10,15,20,26</sup> , but this is now known to be a large complex of several species (Stark 1989; Kondratieff and Myers 2011). <i>Perlesta dakota</i> was recently confirmed for Saskatchewan (see below), but <i>Perlesta</i> specimens from Saskatchewan (LMD, personal collection) and Manitoba (Wallace Roughley Museum, University of Manitoba) could not be confirmed as <i>P. dakota</i> , with at least one specimen not fitting the description of <i>P. dakota</i> (R.E. DeWalt, Pers. Comm.). Further collecting is needed to establish which <i>Perlesta</i> species are present in the Canadian Prairies. Another species, <i>P. decipiens</i> , is reported to be widely distributed in warm streams through the American midwest and in the larger rivers of the plains and foothills of the Rockies <sup>6</sup> , so may occur in the Canadian Prairie Provinces as well.	-	10, 12, 20	3, 15, 26	p

Species, Common Name	Distr.	Orig.	North American Distribution and Notes	Prairie Provinces Distribution				
				AB	SK	MB	Zone	
<i>Perlesta dakota</i> Kondratieff and Baumann 1999 (Fig. 1C).	MW	?	CAN: SK*. USA: ND, SD. <b>Remarks:</b> Specimens of this species from a prairie river in southern Saskatchewan (reported as <i>P. placida</i> ; Phillips <i>et al.</i> 2008) were determined to be <i>P. dakota</i> by B. Kondratieff (*D. Parker, Pers. Comm.).	*				
<b>Perlodidae</b>								
<i>Cultus aestivalis</i> (Needham and Claassen 1925). Summer springfly.	W	SW	CAN: AB <sup>8,9,26</sup> , BC, NT, YK. USA: AZ, CO, ID, MT, NM, UT, WY. <b>Remarks:</b> Western species in and near the mountains <sup>26</sup> ; prairie to the mountain zone in the Waterton River <sup>8</sup> and Bow River <sup>9</sup> drainages in Alberta, as far east as Lethbridge <sup>26</sup> .	8, 9, 26	-	-	p, m	
<i>Cultus tostonus</i> (Ricker 1952). Toston springfly.	W	SW	AB <sup>8,9</sup> , BC, CA, ID, MT, OR, WA, WY. <b>Remarks:</b> Prairies Ecozone in the Waterton River <sup>8</sup> and Bow River <sup>9</sup> drainages, Alberta.	8, 9	-	-	p, m	
<i>Diura bicaudata</i> (Linnaeus 1758). Lapland springfly.	NW	B	CAN: MB, NT, NU, SK, YK. USA: AK. <b>Remarks:</b> Circumpolar northern species <sup>30</sup> ; northern boreal in SK <sup>10,11</sup> and near Churchill in Manitoba <sup>3</sup> .	-	6, 10, 11	3, 6, 10	b	
<i>Diura knowltoni</i> (Frison 1937). Nearctic springfly.	W	SW?	CAN: AB, BC, SK, YK. USA: CA, CO, ID, MT, NM, NV, OR, UT, WY. <b>Remarks:</b> Western mountains; only found above 1800 m elevation in the southern parts of the range <sup>30</sup> .	6, 30	6	-	m, b	
<i>Isogenoides colubrinus</i> (Hagen 1874). Blackfoot springfly.	W	SW	CAN: AB, BC, MB, NT, NU <sup>30</sup> , SK, YK. USA: AK, AZ, CA, CO, ID, MT, NM, OR, UT, WA, WY. <b>Remarks:</b> Rocky Mountains and across the north <sup>30</sup> ; prairie to mountain zones along the Bow River, Alberta <sup>9</sup> ; North and South Saskatchewan Rivers in Saskatchewan <sup>10,20</sup> and Manitoba (near The Pas) <sup>3</sup> .	2, 6, 9, 26, 30	6, 10, 20	3, 6	p, m, b	
<i>Isogenoides doratus</i> (Frison 1942). Indiana springfly.	E, MW	SE?	CAN: BC, MB, PQ. USA: IA, MN, MI, NY. <b>Remarks:</b> Aweme and Assiniboine River in southwest Manitoba (as <i>I. krumholzii</i> ) <sup>3</sup> .	-	-	3, 6	p, b	
<i>Isogenoides elongatus</i> (Hagen 1874). Elongate springfly.	W	SW	CAN: AB, BC, MB. USA: AZ, CO, ID, MT, NM, SD, UT, WA, WY. <b>Remarks:</b> Western Mountains <sup>30</sup> ; described as a cordilleran species which has spread over most of the prairies <sup>26</sup> ; prairies to mountains in Alberta (Lethbridge <sup>26</sup> , Waterton River <sup>8</sup> , Bow River <sup>9</sup> ) and prairies (Aweme <sup>26</sup> ) in Manitoba.	6, 8, 9, 26, 30	-	6	p, m	
<i>Isogenoides frontalis</i> (Newman 1838). Hudsonian springfly.	NE, MW	SE	CAN: MB, NF, ON, PQ, SK. USA: ME, MI, MN, NY, WI. <b>Remarks:</b> Boreal forest in northern Saskatchewan <sup>10,11</sup> and Manitoba <sup>3,17</sup> .	-	6, 10, 11	3, 6, 17	p, b	
<i>Isoperla bilineata</i> (Say 1823). Two-lined stripetal.	E, MW	SC or SE?	CAN: MB, NB, NF, ON, PQ, SK. USA: AL, CO, CT, FL, IA, IL, IN, KS, KY, MA, ME, MI, MN, MO, MS, NC, ND, NE, NY, OH, PA, SD, VA, WI, WV. <b>Remarks:</b> A "northern Great Plains" species in Saskatchewan <sup>10</sup> ; prairie rivers in southern Manitoba <sup>3,26</sup> ; medium to large rivers in Iowa <sup>18</sup> .	-	6, 10, 20, 26	3, 6, 16, 26	p, b	

<i>Isoperla decolorata</i> (Walker 1852). Bear Lake stripetail.	NW	B	CAN: AB, BC, MB, NT, NU <sup>30</sup> , SK, YK. USA: AK. <b>Remarks:</b> Reported from large rivers in or near tundra <sup>30</sup> but is boreal in Saskatchewan and borders the Prairies Ecozone in the North Saskatchewan River <sup>10,20</sup> , where it is reported as a "rare northern species" <sup>7,20</sup> . It is reported from Churchill in Manitoba <sup>7</sup> .	30	6, 10, 20	3, 6	p, b
<i>Isoperla dicada</i> Frison 1942. Sable stripetail.	E, MW	SE?	CAN: MB, NB, ON, PQ. USA: AL, AR, CT, FL, IA, IN, KY, MA, MD, ME, MI, MN, MO, MS, NC, NY, OH, PA, SC, TN, VA, WI, WV. <b>Remarks:</b> Southern boreal in Manitoba <sup>7</sup> ; small to medium sized streams in Iowa and Wisconsin <sup>18</sup> .	-	-	3, 6	b
<i>Isoperla frisoni</i> Illies 1966. Wisconsin stripetail.	NE, MW	SE?	CAN: MB, NB, NS, ON, PE, PQ. USA: CT, DE, IN, ME, MI, MN, NC, NY, PA, WI. <b>Remarks:</b> This species was reported from the southern boreal zone in Manitoba <sup>7</sup> .	-	-	3, 6	b
<i>Isoperla fulva</i> Claassen 1937. Western stripetail.	W	SW	CAN: AB, BC. USA: AZ, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , Prairies Ecozone in Waterton river drainage <sup>8</sup> ; prairie to mountain zone along the Bow River <sup>9</sup> , and boreal zone in northeastern Alberta <sup>2</sup> .	2, 6, 8, 9, 30	-	-	p, m, b
<i>Isoperla fusca</i> Needham and Claassen 1925. Waterton stripetail.	NW	SW?	CAN: AB, BC, YK. USA: ID, MT, OR, WA, WY. <b>Remarks:</b> Northwestern mountains <sup>30</sup> ; boreal in northeastern Alberta <sup>2</sup> ; mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	2, 6, 8, 30	-	-	m, b
<i>Isoperla longiseta</i> Banks 1906. Plains stripetail.	MW, W	SC	CAN: AB, BC, MB, NT <sup>30</sup> , PQ, SK. USA: CO, IA, ID, IL, KS, MN, MO, MT, ND, NM, SD, UT, WY. <b>Remarks:</b> Prairies Ecozone in the Waterton River drainage <sup>8</sup> and prairie to mountain zones along the Bow River <sup>9</sup> ; across the prairies in Alberta <sup>26</sup> , Saskatchewan <sup>10</sup> and Manitoba <sup>7</sup> . Described as a cordilleran species which has spread over most of the prairies <sup>26</sup> ; Rocky Mountains to the Great Plains <sup>26,30</sup> and boreal forest <sup>2</sup> , but considered a typical prairie stonefly <sup>10,18</sup> .	2, 6, 8, 9, 26, 30	6, 10, 20, 26	3, 6, 16, 26	p, m, b
<i>Isoperla marlynia</i> (Needham and Claassen 1925). Midwestern stripetail.	E, MW	SE	CAN: MB, NB, NS, ON, PQ, SK. USA: CO, IA, IL, IN, KS, KY, ME, MI, MN, NE, NH, NJ, NY, OK, PA, SC, VA, WI, WV. <b>Remarks:</b> A common eastern species; southern boreal and in the Saskatchewan River drainage in Saskatchewan <sup>10,20</sup> and both northern (Churchill) and southern (Aweme) locations in Manitoba <sup>3,26</sup> .	-	6, 10, 20	3, 6, 15, 16, 26	p, b
<i>Isoperla petersoni</i> Needham and Christenson 1928. Springs stripetail.	W	SW	CAN: AB, BC, NT <sup>30</sup> , SK, YK. USA: AK, CO, ID, MT, UT, WA, WY. <b>Remarks:</b> Rocky Mountain and northwest Canada in small and mid-sized clear water streams <sup>30</sup> ; prairie-edge to mountain zones along Bow River <sup>9</sup> ; northern boreal zone in Saskatchewan <sup>10,12</sup> .	6, 9, 30	6, 10, 12	-	p, m, b
<i>Isoperla pinta</i> Frison 1937. Checkered stripetail.	Mex, W	SW	CAN: AB, BC. USA: CA, CO, ID, MT, OR, UT, WA, WY. MEX: Baja California. <b>Remarks:</b> Western mountains <sup>30</sup> ; Prairies Ecozone in Waterton River drainage <sup>8</sup> as far east as Lethbridge in Alberta <sup>26</sup> .	6, 8, 26, 30	-	-	p, m

Species, Common Name	Distr.	Orig.	North American Distribution and Notes	Prairie Provinces Distribution				
				AB	SK	MB	Zone	
<i>Isoperla quinquepunctata</i> (Banks 1902). Fivespot stripetail.	Mex, W	SW	CAN: AB, BC, SK. USA: CA, CO, ID, KS, MT, NE, NM, NV, OR, SD, UT, WY. MEX: Baja California. <b>Remarks:</b> Widespread in western North America <sup>30</sup> (as <i>I. patricia</i> ); reported in the Prairies Ecoregions of both the Waterton <sup>8</sup> and Bow <sup>9</sup> Rivers, Alberta; Cypress Hills, South Saskatchewan River, and other streams in the southwest in Saskatchewan <sup>10,12,20</sup> .	6, 7, 8, 9, 26, 30	6, 10, 12, 20	-	p, m	
<i>Isoperla signata</i> (Banks 1902). Transverse stripetail.	NE, MW	SE?	CAN: MB, NB, NS, PQ. USA: AR, CT, IA, ME, MI, MN, MO, NY, OH, OK, PA, VA, WI, WV. <b>Remarks:</b> Southern boreal streams near the prairies in Manitoba <sup>2</sup> ; small cold-water streams that are influenced by groundwater in Iowa <sup>18</sup> .	-	-	3, 6	p, b	
<i>Isoperla sobria</i> (Hagen 1874). Colorado stripetail.	W	SW?	CAN: AB, BC, YK. USA: AK, AZ, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> ; mountain zone in the Waterton River drainage, Alberta (as <i>I. ebrina</i> ) <sup>8</sup> .	6, 8, 30	-	-	m	
<i>Isoperla sordida</i> Banks 1906. Notched stripetail.	NW	SW?	CAN: AB, BC. USA: AK, CA, ID, MT, OR, WA. <b>Remarks:</b> Western mountains <sup>30</sup> ; boreal forest in Alberta <sup>2</sup> .	6, 30	-	-	m, b	
<i>Isoperla transmarina</i> (Newman 1838). Boreal stripetail.	E, MW	SE	CAN: AB, BC, LB, MB, NB, NE, NS, ON, PE, PQ, SK. USA: CT, DE, IA, KY, ME, MI, MN, NC, NJ, NY, OH, PA, SD, VA, WI, WV, WY. <b>Remarks:</b> Widespread across boreal Saskatchewan <sup>10,11</sup> and Manitoba <sup>3,17,26</sup> , but also further south in or near the prairies zone in both provinces (Saskatchewan: North Saskatchewan River; Carrot River area <sup>20</sup> ; Manitoba: Aweme <sup>27</sup> ); medium sized rivers in Iowa <sup>18</sup> .	6, 30	6, 10, 11, 20 16, 17, 26	3, 6	p, b	
<i>Kogotus modestus</i> (Banks 1908). Sickle springfly.	W	SW?	CAN: AB <sup>8,30</sup> , BC. USA: CO, ID, MT, NM, UT, WY. <b>Remarks:</b> Northwestern mountains <sup>30</sup> ; mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	8, 30	-	-	m	
<i>Kogotus notus</i> (Needham and Claassen 1925). Smooth springfly.	W	SW?	CAN: AB <sup>8,30</sup> , BC. USA: AK, CA, ID, MT, OR, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> ; mountain zone in the Waterton <sup>8</sup> and Bow River <sup>9</sup> drainages, Alberta.	8, 9, 30	-	-	m	
<i>Megarcys signata</i> (Hagen 1874). Larimide springfly.	W	SW?	CAN: AB <sup>8,9,30</sup> , BC. USA: AK, CO, ID, MT, NM, NV, UT, WY. <b>Remarks:</b> Widespread in western North American Mountains <sup>30</sup> ; mountain zone in the Waterton <sup>8</sup> and Bow River <sup>9</sup> drainages, Alberta.	8, 9, 30	-	-	m	
<i>Megarcys watertoni</i> (Ricker 1952). Glacier springfly.	NW	SW?	CAN: AB, BC. USA: ID, MT. <b>Remarks:</b> Rocky Mountains (type locality is in Waterton Park) <sup>30</sup> ; mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	6, 8, 30	-	-	m	
<i>Perlinodes aureus</i> (Smith 1917). Longgill springfly.	W	SW?	CAN: AB. USA: CA, ID, MT, OR, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> .	6, 30	-	-	m	

<i>Seviena bradleyi</i> (Smith 1917). Alberta springfly.	NW	SW?	<b>CAN:</b> AB, BC, <b>USA:</b> ID, MT. <b>Remarks:</b> Rocky Mountains (type locality for this species is Lake Louise) <sup>30</sup> , mountain zone in the Waterton River drainage, Alberta <sup>8</sup> .	6, 8, 30	-	-	m	
<i>Skwala americana</i> (Klapálek 1912). American springfly.	W	SW	<b>CAN:</b> AB <sup>8,9,21,30</sup> , BC, MB, SK, YK. <b>USA:</b> AZ, CA, CO, ID, MT, NM, NV, OR, SK, UT, WA, WY. <b>Remarks:</b> Western mountains <sup>30</sup> (as <i>S. parallela</i> ); Prairies Ecozones of the Waterton <sup>8</sup> and Bow Rivers <sup>9,21</sup> , Alberta, Cypress Hills and boreal region in Saskatchewan <sup>10</sup> , boreal (Duck Mountains) in Manitoba <sup>3</sup> .	7, 8, 9, 21, 30	6, 10	3, 6, 14	p, m, b	
<i>Skwala compacta</i> (McLachlan 1872). Holarctic springfly.	W, NE	<b>B</b>	<b>CAN:</b> AB, BC, NT, NU, SK, YK. <b>USA:</b> AK, CO, ME, MI, MT, NH, NY, WY. <b>Remarks:</b> In cold streams and stony shores of lakes in the north <sup>30</sup> , boreal in Alberta <sup>1</sup> , and in Saskatchewan in cold lakes <sup>10,11</sup> , and may have been in Glacial Lake Agassiz <sup>10</sup> .	1a, 6, 30	6, 10, 11	-	m, b	
<b>Pteronarcyidae</b>								
<i>Pteronarcella badia</i> (Hagen 1874). Least salmonfly.	W	SW	<b>CAN:</b> AB, BC, NT, SK, YK. <b>USA:</b> AK, AZ, CO, ID, MT, NM, NV, OR, UT, WY. <b>Remarks:</b> Western mountains <sup>30</sup> , Prairies Ecozone of the Waterton River drainage, Alberta <sup>8</sup> , northern boreal in Saskatchewan <sup>10</sup> .	6, 8, 9, 30	6, 10	-	p, m, b	
<i>Pteronarcella regularis</i> (Hagen 1874). Dwarf salmonfly.	W	SW	<b>CAN:</b> AB, <b>USA:</b> AK, CA, NV, OR, WA. <b>Remarks:</b> Western mountains <sup>30</sup> and into the boreal forest of northeastern Alberta <sup>2</sup> .	2, 6, 9, 30	-	-	m, b	
<i>Pteronarcys californica</i> Newport 1848. Giant salmonfly.	W	SW	<b>CAN:</b> AB <sup>8,9,30</sup> , BC, YK. <b>USA:</b> AK, AZ, CA, CO, ID, MT, NM, OR, UT, WA, WY. <b>MEX:</b> Chihuahua? <b>Remarks:</b> Western mountains <sup>8,9,30</sup> , prairie and mountain zones of Waterton <sup>8</sup> and Bow <sup>9</sup> River drainages, Alberta.	8, 9, 30	-	-	p, m	
<i>Pteronarcys dorsata</i> (Say 1823). American salmonfly (Fig. 1D).	MW, NE, NW	SE	<b>CAN:</b> AB, BC, LB, MB, NB, ON, PQ, NT, SK, YK. <b>USA:</b> AK, AL, GA, FL, KS, KY, IN, LA, MD, ME, MI, MN, MS, MT, NC, NJ, NY, OH, PA, SC, TN, VA, WI, WV, WY. <b>Remarks:</b> Across eastern and northern North America <sup>30</sup> , Boreal Plains Ecozone in northeastern Alberta <sup>2</sup> and widespread across north-central Saskatchewan, including Saskatchewan River drainage <sup>10,20</sup> and near Lake Athabasca <sup>11</sup> ; both the Boreal Shield Ecozone (Churchill and the southeastern Manitoba) and the Prairies Ecozone (Winnipeg and west) in Manitoba <sup>3</sup> .	2, 6, 26, 30	6, 10, 11, 20	3, 6, 16, 26	p, m, b	
<i>Pteronarcys pictetii</i> Hagen 1873. Midwestern salmonfly	E, MW	SE	<b>CAN:</b> MB. <b>USA:</b> AR, CO, CT, IA, IL, IN, KS, KY, MI, MN, MO, ND, NE, PA, SD, TN, WI. <b>Remarks:</b> in streams west and south of Winnipeg in the prairies zone in Manitoba <sup>3,16</sup> .	-	-	3, 6, 15, 16	p	

References: <sup>1</sup>Alexander and Stewart 1999; <sup>2</sup>Barton 1984; <sup>3</sup>Barton 1984; <sup>4</sup>Baumann and Kondratieff 2010; <sup>5</sup>Baumann and Stark 2009; <sup>6</sup>Dewalt *et al.* 2013; <sup>7</sup>Donald 1980; <sup>8</sup>Donald and Anderson 1977; <sup>9</sup>Donald and Mutch 1980; <sup>10</sup>Dosdall and Lehmkühl 1979; <sup>11</sup>Dosdall and Lehmkühl 1987; <sup>12</sup>Dosdall 1992; <sup>13</sup>Flannagan 1978; <sup>14</sup>Flannagan and Cobb 1983; <sup>15</sup>Flannagan and Cobb 1991; <sup>16</sup>Flannagan and Flannagan 1982; <sup>17</sup>Frieson *et al.* 1984; <sup>18</sup>Hemdal *et al.* 2004; <sup>19</sup>Huntsman *et al.* 1999; <sup>20</sup>Miyazaki and Lehmkühl 2011; <sup>21</sup>Mutch and Pritchard 1986; <sup>22</sup>Nebeker and Gaufin 1965; <sup>23</sup>Nelson and Baumann 1987; <sup>24</sup>Nelson and Baumann 1989; <sup>25</sup>Radford and Hartland-Rowe 1971; <sup>26</sup>Ricker 1946; <sup>27</sup>Ricker 1952; <sup>28</sup>Stark *et al.* 1986; <sup>29</sup>Stark *et al.* 1998; <sup>30</sup>Stewart and Oswood 2006; <sup>31</sup>Zenger and Baumann 2004.



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## Chapter 8

# The Dragonflies and Damselflies (Odonata) of Canadian Grasslands

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**Abstract.** The Odonata are energetic aerial predators of other insects; the aquatic larvae are voracious predators of invertebrates and small vertebrates. As of 2010, 5,952 species of the order were described worldwide; 211 species are known from Canada. Grasslands across the country support about 59% of the national fauna. A checklist and systematic overview of 124 species in nine families are presented. Species totals in these families are as follows: Calopterygidae, 2; Lestidae, 7; Coenagrionidae, 31; Aeshnidae, 16; Gomphidae, 15; Cordulegastridae, 1; Macromiidae, 2; Corduliidae, 13; and Libellulidae, 37. The geographical ranges of the species are defined and summarized; according to the definitions herein, 20 species have boreal ranges, 17 are transition species, 12 are Cordilleran, 1 is Pacific coastal, 10 are western, 4 are more or less restricted to the Great Plains, 16 have southern ranges, 38 are considered eastern, and 6 are widespread species. A summary of studies on grassland Odonata and recommendations for inventory and taxonomic research are provided. The geographical scope of the Canadian grassland fauna is described briefly with respect to lotic and lentic habitats in grasslands of the Cordillera, the Great Plains, and southern Ontario.

**Résumé.** Les odonates sont de féroces prédateurs aériens d'autres insectes ; leurs larves aquatiques sont aussi des prédateurs voraces d'autres invertébrés et petits vertébrés. En 2010, 5 952 espèces d'odonates avaient été décrites dans le monde. De ce nombre, 211 sont connues au Canada. Environ 59 % des odonates de la faune canadienne s'observent dans les prairies. Ce chapitre présente une liste et un aperçu de la systématique de 124 espèces, réparties en neuf familles comme suit : caloptérygides, 2 ; lestidés, 7 ; coenagrionidés, 31 ; aeshnidés, 16 ; gomphidés, 15 ; cordulégastridés, 1 ; macromiidés, 2 ; corduliidés, 13 ; libellulidés, 37. Les aires de répartition de ces espèces sont par ailleurs définies, ce qui permet de conclure que 20 espèces ont une aire de répartition boréale, 17 sont des espèces de transition, 12 vivent dans la Cordillère, 1 vit sur la côte du Pacifique, 10 sont occidentales, 4 sont plus ou moins limitées aux Grandes Plaines, 16 ont une aire de répartition méridionale, 38 sont considérées orientales, et 6 sont des espèces largement répandues. Le chapitre présente un résumé des études réalisées sur les odonates des prairies ainsi que des recommandations concernant les travaux d'inventaire et les études taxonomiques à réaliser. La portée géographique de la faune de la prairie canadienne est brièvement décrite en ce qui a trait aux habitats lotiques et lenticques des prairies qui se trouvent dans la Cordillère, dans les Grandes Plaines et dans le sud de l'Ontario.

### Introduction

The Odonata (dragonflies and damselflies) is a small order of insects of 5,952 named species (as of 2010) in 30 families worldwide (Dijkstra *et al.* 2013). It is predominantly tropical in distribution and is not as diverse at higher latitudes. Canada records 211 species (Catling *et al.* 2005; RAC and P. Catling, unpublished data).

The Odonata and their ancestors are some of the most ancient of insects; there is a considerable fossil record containing many extinct groups. Dragonflies and damselflies have many primitive features, but also possess specializations that reflect their aerial

and predatory life. Odonata are usually divided into three suborders: the Zygoptera (damselflies), the Anisoptera (dragonflies), and the Anisozygoptera (a small group of four species from Asia that is intermediate in appearance between the other two suborders). The Zygoptera is normally considered the sister group to the Anisoptera plus Anisozygoptera. A brief summary of the issues and relevant literature in Odonata phylogenetics is found in Trueman and Rowe (2009), and the most recent and widely accepted classification is given in Dijkstra *et al.* (2013). The Canadian fauna is treated here in two suborders, Zygoptera and Anisoptera.

The two suborders differ in structure and behaviour. Damselflies are slimmer and often smaller, and they usually fly more slowly than dragonflies. At rest, their equal-sized wings are usually held together above the body (Zygoptera means “joined wings”). The compound eyes are spaced widely apart on the head. Dragonflies are robust and often fast flying, with the hind wings broader at the base than the fore wings (Anisoptera means “unequal wings”); when perched, they hold their wings out and away from the body. The eyes usually touch on the midline, although in some families they are separated, but not to the extent seen in the Zygoptera. There are significant differences between damselflies and dragonflies in wing venation and sexual structures.

### Biology

Corbet (1999) provides comprehensive detail on the biology of Odonata in a global context; more general summaries related to North America and Canada are found in Walker (1953), Cannings (2002), Acorn (2004), Paulson (2009, 2011), and Hutchings and Halstead (2011). Most of the following short summary is taken from Cannings (2002).

Members of the Odonata are large and abundant predatory aquatic invertebrates; because of this, the order forms one of the predominant groups in freshwater communities. Some species prefer lakeshores, whereas others are found only along streams and rivers and in springs. Ponds and marshes rich in aquatic vegetation support the greatest diversity. The aquatic larvae are armed with an enormously enlarged, hinged labium, which is used as an extendible grasping organ for capturing prey. Larvae are voracious, eating aquatic insects, small crustaceans, and even fish and tadpoles. Larvae can be placed in three categories according to their feeding behaviour (Corbet 1999). Claspers (Zygoptera, Aeshnidae) are streamlined stalkers that live in submerged vegetation and use their clasping legs to hold on to vegetation. Sprawlers (Macromiidae, Corduliidae, and most Libellulidae) lie spread-eagled on the bottom mud, debris, or vegetation, waiting in ambush; they often hide under a coating of mud and algae. Burrowers (Gomphidae, Cordulegastridae) dig into sand and mud and await their prey. Metamorphosis in odonates is striking. Larvae go through 8 to 17 (usually 10 to 14) moults before emerging as terrestrial flying adults.

Adults are often colourfully patterned and exhibit a wide variety of readily observed behaviour. They are aerial, visually oriented predators and are large, strong-flying insects with big eyes, strong mandibles, and spiny legs. Their prey includes a wide range of flying insects that are normally captured in flight, although some groups, such as the coenagrionids (except for *Argia*), usually take their prey from the substrate (Paulson 2009). Mature males often patrol the breeding habitats, aggressively searching for mates and may, like birds, defend a territory against other males of the species. These territories limit aggression and prevent undue disturbance of egg-laying females. Sometimes in crowded situations group territories with dominance hierarchies are established.

Developmental timing varies depending on the group and geographical location. In the damselflies and many dragonflies, development from egg to mature adult may be rapid, requiring only a year, even in the north and at higher elevations. *Lestes* and some *Sympetrum* species overwinter as diapausing eggs, hatch in the spring, and emerge as adults in the summer. Others overwinter as larvae and emerge the following spring or summer, although probably in some species and conditions, the larvae overwinter two years. However, in many larger dragonflies, such as *Aeshna* or *Somatochlora*, the short summers of high altitudes and northern regions often mean that four or five years are spent in the larval stage. In Canada, most adults live for one to two months.

## Summary of Taxonomic and Biodiversity Studies in the Region

### *General Faunal Treatments and Annotated Lists*

The major early works on Odonata of the Canadian fauna, including grassland species, are Walker (1912*a*, 1912*b*, 1925, 1927, 1933, 1940, 1941*a*, 1941*b*, 1943), Buckell (1938), and Whitehouse (1917, 1918*a*, 1918*b*, 1941). Walker (1953, 1958) and Walker and Corbet (1975) used data from some of these baseline publications in their work on the Odonata of Canada and Alaska, including records of dragonflies in grassland habitats, and added considerable ecological information.

Several subsequent regional treatments also covered grassland areas across Canada. In the West, Scudder *et al.* (1976) and Cannings and Stuart (1977) updated and summarized the distributional information known for British Columbia. Since then, inventories and general collecting have improved knowledge considerably. Cannings *et al.* (1991) and Cannings and Cannings (1997) documented extensive surveys in Yukon and, in British Columbia, Cannings *et al.* (1998, 2000, 2008) undertook detailed inventories, from 1996 to 2005, jointly sponsored by the Royal BC Museum and the British Columbia Conservation Data Centre (British Columbia Ministry of Environment). Many of these dealt with grassland habitats in the Yukon and the Okanagan, Kootenays, Peace River, and Chilcotin/Cariboo regions of British Columbia. Other surveys were made for more specific reasons, such as investigations on the possible impact of the Site C Dam proposal along the Peace River (Cannings 2012). Data and distribution maps for British Columbia species are available at the Royal BC Museum, British Columbia Conservation Data Centre (2013), and E-Fauna BC (2013).

In the Prairie Provinces, inventories and annotated provincial lists have been undertaken by various institutions and have resulted in provincial databases, websites, and publications for Alberta (Acorn 2004; Strickland Museum 2013), Saskatchewan (Lehmkuhl 1975; Hutchings and Halstead 2011; Parker 2013), and Manitoba (Hughes and Duncan 2003; Manitoba Dragonfly Survey 2004). The Manitoba Dragonfly Survey, a volunteer project organized by NatureNorth and the Manitoba Wildlife and Ecosystem Protection Branch, has provided data to the Manitoba Conservation Data Centre. Acorn's (2004) publication (noted above) on the damselflies of Alberta is a superb example of a regional treatment, useful both in scientific terms and as a popular stimulus for student and naturalist involvement in the study of Odonata. Systematic research into other groups has sometimes resulted in useful information on Odonata. For example, Conroy and Kuhn (1977) improved the Manitoba Odonata list during their study of water mites that parasitized aquatic insects; such mites are frequently found on adult Odonata.

Ontario has been a leader in Odonata study ever since E.M. Walker's superb work started the trend. Catling and Brownell (2000) published a summary of species and



distribution that complements the volumes of *Ontario Odonata* (Catling *et al.* 2000, 2001, 2002, 2004a, 2004b, 2005, 2007), an annual summary of Odonata records published by the Toronto Entomologists' Association. This publication also supplies notes on observations, range extensions, and regional lists. All these data are summarized in the Ontario Odonata Atlas (2005), an outgrowth of the extensive database of the Natural Heritage Information Centre, Ontario Ministry of Natural Resources. Websites such as that for Ojibway Prairie (Pratt 2010) and for regional Ontario lists (Pratt 2012) are ongoing resources for Odonata study in the grassland pockets in southern Ontario. A field guide to species of southwestern Ontario (Carmichael *et al.* 2002) covers most of the species considered grassland inhabitants in the region.

### ***Studies of Particular Areas or Sites***

Several studies have examined the odonate fauna of particular areas, including grassland sites. Not all of these studies were made for faunistic or systematic reasons; the purpose of the work was often ecological. For example, in British Columbia's Chilcotin region, Cannings and Cannings (1987) documented 22 species in 18 saline lakes at Riske Creek. The distribution of the genus *Lestes* was studied in detail across these water bodies, whose chemistry varied widely (Cannings *et al.* 1980). Conference-related field trips can also contribute to regional faunal information. In 1983, the Seventh International Symposium of Odonatology held in Calgary resulted in field trips to grasslands around Calgary and the southern Rocky Mountain Trench in British Columbia (Invermere/Radium Hot Springs area) that produced new and important records and range extensions (Cannings 1983, 1984). Intensive life history studies on *Argia vivida* in non-grassland habitats in hot springs in Banff, Alberta, and similar montane localities in British Columbia (Pritchard 1989; Conrad 1992) should be mentioned here, as they give significant insight into the biology of this rare species in British Columbia grasslands.

Insect surveys that include Odonata have been published from several localities in Alberta, mostly in the Aspen Parkland near Edmonton: Clifford E. Lee Nature Sanctuary (G.C.D. Griffiths and D. Griffiths 1980, unpublished report), Devonian Botanic Garden (Stoyke 1987), Wagner Natural Area (Page 1998), and Beaverhill Lake (Rice 1999). As the wetlands in these sites often lie in a mosaic of parkland, forest, and peatland, many of the species listed are not typical grassland species. The same is true for the species of Cypress Hills in Alberta (Hilton 1985) and Saskatchewan (Catling and Kostiuk 2004b), although some of the localities are predominantly fescue grasslands. Rice (2003) studied 16 wetlands near Brooks, Alberta, as part of a larger ecological study of dragonflies and damselflies in Prairie marshes. This study primarily dealt with the effects of cattle grazing on odonates and wetland quality (Hornung and Rice 2003) and on the use of odonates as biological indicators of grazed and ungrazed sites (Foote and Rice 2005). The study is summarized by Wrubleski and Ross (2011: 104). The collections produced 25 species of Odonata typical of marshes in the dry mixed grassland of southeastern Alberta, and one, *Ichnura verticalis*, was the first Alberta record of this primarily eastern damselfly.

Other ecological and faunistic studies emphasize the rudimentary nature of our knowledge of the Great Plains odonate fauna. Catling and Kostiuk (2004a) published abbreviated lists of the more notable results of odonate collecting along a few streams in southern Saskatchewan, resulting in significant numbers of unusual records from sites along Frenchman Creek, Lodge Creek, and Souris River. Unusual records and distributional data also often result from studies that have their origins in fields far from Odonata systematics, such as the pollution work of Dossdall and Lehmkühl (1989). They found that the larvae of

the rare *Stylurus intricatus* in the North Saskatchewan River were affected in a catastrophic kill of aquatic insects, 21 and 38 km downstream from an application site of methoxychlor to control black fly larvae. In Manitoba, Ackerman and Galloway (2003) collected Odonata larvae of 22 species in 10 stormwater retention ponds in Winnipeg. This highly modified urban habitat within the tallgrass prairie ecosystem produced almost one quarter of the species known in Manitoba.

Inventories in Ontario have also contributed to the knowledge of grassland Odonata. For example, the fauna of Ojibway Prairie in Windsor, Ontario, is well-known (Pratt 2010). Paiero *et al.* (2010) discusses the locality in the context of insects and remnant grassland localities in the province. Skevington *et al.* (2000) inventoried the insects of north Lambton County, including a number of grassland and oak savanna sites, and produced a list of Odonata.

### **Conservation Studies**

Most conservation studies involve general surveys searching for particular target species to improve knowledge of the species' status. A major goal of the surveys in British Columbia noted earlier was the clarification of the conservation status of all provincial species; in the process, many grassland species were studied. This improved understanding has allowed more accurate estimates for conservation ranking of British Columbia Odonata, which has, since 2005, become an important part of provincial and national research and conservation efforts (Ramsay and Cannings 2005; Cannings *et al.* 2007). The distribution, status, and ecological requirements of the fauna are relatively well-known for the Thompson-Okanagan and Columbia-Kootenays and moderately known for the remaining southern valleys. The grassland populations in the Cariboo-Chilcotin Plateaus and the Peace River region are probably less accurately assessed. The British Columbia Conservation Data Centre, the Ontario Natural Heritage Information Centre, and the equivalent agencies for each province give conservation ranks to all odonate species. Many of the most vulnerable, because of habitat destruction and disturbance, are grassland species.

Nationally, all species are given a general conservation rank (Wild Species 2005, 2010). In addition, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has commissioned status reports on a few odonates of national rarity and concern that have grassland populations: *Argia vivida* (British Columbia), *Stylurus olivaceus* (British Columbia), and *Stylurus amnicola* (Manitoba). Provincial jurisdictions have sometimes produced status reports on species of provincial concern; for example, in British Columbia, Cannings (2003) studied *Macromia magnifica*. Hall *et al.* (2011) summarized some conservation issues on the grasslands of the Great Plains. They list some odonate species that may be at risk based on national general status rankings: *Somatochlora ensigera* (Saskatchewan 5, Manitoba 2), *Gomphus externus* (Saskatchewan 5, Manitoba 2), and *Stylurus intricatus* (Alberta 3, Saskatchewan 5) where 2 = may be at risk, 3 = sensitive, and 5 = undetermined (based on low search effort).

### **Other Studies**

Other specific studies dealing with taxonomy, morphological variation, distribution, life histories, and other aspects of Odonata biology in Canadian grasslands are cited under the relevant genus or species in the systematic treatment below.

### **Research Priorities**

The taxonomy of the Nearctic Odonata is relatively well-known compared with that of

many other insect groups; there are only a few problematic taxa. Certain closely related pairs of taxa such as *Erythemis collocata* (West) and *E. simplicicollis* (East), and especially *Amphiagrion abbreviatum* (West) and *A. saucium* (East), require more study to ascertain whether they should remain separate species. Phylogenetic examination lumped together the widespread grassland taxa *Sympetrum occidentale* Bartenev (West) and *S. semicinctum* (East) (Pilgrim and von Dohlen 2007), but further work on these and other such variable taxa is desirable. *Aeshna interrupta* is another good example of a species with widespread geographical variation (Catling *et al.* 2005). Genetic work may also help determine the relationships among Palaearctic and Nearctic taxa, as was done with the separation of the Nearctic *Enallagma annexum* Hagen from the Palaearctic *E. cyathigerum* (Charpentier) (Turgeon *et al.* 2005).

Despite the excellent inventories and data compilations described earlier, more studies are required to better define occurrence and abundance for almost all species of odonates in grasslands. This is especially true in the Prairies Ecozone where some areas (southern Saskatchewan, in particular) have not been well collected. Detailed, annotated site lists developed over several years would be extremely valuable in all regions, as would autoecological research on species to determine habitat requirements. With potential habitat changes because of climate change, baseline data on distribution and habitat (with detailed vegetational and water characteristics) are of the utmost value, and continuous monitoring of sites, especially in areas of transition between grassland and forest, would be most useful. Studies that examine the effects of disturbance and habitat change on species are needed. Several species new to particular regions will likely be recorded in southern grasslands if monitoring is increased. For example, *Hetaerina americana* (Calopterygidae), which ranges into northern Montana, will probably be recorded in Alberta and Saskatchewan before long.

Ongoing monitoring of conservation status is also a priority as habitats and climate fluctuate in character. Even when species have already been assessed, COSEWIC and provincial agencies require regular updates, and so more status reports will likely be required as drying wetlands and reduced stream flows affect populations of rare species.

## Overview of the Odonata of Canadian Grasslands

### *Odonata Habitats*

The correlation of Odonata distribution and habitat requirements with detailed schemes of wetland classification are largely lacking in Canada. Cannings *et al.* (2008) and Cannings and Cannings (2011) matched odonate species presence with site associations in the classification of British Columbia wetlands by MacKenzie and Moran (2004). Habitats for odonates in grasslands are diverse; a few generalized habitats are summarized here with some typical odonate species given for each. Many species live in more than one of these general habitat types. Various kinds of peatlands that harbour northern, eastern, or montane forest species in grassland transition areas are omitted.

Alkaline water bodies typically occur in areas of low precipitation and high evaporation. Some odonate species are able to live in these sites despite the often high salinity, and their life histories enable them to take advantage of the ephemeral nature of the shallower lakes and ponds; these species include *Enallagma boreale*, *E. clausum*, *Lestes congener*, *L. unguiculatus*, *Aeshna interrupta*, *Sympetrum internum*, *S. corruptum*, and *S. costiferum*. They are not restricted to this habitat. In addition to some saline ponds that may disappear during hot weather, fresher ephemeral waters may support species such as *Lestes dryas*,

*L. unguiculatus*, *Sympetrum internum*, *S. madidum*, and *S. pallipes*. In some years, large numbers of *Anax junius* (and probably other species) emerge in August from seasonally flooded fields in southern Manitoba (M. Hughes, pers. comm.).

Marshes are permanently to seasonally flooded mineral wetlands dominated by emergent grass-like vegetation. Tall stands of cattails (*Typha*) and bulrushes (*Shoenoplectus*) are most common in nutrient-rich warm waters and often form rather uniform beds in basins or margins around otherwise open ponds and lakes. Odonata are diverse here; some species associated with these habitats include *Lestes congener*, *L. disjunctus*, *L. dryas*, *L. unguiculatus*, *Coenagrion angulatum*, *Enallagma annexum*, *E. carunculatum*, *E. civile*, *E. ebrium*, *Ischnura cervula*, *I. perparva*, *I. verticalis*, *Aeshna canadensis*, *A. constricta*, *A. interrupta*, *A. palmata*, *Anax junius*, *Rhionaeschna californica*, *R. multicolor*, *Epithea cynosura*, *E. princeps*, *E. spinigera*, *Erythemis collocata*, *E. simplicicollis*, *Leucorrhinia intacta*, *Libellula forensis*, *L. luctuosa*, *L. pulchella*, *L. quadrimaculata*, *Pachydiplax longipennis*, *Pantala hymenaea*, *Perithemis tenera*, *Plathemis lydia*, *Sympetrum costiferum*, *S. danae*, *S. internum*, *S. obtrusum*, *S. rubicundulum*, *S. semicinctum*, *S. pallipes*, and *Tramea lacerata*.

Sedge marshes are widespread, especially in the regions of grassland–forest transition in the Cordillera or northern Prairies. Sedge marshes grow in places such as flooded beaver ponds, lake margins, and flood plains. Some typical species are *Lestes congener*, *L. disjunctus*, *L. dryas*, *Coenagrion resolutum*, *Enallagma annexum*, *E. boreale*, *Nehalennia irene*, *Aeshna canadensis*, *A. interrupta*, *A. juncea*, *A. palmata*, *Epithea canis*, *Somatochlora hudsonica*, *S. semicircularis*, *Libellula quadrimaculata*, *Leucorrhinia borealis*, *L. hudsonica*, *Sympetrum internum*, and *S. obtrusum*.

Lakes, both those that are ringed by emergent vegetation and those that lack the abundant vegetation typical of marshes, have considerable open water. Typical species include *Enallagma carunculatum*, *E. clausum*, *Aeshna eremita*, *Gomphus graslinellus*, *Macromia magnifica*, *Epithea cynosura*, *E. spinigera*, *Libellula forensis*, and *L. quadrimaculata*.

Odonata of running waters are most diverse east of the Cordillera, probably owing to the mainly cold waters of the mountains. In southern British Columbia, the following species, when living in running water, are generally restricted to lowland streams or warm montane streams that drain lake basins, beaver ponds, or peatlands: *Argia emma*, *Ophiogomphus occidentis*, *Stylurus olivaceus*, and *Macromia magnifica*. Damselflies found in Prairie streams include *Argia fumipennis*, *Enallagma anna*, *E. antennatum*, and *Ischnura damula*, while *E. antennatum* and *E. exulans* occur in streams in southwestern Ontario tallgrass prairie. *Calopteryx aequabilis* lives in western grassland streams; *C. maculata* is common in eastern streams. The stream-dwelling *Archilestes grandis* is rare in Ontario Ojibway Prairie grasslands. *Ophiogomphus severus* is widespread in the West and is one of the more common lotic species across the Cordillera and Great Plains, in the latter region sharing the rivers with other gomphids such as *Gomphus externus*, *G. fraternus*, *Ophiogomphus rupinsulensis*, *Stylurus amnicola*, *S. intricatus*, and *S. notatus*.

Some of the more uncommon species of Odonata are associated with small springs and shallow seeps, although most of these species are not restricted to these places. *Amphiagrion abbreviatum* and *A. saucium* are widespread in such habitats in the West and East, respectively. *Argia vivida* is most often found in outlets of hot springs in the mountains, although it occurs in some tiny spring-fed cool streams in the grasslands of British Columbia's southern valleys. In the same region, *Cordulegaster dorsalis* is a rare inhabitant of small streams usually arising from springs.

## Odonata Faunas of Regional Grasslands

### Cordillera

#### *Yukon*

The most familiar Yukon grasslands are those on south-facing slopes in xeric parts of the Yukon, dominated by *Artemisia frigida* Willd., as well as grasses such as *Poa glauca* Vahl and *Festuca brachyphylla* Schult. ex Schult. and Schult. (Scudder 1997; Shorthouse 2010b). These grasslands have little relevance to the Odonata, however, except as hunting areas above wetlands lying below. Grasslands with wetlands supporting Odonata are few; those treated here lie in the main valleys of the southern Yukon, especially northwest of Lake Laberge and in the Takhini River Valley. Prominent species include those common across western grasslands to the south, but there is a strong boreal flavour to the list. Salt flats occur along the Klondike Highway about 25 km northwest of Upper Laberge in one of the driest parts of the Yukon; these are found in *Pinus* and *Populus* parkland, with scattered vegetation consisting of grasses, rushes, *Chenopodium*, and *Salicornia*. Ponds in these areas support species such as *Lestes dryas*, *L. disjunctus*, *Enallagma annexum*, *E. boreale*, *Aeshna eremita*, *A. juncea*, *A. septentrionalis*, *Sympetrum danae*, and *S. internum*. Among the aspen groves of the Takhini River Valley along the Alaska Highway, a series of small, rich, prairie kettlehole ponds bordered with emergent sedges provide habitat for *Lestes disjunctus*, *L. dryas*, *Coenagrion resolutum*, *Enallagma annexum*, *E. boreale*, *Aeshna eremita*, *A. interrupta*, *A. juncea*, *A. septentrionalis*, *Somatochlora hudsonica*, *Leucorrhinia borealis*, *L. hudsonica*, *Libellula quadrimaculata*, *Sympetrum danae*, and *S. internum*. *Aeshna palmata* is restricted to small warm marl-bottomed lakes in parkland in the southern Yukon.

#### *British Columbia*

Shorthouse (2010b) discusses the wide distribution and complexity of grasslands in British Columbia. About 50 of the province's 87 known Odonata species are recorded in grasslands (Cannings 2008). Odonata diversity is greatest in intermontane grasslands in the Montane Cordillera Ecozone east of the Coast Mountains (Cannings and Cannings 2011), especially in the warm valleys south of 51°N. Two biogeoclimatic zones, the Bunchgrass and Ponderosa Pine zones in the Thompson-Okanagan, Cariboo-Chilcotin, and East Kootenay regions, are the main focus. Big sagebrush (*Artemisia tridentata* Nutt.) and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve) grow in the bottomlands of the Thompson and Okanagan Valleys, usually below 500 m. At higher elevations and in more northern plateaus in the Cariboo-Chilcotin, other grass ecosystems develop. East Kootenay grasslands lie in the Ponderosa Pine Zone at low elevations in the Rocky Mountain Trench, immediately west of the Rockies. Although these grasslands are similar to those in the Bunchgrass Zone to the west, in some areas they support species typical of the Great Plains east of the Rockies, such as blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths). Damselfly and dragonfly species found in British Columbia grasslands that are absent or rare elsewhere in Canadian grasslands include *Argia emma*, *A. vivida*, *Stylurus olivaceus*, and *Macromia magnifica*. Other characteristic species are *Enallagma clausum*, *Aeshna constricta*, *Rhionaeschna californica*, *R. multicolor*, *Gomphus graslinellus*, *Ophiogomphus occidentis*, *Libellula pulchella*, *Sympetrum costiferum*, and *S. vicinum*.

In the Boreal White and Black Spruce Biogeoclimatic Zone east of the Rockies (Boreal Plains Ecozone), special grasslands occur on the south-facing slopes of the Peace River Valley. These river valley "breaks" are related to the mixed grasslands of the Prairies Ecozone. Other grasslands on the level plains have mostly been converted to agriculture.

The odonate fauna in this region is similar to that of the Aspen Parkland of Alberta; species such as *Coenagrion angulatum* and *Leucorrhinia borealis* are typical.

The Garry oak meadows of southeastern Vancouver Island and the Gulf Islands are coastal grassland and savanna, the driest part of the Coastal Douglas-fir Biogeoclimatic Zone (Pacific Maritime Ecozone). Summer drought produces meadows and open parkland characterized by two broad-leaved trees, Arbutus (*Arbutus menziesii* Pursh) and Garry oak (*Quercus garryana* Douglas ex Hook.). Characteristic odonate species include *Ischnura cervula*, *Rhionaeschna californica*, *R. multicolor*, *Libellula forensis*, *Pachydiplax longipennis*, and *Erythemis collocata* (all shared with the intermontane grasslands); *Ischnura erratica* and *Sympetrum illotum* are found in no other Canadian grasslands.

### **Great Plains**

Shorthouse (2010a) gives an overview of the grasslands of the Central Plains of western Canada. The Prairies Ecozone has a diverse Odonate fauna with several notable, but not surprising, patterns. Cordilleran species such as *Ischnura cervula*, *Aeshna palmata*, and *Somatochlora semicircularis* range into the western Prairies Ecozone and the Cypress Upland Ecoregion, and some, such as *Argia emma*, apparently have spread from the south into the Mixed Grassland Ecoregion. In southeastern Manitoba, eastern forest species (e.g., *Lestes rectangularis*, *Chromagrion conditum*, *Ischnura posita*, *Arigomphus cornutus*, *Stylurus amnicola*) have penetrated tallgrass prairie around Winnipeg or grasslands in the Lake Manitoba Plain Ecoregion. Boreal and transition species common in the Boreal Plains Ecozone to the north appear in grassland–forest interface areas, especially in the Aspen Parkland, but also sometimes in isolated forested uplands such as Cypress Hills: *Coenagrion interrogatum*, *Nehalennia irene*, *Aeshna eremita*, *A. juncea*, *Cordulia shurtleffii*, *Ladona julia*, *Leucorrhinia hudsonica*, *L. proxima*, *Sympetrum obtusum*, and others. Species more or less restricted to the Prairies Ecozone in Canada are *Enallagma anna*, *Gomphus externus*, *Stylurus intricatus*, and *Somatochlora ensigera*. Several others, such as *Ischnura damula* and *Coenagrion angulatum*, have most of their Canadian population in this region.

### **Southern Ontario**

Small remnant patches of tallgrass prairie are scattered in southern Ontario, part of a transition zone between the Great Plains and the eastern forests. In the warm Hypsithermal period, about 6,000 to 8,000 years ago, extensive prairies reached into what is now southern Ontario; these grasslands were maintained by dry microclimates, well-drained soils, and seasonal fires. When cooler modern temperature regimes were established, these prairies were severely fragmented by increased forest development and, later, by human activity (Paiero *et al.* 2010; Shorthouse 2010b).

### **Ojibway Prairie**

The Ojibway Prairie Complex in Windsor is an important protected remnant of tallgrass prairie in extreme southwestern Ontario. Its relevance to studies of insects in this unusual eastern ecosystem is documented by Paiero *et al.* (2010). The site consists of five separate areas of tallgrass prairie, oak savanna, and open oak woodland totalling 320 ha, second only to nearby Walpole Island (650 ha) (Paiero *et al.* 2010; Shorthouse 2010b).

Ojibway Prairie was chosen to represent the tallgrass prairies of Ontario because a list of Odonata has been developed and maintained there for many years. Sixty-one species have been recorded (2013). Although the list contains a mixture of species typical of both open and forest habitats, it gives an excellent picture of the odonate fauna of this

transitional ecosystem in Ontario. Typical eastern species recorded, among many, are *Archilestes grandis*, *Lestes rectangularis*, *Enallagma geminatum*, *Enallagma signatum*, *Ischnura posita*, *Anax longipes*, *Epiaeschna heros*, *Gomphus vastus*, *Macromia taeniolata*, *Epitheca priceps*, *Celithemis elisa*, *Erythemis simplicicollis*, *Leucorrhinia frigida*, *Libellula incesta*, *Perithemis tenera*, and *Tramea carolina*. A comparable list from Pinery Provincial Park and dunes at Port Franks on Lake Huron (localities containing mostly oak savanna and other transitional grassland habitats in north Lambton County) includes 62 species of Odonata (Skevington *et al.* 2000). Other localities in southern Ontario containing grassland remnants or similar environments include the Rice Lake Plains (Catling 2008) and various alvars (areas of flat limestone with shallow soils) (Shorthouse 2010b).

### Defining Grassland Odonata

There is no specialized Odonata fauna in Canadian grasslands; the species that live in grasslands also mostly occur in marshes, at pond edges, and in streams in other nearby ecosystems (Euliss *et al.* 1999; Scudder *et al.* 2010; Wrubleski and Ross 2011). The distribution patterns of these grassland Odonata might appear less defined than in many other grassland insect groups, at least terrestrial groups. This may be partially due to the strong flying abilities of most dragonflies and damselflies, but the important factor is that aquatic environments spread throughout a diverse landscape may possess similar habitats. To individuals of *Aeshna interrupta*, a *Typha* marsh in a dry prairie grassland might be equivalent to a similar pond in a spruce fen in the Aspen Parkland or boreal forest. To *Libellula forensis*, a pond on a hot sagebrush steppe in the Interior of British Columbia might be no different from a similar pond in a wet coastal hemlock forest, yet few terrestrial organisms would live in both places (Paulson 1970; Cannings and Stuart 1977). In British Columbia, for example, the close proximity of forest and grassland areas promotes the mixing of montane or northern species such as *Somatochlora semicircularis*, *Aeshna juncea*, and even *A. subarctica* with more typical grassland inhabitants in waters in, or at the margins of, grasslands. This also happens at the interface of grassland and forest in the Prairie Provinces, where northern species, such as *Coenagrion interrogatum*, *Aeshna eremita*, and *Cordulia shurtleffii*, encroach on the grasslands. This occurs primarily in the Aspen Parkland but also in more discrete areas such as the forest “islands” of southern Manitoba and the Cypress Hills of Alberta and Saskatchewan. In extreme southeastern Manitoba, a similar phenomenon occurs where the eastern forest fauna meets that of the Prairies. Some eastern species that are at home in open habitats have spread into grasslands (or urban or agricultural areas that once were grassland), but many eastern forest species remain tied to the forests near the Ontario–Manitoba border. Nevertheless, some species are more often found in grassland waters than are their close relatives, and some can develop in a wide range of habitat types. A few, such as *Lestes congener*, *Enallagma boreale*, and *Sympetrum costiferum*, are able to withstand the high salinities of alkaline ponds that are typical of many grassland environments. Others, such as *Lestes dryas* and *S. internum*, have life histories that allow them to live in water bodies that dry up in summer, another characteristic of many grassland waters. These species overwinter as eggs, and larval development is unusually rapid (Sawchyn and Gillott 1974a, 1974b). A core list of typical grassland species can thus be established, but constructing a complete and accurate list is complicated by the difficulty in defining a grassland species because of this encroachment of predominantly forest taxa. In this examination of the fauna, I have arbitrarily included all species recorded within the ecological regions and localities that I use to represent the grassland environments of Canada. Except for a few lists from specific

grassland sites, I do not know of any other compilations of Odonata species living in Canadian grasslands. However, Wrubleski and Ross (2011) indicate that 49 species from seven families were recorded in North American Prairie wetlands by Eulis and Mushet (1999).

The Odonata species shared by all the various types of Canadian grasslands discussed here, from Yukon to southern Ontario, are few: *Lestes congener*, *L. dryas*, *Coenagrion resolutum*, *Enallagma boreale*, and *Libellula quadrimaculata*. If the southern Ontario grasslands are omitted, the number of species rises dramatically because the Ojibway Prairie fauna is dominated by eastern species and lacks many of the northern transcontinental species common to the other regions. The small Yukon list results in the omission of many common, more southerly species. Thus, typical grassland species that are widespread in most Canadian grasslands (British Columbia and the Prairie Provinces) include *Lestes congener*, *L. disjunctus*, *L. unguiculatus*, *Coenagrion angulatum*, *C. resolutum*, *Enallagma annexum*, *E. boreale*, *E. carunculatum*, *E. clausum*, *E. ebrium*, *E. hageni*, *Ischnura perparva*, *Aeshna constricta*, *A. interrupta*, *Anax junius*, *Ophiogomphus severus*, *Leucorrhinia borealis*, *L. intacta*, *Libellula quadrimaculata*, *Sympetrum corruptum*, *S. costiferum*, *S. danae*, *S. internum*, *S. madidum*, and *S. semicinctum*. Species more or less restricted to the various grassland regions of Canada were indicated earlier in the Odonata Faunas of Regional Grasslands section.

Some grassland populations are distinctive in that there is a trend toward a lighter colour in adults within species and within species groups (Catling and Hughes 2008). *Gomphus externus* and *Stylurus intricatus*, both of the Great Plains, are among the palest species in their genera. In *Gomphus fraternus*, *Macromia magnifica*, and *Ophiogomphus severus*, pale subspecies occupy grassland regions. Paleness in grassland Odonata may serve to reduce body temperature and avoid predation. The grassland environment is often hot and dry during the flight period and the vegetation is often yellow or pale brown.

## Systematic Review of the Grassland Odonata

An annotated systematic checklist of the 124 species, including the biogeographical faunal elements that they represent, is included in Table 1. English names of the species are included in this list. The nomenclature follows that of the Dragonfly Society of the Americas (2013). A brief review of the taxa of Canadian grasslands with biological and distributional information is presented in the following sections. Localities listed, unless otherwise noted, are sites selected as examples only. These localities are often reduced to the name of the closest town or city.

### Order Odonata (Dragonflies and Damselflies)

#### Suborder ZYGoptera (Damselflies)

#### Family Calopterygidae (Broad-winged Damselflies)

North America: 8 species; Canada: 5 species; Canadian grasslands: 2 species

The Calopterygidae, a family of large, elegant, and colourful damselflies, is represented by two species in Canadian grasslands, although typically species in the family live in woodlands. They fly with a beautiful dancing flight along clear streams, where the larvae cling to submerged vegetation.

*Calopteryx* species are large and spectacular with metallic green or blue bodies and with wings or wingtips that are often black; they are the showiest damselflies in North America. Males and females perform fascinating courtship displays. *Calopteryx aequabilis* is the more widespread species in Canada, occurring across much of the transition and

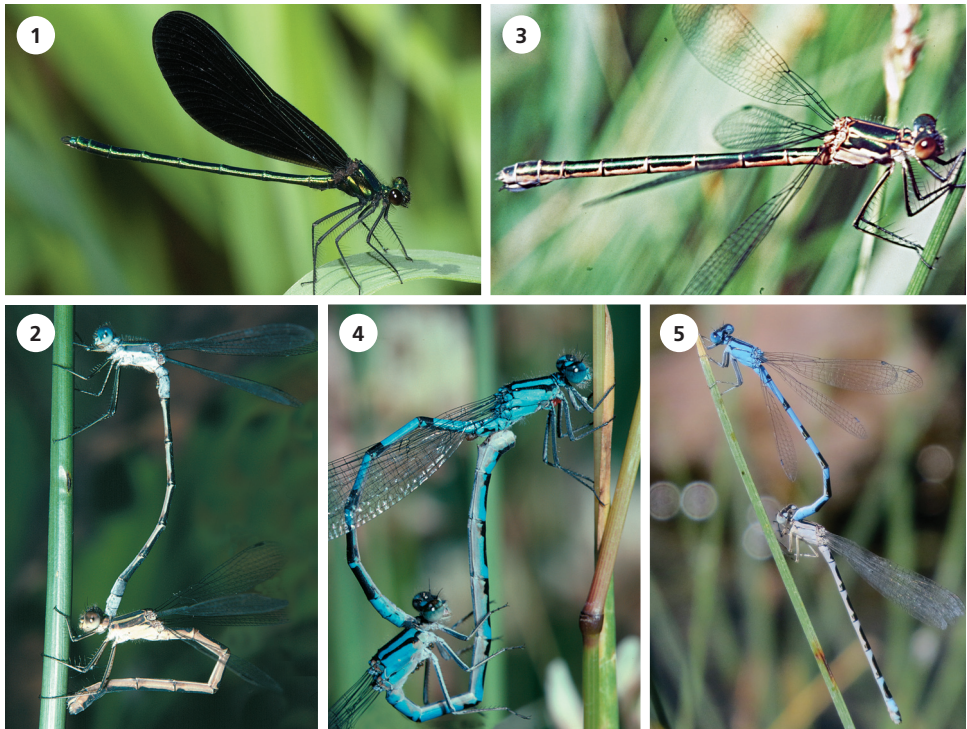


southern boreal regions and south to varying degrees all across the country. Only three localities are known in British Columbia and two of these are at the edge of grasslands: one at 100 Mile House in the Cariboo region and the other immediately north of the United States boundary at Christina Creek near Grand Forks. The species occurs in central Alberta and Saskatchewan, mostly north of grasslands, and south to southern Manitoba. Although it is common in Ontario it has not been recorded from Ojibway Prairie. The strictly eastern *C. maculata* (Fig. 1) is recorded at Ojibway but, although it lives in extreme southeastern Manitoba, it is not known from prairie sites there.

### Family LESTIDAE (Spreadwings)

North America: 18 species; Canada: 10 species; Canadian grasslands: 7 species

The Lestidae is a cosmopolitan zygopteran family. Although it is a small group in Canadian grasslands, several of its members are abundant and widely distributed. Two genera are represented: *Lestes*, with six species and *Archilestes*, with one. Adults are metallic green or bronze, but parts of the body become pruinose-gray with age. They characteristically perch with wings half-spread. Females oviposit in tandem with males, and eggs are usually placed in plants above the surface of the water. Larvae have unusually elongate labia. Some species



**Fig. 1.** *Calopteryx maculata* (Ebony Jewelwing), male. Photo: Dennis Paulson. **Fig. 2.** *Lestes disjunctus* (Northern Spreadwing), male guarding ovipositing female. Photo: George Doerksen, Royal British Columbia Museum. **Fig. 3.** *Lestes dryas* (Emerald Spreadwing), female. Photo: George Doerksen, Royal British Columbia Museum. **Fig. 4.** *Enallagma boreale* (Boreal Bluet), male and female mating. Photo: George Doerksen, Royal British Columbia Museum. **Fig. 5.** *Enallagma clausum* (Alkali Bluet), male and female mating. Photo: Dennis Paulson.

are adapted to temporary ponds; in these situations, larvae grow rapidly after overwintering as eggs. *Archilestes grandis* is known in Canada only from Ojibway Prairie, where it was first discovered in 2002 (Pratt and Paiero 2004). It normally lives along slow streams with wooded banks. Most of the recorded species of *Lestes* are typical of various types of grasslands from British Columbia to Ontario. Four species, *L. congener*, *L. disjunctus* (Fig. 2), *L. dryas* (Fig. 3), and *L. unguiculatus*, are particularly common and widespread. *Lestes disjunctus* is the most frequently observed grassland species from Yukon to Manitoba, but is not yet recorded from Ojibway Prairie, although it is known from Essex County. *Lestes dryas* is the only Holarctic member of the family. These *Lestes* species possess ecological traits and life history adaptations that allow them to inhabit prairie ponds that may vary in water chemistry and hydrology. In prairie ponds near Saskatoon, Saskatchewan, all four oviposit above the water surface and overwinter as eggs (Sawchyn and Gillott 1974a, 1974b). With the exception of those of *L. congener*, eggs are laid in green *Shoenoplectus* (*Scirpus*) stems and enter diapause after embryonic development is complete. Eggs of *L. congener* are placed in dead, dried stems and start diapause at an earlier stage. Wetting of the eggs at snowmelt in spring stimulates post-diapause development and helps synchronize larval development and adult emergence. *Lestes dryas* emerges earlier than the other species in both British Columbia and Saskatchewan (Sawchyn and Gillott 1974a, 1974b; Cannings *et al.* 1980), which may allow it to colonize temporary ponds, a strategy for which it is well-known. In British Columbia, *L. dryas* emerged about 10 days before *L. disjunctus*, which preceded *L. congener* by nine days. The main emergence of *L. disjunctus* occurred 20 days before the peak of the *L. congener* emergence (Cannings *et al.* 1980). The last species to emerge in both areas is *L. congener*, which has more egg development to undergo in the spring (Sawchyn and Gillott 1974a, 1974b). The lakes and ponds where these species were studied on British Columbia's Chilcotin Plateau range greatly in salinity (Cannings *et al.* 1980). *Lestes dryas* colonized only the freshest ponds, *L. disjunctus* occurred in lakes up to medium salinities, and *L. congener* lived in the complete range of salinities and occurred in very large numbers even at the highest concentrations (conductivity of 15,524 microSiemens, or about 1 ppt salinity).

Two other *Lestes* species should be noted here. *Lestes forcipatus* is primarily an eastern species, but was discovered in British Columbia in 1998 (Cannings *et al.* 2000, 2005) and is now known from many localities there (Cannings and Simaika 2005). Although largely restricted to forest fens north of grasslands in the West (and still unknown from Alberta), it is found at some sites adjacent to grassland in British Columbia. In Nebraska, it is common at grassland ponds (D. Paulson, pers. comm.). In western Canada, the species is more common than records indicate; it has certainly been overlooked over much of its range west of Ontario because of its similarity to the common *L. disjunctus* (Simaika and Cannings 2004). *Lestes rectangularis* is an eastern species recorded from Ojibway Prairie and southeastern Manitoba as far west as Winnipeg.

### Family COENAGRIONIDAE (Pond Damsels)

North America: 105 species; Canada: 42 species; Canadian grasslands: 31 species

Seven genera and about 31 species of coenagrionids occur in Canadian grasslands (as defined here). They are usually the most common damselflies in ponds and marshes anywhere. Adult males are frequently blue marked with black, but the ground colour may be green, yellow, orange, red, or purple. Females may be similar to males (andromorphs) or coloured differently. Eggs are laid in the tissues of water plants, and females may

completely submerge for considerable periods during oviposition. The larvae are less elongate and have shorter labia than those of the Lestidae.

*Enallagma* is the most diverse and abundant genus of damselflies in Canada; 14 species live in grasslands. Most males are blue and black, while females are similarly coloured or have the blue replaced by brown or green. Most live in ponds and the marshy edges of lakes and streams, while a few are at home in saline lakes, and others are restricted to flowing water. *Enallagma boreale* (Fig. 4) and *E. annexum*, with widespread boreal distributions, are perhaps the most common species of the genus in Canada, and both extend into grasslands from Yukon to Ontario. *Enallagma boreale* swarms around the grassland kettle lakes and ponds from British Columbia's central plateau east across the Great Plains. *Enallagma annexum* is not recorded yet from Ojibway Prairie, but occurs nearby. It once was considered the only Holarctic member of the genus and family (as *E. cyathigerum*), but it has recently been split into two: the original Old World species (*E. cyathigerum*) and a New World species (*E. annexum*) (Turgeon *et al.* 2005). *Enallagma clausum* (Fig. 5) is a western species characteristic of alkaline ponds and lakes in dry grasslands in British Columbia and the Prairies, where it can be extremely abundant, even at sites so salty that other odonates are absent. *Enallagma ebrium* and *E. hageni* are common species across much of Canada. In British Columbia, *E. hageni* is restricted to the central plateau and does not enter the southern valley grasslands as *E. ebrium* does, but both species are common across the Prairies; in Ontario, *E. hageni* is less abundant at Ojibway than is *E. ebrium*. *Enallagma civile* occupies a wide range of marshy habitats, including newly created wetlands, and although it can be abundant in some sites, it is often only locally distributed. Apparently, it is an early successional species and may disappear from some wetlands as they age (Paulson 2011). Its range is expanding in Ontario (Catling and Brownell 2000), and it is common in southern Manitoba grasslands, uncommon in Saskatchewan, and unknown in Alberta. In British Columbia, *E. civile* is recorded only from Bridge Lake on the Cariboo Plateau, where it has been collected only once, in 1934 (Scudder *et al.* 1976). Two close relatives of *E. civile* are found in grassland habitats: *E. carunculatum* is widespread throughout much of southern Canada, and *E. anna* (Fig. 6) is predominantly western in Great Plains streams. *Enallagma carunculatum* can develop in moderately saline waters and is often the sole *Enallagma* species of *Shoenoplectus* beds and rocky or gravelly shorelines in the large lakes of southern British Columbia valleys (some, like the Okanagan, once largely clothed in grasslands). It is less common on the Great Plains, where it is considered a grassland species. It is listed as uncommon at Ojibway Prairie. Most of the few records of *E. anna* are from Alberta, where it was first discovered in Canada at Ross Creek, Medicine Hat, in 1980 (Acorn 2004), and has been collected from Fish Creek, Calgary (Cannings 1984; Beukeboom and Wasscher 1986). It is also known from several Saskatchewan localities, for example, Highway 630 SW Swift Current (Cannings 1984) and on the Souris River at Highway 39 (Catling and Kostiuik 2004a). *Enallagma anna* probably occurs in southern Manitoba streams, but it is not recorded there. Although it is known in Ontario only from several localities in Essex County, it is not listed from Ojibway Prairie. Four of the common *Enallagma* species (*E. carunculatum*, *E. clausum*, *E. ebrium*, and *E. hageni*) may be relatively recent migrants to the western Great Plains, because Whitehouse (1918a, 1918b) failed to find them. Acorn (2004) believes they have colonized Alberta (and perhaps other parts of the Prairies) over the last 100 years because of the proliferation of man-made wetlands, irrigation schemes, and water storage areas. Six *Enallagma* species recorded in grasslands are eastern in distribution and are known from Ojibway Prairie, although one, *E. antennatum*, is a stream species that occurs rarely on the Great Plains (e.g., Saskatchewan in Frenchman Creek at Highway 21, Souris River at Highway 39; Catling and Kostiuik



**Fig. 6.** *Enallagma anna* (River Bluet), male. Photo: Dennis Paulson. **Fig. 7.** *Ischnura damula* (Plains Forktail), male and female mating. Photo: George Doerksen, Royal British Columbia Museum. **Fig. 8.** *Ischnura verticalis* (Eastern Forktail), male. Photo: Dennis Paulson. **Fig. 9.** *Coenagrion angulatum* (Prairie Bluet), female. Photo: John Acorn.

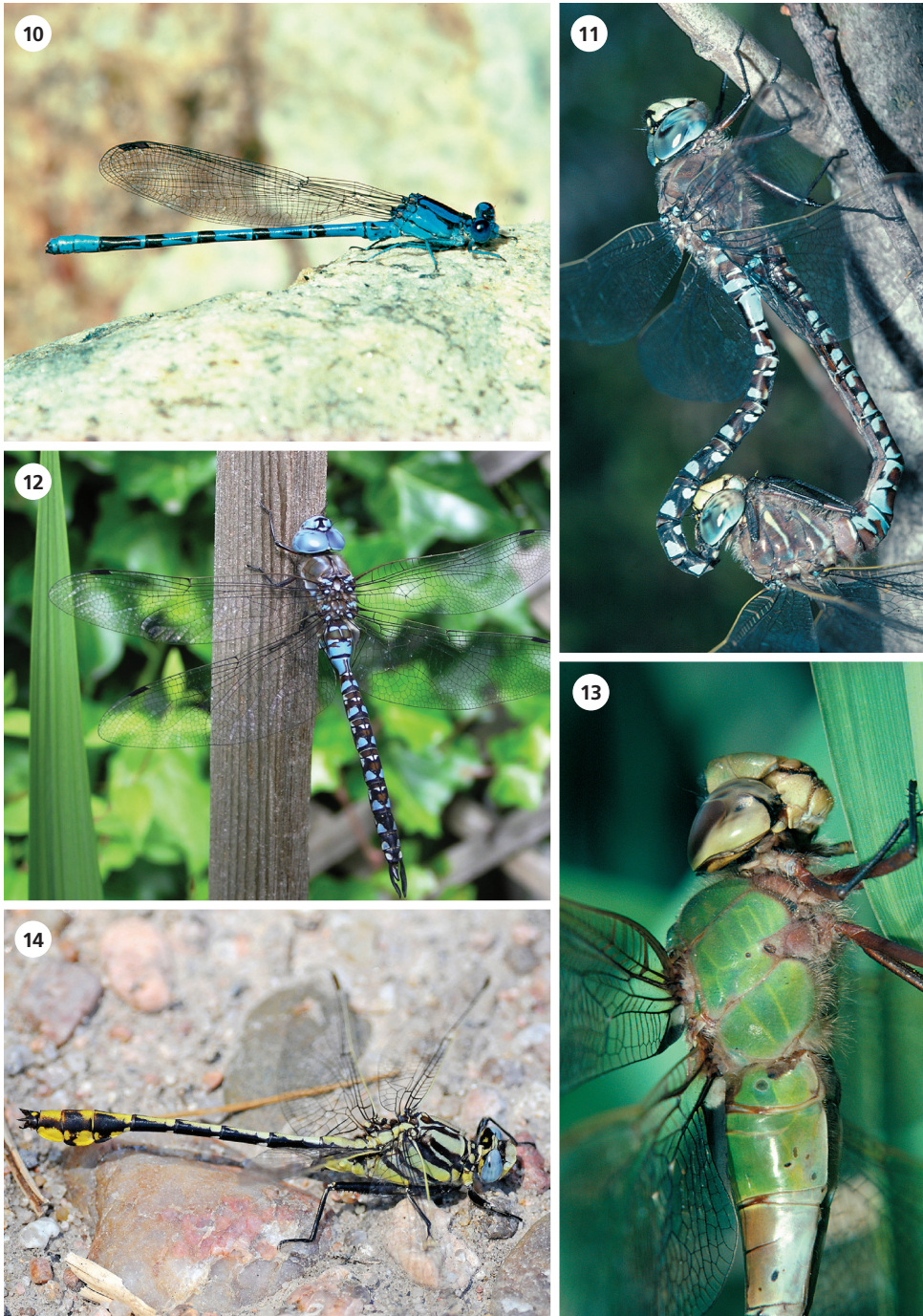
2004a). *Enallagma basidens* has dramatically expanded its range in the last century all the way to New England from the American Southwest (Paulson 2011). Cunnings (1989) first reported *E. basidens* in Canada in 1985 and attributed the rapid range expansion, at least in part, to its ability to colonize man-made habitats. The other eastern species are *E. aspersum*, *E. exsulans*, *E. geminatum*, and *E. signatum*.

*Ischnura* is a cosmopolitan genus whose distribution in North America is decidedly southern in character. In Canada, seven species are recorded in grasslands: *I. cervula*, *I. erratica*, *I. perparva*, and *I. damula* (Fig. 7) are western, and *I. verticalis* (Fig. 8), *I. posita*, and *I. hastata* are mostly eastern in distribution. *Ischnura cervula* is common in ponds and lakes with *Typha* and *Schoenoplectus* margins in both coastal Garry oak meadows and interior grasslands in southern British Columbia. In Alberta, it is mainly a montane species at Banff, a Cordilleran relict in the Cypress Hills (Acorn 2004), and recorded rarely in Saskatchewan grasslands (e.g., Frenchman Creek at Highway 21, where it flies with *I. verticalis*; Catling and Kostiuk 2004a). *Ischnura erratica* is restricted to the Pacific Coast from southern British Columbia south to northern California. It is a large forktail, commonly perching on the leaves of water lilies. *Ischnura perparva* is also common and widespread in southern British Columbia grasslands but is rarer east of the Rockies. For example, it is recorded at Medicine Hat, Alberta (Acorn 2004); in Lodge Creek, Saskatchewan (Catling and Kostiuk 2004a); and at Fort Whyte Centre and Winnipeg Beach in the southern Manitoba prairies (Hughes and Duncan 2003). *Ischnura damula* is predominantly a species of the Great Plains and the American Southwest and, in Canada, is more widespread in grasslands east of the Rockies than the other western species. It is rare in northern British Columbia and Yukon, where it is not associated with grasslands but inhabits warm springs in forests (it is considered a relict of a more widespread distribution during warmer climatic periods). In Alberta, it ranges from the Edmonton area to Medicine Hat (Acorn 2004) and in Saskatchewan from

Prince Albert National Park (Walker 1953) to Lodge Creek at Highway 13 and Souris River at Highway 39 (Catling and Kostiuk 2004a). It is rare in southeastern Manitoba. The three eastern species recorded at Ojibway Prairie make up the rest of the *Ischnura* grassland complement. *Ischnura hastata* prefers shallow temporary pools at Ojibway (P. Pratt, pers. comm.) and at some other southern Ontario grassland sites such as the Rice Lake Plains (P. Catling, pers. comm.). *Ischnura posita* and *I. verticalis*, the common eastern members of the genus, are abundant at Ojibway and also range west onto the Great Plains. *Ischnura verticalis* is fairly common in the Winnipeg area, in some southern Saskatchewan localities, and in several sites in southeastern Alberta. It was first reported in Alberta near Rolling Hills in 1999 (Hornung and Rice 1999). *Ischnura posita* is recorded from the Fort Whyte Centre, Winnipeg (Conroy and Kuhn 1977; Hughes and Duncan 2003).

*Coenagrion* is a predominantly Palearctic genus with three Nearctic species, two of which, *C. interrogatum* and *C. resolutum*, range across most of boreal North America. The third, *C. angulatum* (Fig. 9), is a Great Plains species. *Coenagrion interrogatum* typically develops in water bodies with aquatic moss in northern forest peatlands; it is the most boreal of Nearctic damselflies (Cannings and Cannings 1997). It is included here because it encroaches on grassland habitats in the southern Yukon and is recorded in a few ponds and marshes in the Aspen Parkland in central Alberta (e.g., Wagner Natural Area; Page 1998) and the prairies of Saskatchewan (e.g., Saskatoon; Sawchyn and Gillott 1975). *Coenagrion resolutum* is one of the most widespread odonates in Canada and mainly a northern forest species, but is a common early-season flyer in many grassland habitats from Yukon to southern British Columbia and across the Great Plains. It reaches the grassland pockets of southern Ontario, but is rare at Ojibway, not being found there until 2001 (Pratt 2010). *Coenagrion angulatum* is one of the most frequently seen damselflies on grasslands of the Great Plains and is widespread in ponds and marshes of the prairies, Aspen Parkland, and southern boreal forest from the Peace River region of British Columbia to southern Manitoba. It is known in a few northwestern Ontario sites, but not in grassland habitats. Sawchyn and Gillott (1975) studied the life histories of *C. resolutum* and *C. angulatum* in a pond near Saskatoon. Both species overwinter in late larval stages and emerge synchronously over about 10 days beginning in the last week of May.

*Argia* is the largest genus of Odonata in the New World, with over 110 species. It is primarily a stream-dwelling group, although many species do show up along lakeshores. The two western Canadian species, *A. emma* and *A. vivida* (Fig. 10), are both found in grasslands. The Canadian range of both is mostly in British Columbia, where most grassland populations are in the Okanagan Valley. There, *A. emma* is most common in the Okanagan River but also develops along lakeshores. In Alberta, there is a single photographic record of *A. emma* from Milk River at Writing-on-Stone Provincial Park in 2010 (K. Allen, pers. comm.). *Argia vivida* lives mostly in warm springs in southern British Columbia mountains and in Alberta at Banff, but also lives in Okanagan grasslands in cool, constant-temperature seeps and spring-fed streamlets (Cannings *et al.* 1998). Both species are considered threatened or vulnerable in British Columbia. Pritchard (1989) and various students published many papers documenting the development and behaviour of *A. vivida* in hot springs, and their findings are probably relevant to grassland situations. *Argia fumipennis* is mainly an eastern species that ranges into the Great Plains, especially in the United States. In Canada, *A. fumipennis* populations consist of the subspecies *A. f. violacea* Hagen. In 2004, it was found in Saskatchewan on the Souris River at Highway 39 (Catling and Kostiuk 2004a), the first Canadian record west of southern Ontario. It is not recorded at Ojibway Prairie, although it occurs nearby. At the Souris River, it flew with *Calopteryx aequabilis*, *Enallagma anna*, *E. antennatum*, *E. civile*, and *E. ebrium*.



**Fig. 10.** *Argia vivida* (Vivid Dancer), male. Photo: George Doerksen, Royal British Columbia Museum. **Fig. 11.** *Aeshna interrupta* (Variable Darner), male and female mating. Photo: George Doerksen, Royal British Columbia Museum. **Fig. 12.** *Rhionaeschna multicolor* (Blue-eyed Darner), male. Photo: Derrick Ditchburn. **Fig. 13.** *Anax junius* (Common Green Darner), female. Photo: George Doerksen, Royal British Columbia Museum. **Fig. 14.** *Gomphus externus* (Plains Clubtail), male. Photo: Steve Mlodinow.

Three other coenagrionid genera have members in Canadian grasslands. The two species of *Amphiagrion*, *A. abbreviatum* and *A. saucium*, are possibly one and the same, and more research in the Great Lakes region is required to clarify their status (Paulson 2011). They are red and black species inhabiting seeps and marshy areas that are often spring-fed in both grassland and forest habitats. Manitoba specimens, which are scarce (e.g., Treesbank), are considered to be *A. saucium* by Hughes and Duncan (2003), although recent evidence suggests that in Canada the species does not range west of Ontario (D. Paulson, pers. comm.). Thus, populations from Manitoba need more study, but those from Saskatchewan west to British Columbia are *A. abbreviatum*. This species is more common in British Columbia than it is farther east. The delicate, metallic green *Nehalennia irene* is widespread across much of Canada, mainly in marshes and fens with dense stands of sedges. In the West, it is generally absent from the hottest and driest grasslands of extreme southern British Columbia and the western Prairies Ecozone. *Chromagrion conditum* is an eastern damselfly not recorded at Ojibway Prairie, which is well within its range, but known from an extralimital record at Fort Whyte grasslands, Winnipeg, Manitoba (Hughes and Duncan 2003).

### Suborder ANISOPTERA (Dragonflies)

#### Family AESHNIDAE (Darners)

North America: 42 species; Canada: 24 species; Canadian Grasslands: 16 species

Members of the Aeshnidae are large dragonflies with big eyes and long abdomens; they are usually marked with blue, green, or yellow. In *Aeshna* and *Rhionaeschna*, females have several colour forms; the typical male colour form with a blue-marked abdomen is usually less common in females than yellow or green forms. Adults tirelessly hunt for insects over ponds, lakes, and streams and wander widely in search of prey. They fly swiftly, hover here and there, and perch vertically. *Rhionaeschna* males tend not to hover. Females have well-developed ovipositors at the tip of the abdomen, and oviposit in water plants or floating wood above or below the waterline. The larvae are slender and sleek, with flattened labia lacking setae. They are rapacious hunters among water plants. Darners are represented in Canadian grasslands mainly by three genera, *Aeshna*, *Rhionaeschna*, and *Anax*; a fourth, *Epiaeschna*, normally an eastern forest species, is included because of its presence at Ojibway Prairie. Cannings (1996) provides pictorial identification keys and outlines the biology and distribution of *Aeshna* and *Rhionaeschna* species in British Columbia, a fauna that includes all Canadian grassland species. Peters (1998) discusses the ecology of some of these darners and gives a key to adults based on wings only. This allows the identification of specimens that have been eaten by birds, a situation often encountered in the field, especially at grassland marshes.

Eleven of the 13 Canadian *Aeshna* species are grassland inhabitants, although some are more typical of grasslands than others. The most characteristic grassland species is *Aeshna interrupta* (Fig. 11); this is one of the most widespread dragonflies in Canada, living in many habitats from northern peatlands to alkaline lakes and temporary ponds. It is the most abundant species of grassland ponds and marshes from Yukon to Manitoba and can occur in impressive numbers. Catling and Brownell (2002) counted about 2,000 flying over the largely agricultural landscape near Grenfell, Saskatchewan, in 2001, and Catling and Kostiuk (2008) estimated (from roadkill counts) that about 10 million individuals crossed 4 km of the Trans-Canada Highway east of Brandon, Manitoba, over a few days in July 2007. In some years, massive aggregations move up the eastern slopes of the Rockies in midsummer (Paulson 2009; J. Acorn, pers. comm.). Three subspecies (*A. i. interrupta*, *A. i. interna*, and *A. i. lineata*) have been described for Canadian *A. interrupta* populations (Walker 1912a,

1958); the common one in Canadian grasslands (except for southern Ontario and coastal British Columbia grasslands) is *A. i. lineata* Walker. However, the subspecies are problematic (Cannings and Stuart 1977; Catling *et al.* 2005), as they do not form clear, geographically separate populations. *Aeshna constricta* lives across much of southern Canada, where it prefers small, rich marshy habitats. It is rare in British Columbia's southern Interior valleys and is of management concern because its habitat is often threatened by human development; some of the few sites are in grasslands (Cannings *et al.* 1998). It becomes more common eastward across the Great Plains to Ontario and is abundant in southern Manitoba and at Ojibway Prairie in southwestern Ontario. The primarily forest-dwelling *A. palmata* and *A. umbrosa* are close relatives that venture into grasslands. *Aeshna palmata* is a Cordilleran dragonfly and is perhaps the most widespread and common dragonfly in British Columbia. It is much less common northward and, in Yukon, it is restricted to shallow, marl-bottomed lakes in southern parkland (Cannings and Cannings 1997). It spills out onto the foothills and plains from the Rockies in southern Alberta, at least as far east as Calgary. It is also one of the many montane animals that live in the forested enclave of the Cypress Hills, straddling the Alberta–Saskatchewan boundary (Hilton 1985; Catling and Kostiuk 2004b) and also occurs in the Maple Creek area in Saskatchewan (Cannings 1984). Cordilleran and boreal flora and fauna in the Cypress Hills are considered isolated relicts of a cooler postglacial period when coniferous forest linked the Cypress Hills and the Rocky Mountain foothills (Hilton 1985). *Aeshna umbrosa*, on the other hand, is a common transcontinental darner that also occurs in grasslands from British Columbia to Ontario. The specimens collected in the Alberta Cypress Hills (Hilton 1985) are the blue Cordilleran form rather than the green transcontinental form (Cannings and Stuart 1977; Catling *et al.* 2005). *Aeshna verticalis* is an eastern species that ranges from southern Ontario to Nova Scotia but extends to the prairies of southern Manitoba. The other darners recorded in grassland habitats are mainly northern forest species that are sometimes recorded along the northern (or montane) borders of grassland regions. *Aeshna canadensis* is the most southerly of these species, found in numerous sites in warm British Columbia valleys (e.g., Athalmer in the East Kootenay and Cosens Bay near Vernon) and on the Prairies, especially northward (e.g., Stoyke 1987). *Aeshna eremita* is a widespread and common boreal darner; in British Columbia it is one of the most widespread forest dragonflies that also inhabits grassland wetlands. It is common in the Cypress Hills and occurs in many sites along the northern borders of grasslands on the Great Plains (e.g., G.C.D. Griffiths and D. Griffiths, 1980, unpublished report; Stoyke 1987; Page 1998; Rice 1999), but is absent from Ojibway Prairie, which is too far south in Ontario to support it. The Holarctic *Aeshna juncea*, common in northern sedge marshes, has a similar distribution to *A. eremita* but with less movement into grasslands, especially in the Prairies Ecozone. *Aeshna subarctica* is closely related to *A. juncea*, but prefers peatland ponds and lakes with submerged mosses, which are rare in and near grasslands. However, the species breeds at several grassland ponds on the Chilcotin Plateau in central British Columbia (Riske Creek; Cannings and Cannings 1987) and in East Kootenay (Athalmer; Cannings 1984). The northern boreal *A. septentrionalis* is a peatland obligate in northern British Columbia and farther east, but lives in a wide range of wetland types from roadside ditches to marl lakes and from sedge marshes to deep mossy fens in the Yukon, where it is the most widespread large dragonfly (Cannings *et al.* 1991; Cannings and Cannings 1997). Such wide habitat tolerance results in its presence at grassland ponds in southern Yukon (e.g., salt flats northwest of Upper Laberge). The related *A. sitchensis*, however, is a peatland obligate wherever it occurs; it gains a place on this grassland list only as a species in forest–grassland interface sites such as Devon and Red Deer in Alberta and Tolstoi in Manitoba.



*Rhionaeschna* is characteristic of South and Central America, with a few species reaching the United States and Canada, mostly in the West. Both species of *Rhionaeschna* treated here, *R. californica* and *R. multicolor* (Fig. 12), occur in British Columbia grasslands but are not normally found eastward in Canada, although there is a record of *R. multicolor* in the Alberta Cypress Hills (Hilton 1985). Either species, especially *R. multicolor*, which is found in Montana, may expand northward into the Canadian Prairies, given trends in climate warming. *Rhionaeschna multicolor* is one of the most common dragonflies of southern British Columbia grassland ponds and marshes in midsummer. In contrast, *R. californica* is remarkable for its springtime flight season, emerging with the earliest dragonflies. In the southern valleys of British Columbia, and especially in the Garry oak grassland habitats around southern Vancouver Island, it usually appears by mid-April. It normally disappears by early August, just when many damner species are reaching their peak abundance. The only other Neotropical damner in Canada is the eastern *R. mutata*, which is strikingly similar to *R. multicolor*. It is a rare species of extreme southern Ontario and has not yet been reported in grassland habitats, although it is known from Essex County near Ojibway Prairie.

*Anax* species are among the largest dragonflies. *Anax junius* (Fig. 13) has a southern transcontinental distribution and is found in grasslands from Vancouver Island to southern Ontario. At least some populations migrate, with spring migrants moving north in the spring before any emerge locally. These migrants breed; their offspring emerge in late summer and fly south in August and September. Other populations are resident, with adults emerging in spring from larvae that have overwintered locally. This species swarms over Ojibway Prairie in August and September (P. Pratt, pers. comm.). The eastern *Anax longipes* has a spectacular male with a green thorax and red abdomen. It is rare in southern Ontario but has been recorded at Ojibway Prairie (Pratt 2010).

*Epiaeschna heros* is a forest species; the majority of Canadian records are from southern Ontario. Although it is atypical of grasslands, it is included because it is recorded at Ojibway Prairie, where it commonly hunts over the open grassland (P. Pratt, pers. comm.).

### Family GOMPHIDAE (Clubtails)

North America: 101 species; Canada: 42 species; Canadian grasslands: 15 species

The Gomphidae is a large family of mostly stream dwellers that, in Canada, is largely eastern in distribution. Six genera (14 species) are listed here as grassland inhabitants. Gomphids are not observed as frequently as some other odonate families because many species are rare and their short flight seasons, cryptic coloration, and tendency to rest often makes them a challenge to find. When they are encountered, they are readily recognized by their relatively small, widely separated eyes and their green or yellow bodies striped in brown and black. The tip of the abdomen in males is usually swollen into a club. The female lacks an ovipositor and drops the eggs directly into streams or along the sandy shores of larger lakes. The larvae burrow in the bottom sediments of streams and lakeshores.

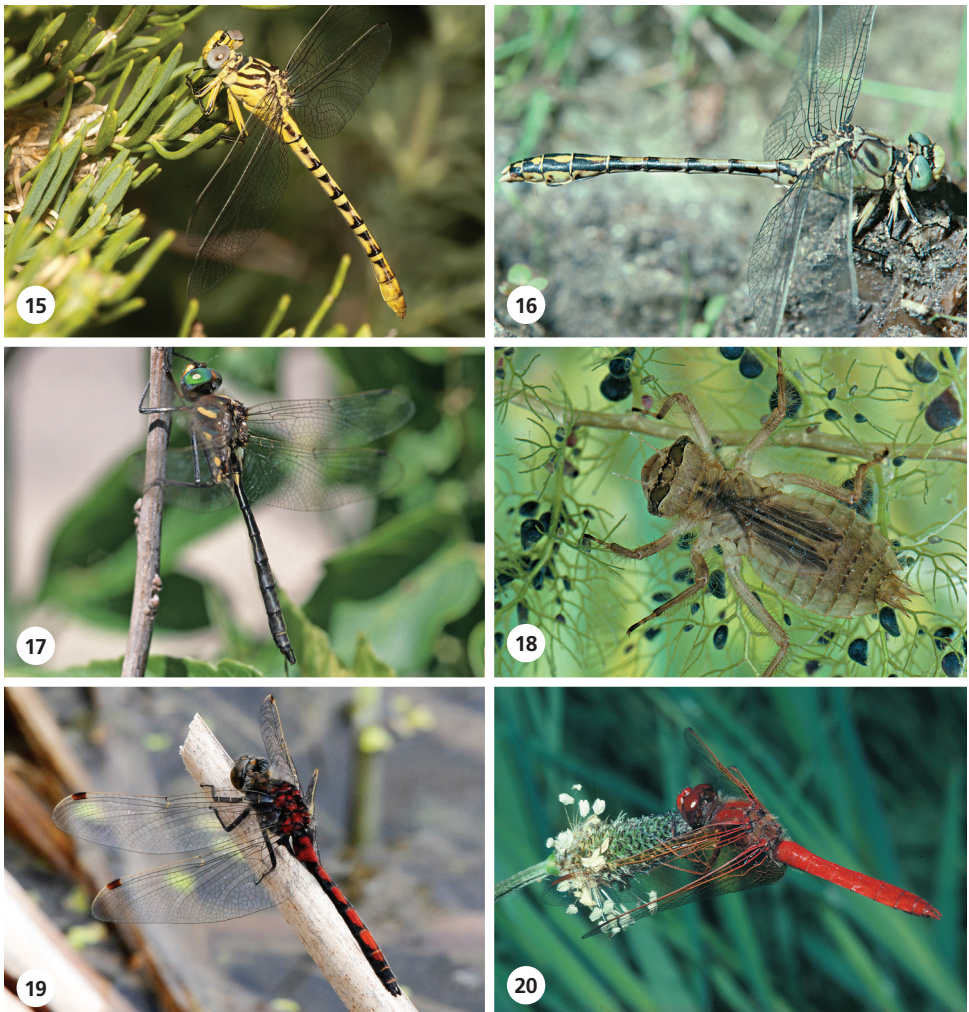
Three gomphid genera have only one or two species in grassland habitats. *Progomphus obscurus* is a clubtail of sandy sites, where the larva is a highly adapted burrower; the species is restricted in Canada to southern Ontario. It is rare at Ojibway Prairie (Pratt 2010). The genus *Arigomphus* is mainly distributed in central and eastern North America, but in contrast to other related gomphids, species are likely to live in lakes and ponds. Two species are recorded in grasslands in Canada. In southern Manitoba, *Arigomphus cornutus* has been collected in diverse habitats around Winnipeg, for example, in urban stormwater retention ponds (Ackerman and Galloway 2003), in the Red and La Salle rivers (Walker

1958), and in the oxbows of the Assiniboine River (M. Hughes, pers. comm.). In 2013, *Arigomphus villosipes* appeared at Ojibway Prairie for the first time (P. Pratt, pers. comm.). *Dromogomphus spinosus* is a widespread eastern forest gomphid that, at the extreme northwestern edge of its range in southern Manitoba, has been recorded in grassland near Oak Hammock Marsh north of Winnipeg and at the edge of prairie near Marchand (Hughes and Duncan 2003).

*Gomphus* is the most diverse genus of odonates in North America, with 38 species; there are 51 worldwide (Paulson 2011). Four are considered here. *Gomphus graslinellus* lives along valley bottom lakeshores in the Okanagan, Shuswap, and Boundary regions of British Columbia, where grasslands were once common but are now scarce. It is rare on the Great Plains, where there is one record for the Cypress Hills in Alberta, several near Armit, Saskatchewan (almost 53°N; Halstead 2013), and a few in southern Manitoba. It is restricted to the south in Ontario; it is uncommon at Ojibway Prairie (Pratt 2010). One of the few odonates that is more or less restricted to the Great Plains is *Gomphus externus* (Fig. 14). The larvae develop in sandy or muddy streams or rivers with moderate current. In Canada, *G. externus* is recorded only in southern Manitoba, where it can be common locally along the Red River north to Winnipeg Beach and on the Assiniboine River west to Treesbank (Hughes and Duncan 2003). The two other *Gomphus* species are mainly eastern in distribution. *Gomphus fraternus fraternus* is fairly common in Manitoba along the Winnipeg River and southeastern Lake Winnipeg in largely forested habitat, immediately east of the grasslands. It ranges eastward through southern Ontario to Québec, although it is not recorded at Ojibway Prairie. Prairie populations along the Red and Assiniboine rivers in Manitoba are smaller and paler than others and are designated as subspecies *G. f. manitobanus* Walker (Walker 1933; Walker 1958; Catling and Hughes 2008). Although not known outside Manitoba, this subspecies could occur in other Great Plains localities in the United States (Catling and Hughes 2008). *Gomphus vastus* has a wide range in the eastern United States and a few small areas of southern Canada, but like so many other eastern forest plant and animal species, it barely enters the southeastern Manitoba woodlands. It is included in the grassland Odonata list because it is recorded at Ojibway Prairie (Pratt 2010).

*Stylurus* also has four species on the Canadian grassland Odonata list. When perched, individuals often hang down from the leaf or twig, or sit tail down on large leaves. *Stylurus olivaceus* lives strictly west of the Rockies and, in British Columbia, it mainly inhabits warm rivers such as the Okanagan and Thompson that flow through grasslands. It ranges east to Christina Creek in the Boundary region. Most of its habitats are strongly affected by humans (Cannings 2011) and it is assessed as “Endangered” by COSEWIC (2011). *Stylurus intricatus* (Fig. 15) is a small, mostly yellow clubtail living in scattered populations across the arid West, typically developing in warm, muddy, slowly moving rivers (Paulson 2009) such as the Milk (e.g., Lost River Ranch, Milk River; Acorn 1983) and Saskatchewan (e.g., Maidstone, Catling and Kostiuk 2004a; Saskatoon, Prince Albert, Walker 1958). *Stylurus amnicola* is an eastern clubtail that was recently (2004) recorded on the southern Manitoba prairies along the Assiniboine and Red rivers (Hughes and Catling 2005) and is now also known from a few other locations in the region. The Great Plains population is believed to be at some risk from agricultural impacts, but more data are needed to determine its status; a recent COSEWIC assessment resulted in an assessment of “data deficient” (COSEWIC 2013). Another eastern *Stylurus*, *S. notatus*, is recorded in grasslands from Saskatchewan east, although the northern parts of its range are in the boreal forest. For example, the only record for Alberta is at Fort McMurray (J. Gatten, pers. comm.), and two of the Saskatchewan records (Frenchman Butte, Hutchings 2004; Prince Albert, Halstead 2013) are at the interface of the boreal forest.

Records from Saskatchewan grasslands also include Maidstone (Catling and Kostiuk 2004a). *Stylurus notatus* is called the Elusive Clubtail; in most places, it is seen much less often than its true abundance warrants. Experienced observers in Manitoba seldom see a mature adult, but sometimes lucky people have come across a mass emergence or thousands of exuviae on a river bank (M. Hughes, pers. comm.). The species is uncommon at Ojibway Prairie, where it spends considerable time hunting and resting out on the prairie (P. Pratt, pers. comm.). *Stylurus notatus* is the sole odonate species living in grasslands that is considered of global conservation concern; it is designated G3 (vulnerable) (Hall *et al.* 2011).



**Fig. 15.** *Stylurus intricatus* (Brimstone Clubtail), female. Photo: Dennis Paulson. **Fig. 16.** *Ophiogomphus severus* (Pale Snaketail), male. Photo: George Doerksen, Royal British Columbia Museum. **Fig. 17.** *Somatochlora ensigera* (Plains Emerald), male. Photo: Sid Dunkle. **Fig. 18.** *Libellula quadrimaculata* (Four-spotted Skimmer), larva. Photo: Robert A. Cannings, Royal British Columbia Museum. **Fig. 19.** *Leucorrhinia borealis* (Boreal Whiteface), male. Photo: Dennis Paulson. **Fig. 20.** *Sympetrum illotum* (Cardinal Meadowhawk), male. Photo: George Doerksen, Royal British Columbia Museum.

Species in the beautiful genus *Ophiogomphus* have green thoraxes and yellow abdomens marked in black. Two western and one eastern species are regularly found in grassland habitats. In Canada, *O. occidentis* is known only from British Columbia, where it ranges from southern Vancouver Island east to the Shuswap and Boundary regions, all south of 51°N. It is most common in the Okanagan Valley, where it breeds in rivers and along sandy lakeshores. *Ophiogomphus severus* (Fig. 16) is the most frequently recorded gomphid west of Manitoba. It develops in small streams, rivers, and lakes in both grasslands and forests from British Columbia east to Saskatchewan and north into the boreal forest. The montane populations in British Columbia and Alberta are part of the subspecies *O. s. montanus* (Selys) and are more heavily marked than the pale populations of the nominate subspecies on the Great Plains. This snaketail is common in the Saskatchewan River system (Miyazaki and Lehmkuhl 2011) and other streams such as the Milk River. The eastern *O. rupinsulensis* is recorded in Canadian grasslands only in Saskatchewan and Manitoba. Typically, it inhabits streams and rivers that are more sluggish and muddy than those used by most other *Ophiogomphus* species. It is uncommon in extreme southern Manitoba (prairie records along the Assiniboine River include Treesbank, Griswold, and Virden) and it is rare in central Saskatchewan (Saskatoon, Prince Albert).

#### **Family CORDULEGASTRIDAE (Spiketails)**

North America: 9 species; Canada: 5 species; Canadian grasslands: 1 species

Spiketails are large black and yellow dragonflies with relatively small blue or green eyes that usually touch at a single point. The dragonflies live along creeks and streams, sometimes even small trickles, usually in woodland. Adults patrol these streams, and the female, hovering vertically, shoves eggs in the sand and silt of the stream bed using her spade-like ovipositor. The large, squat, hairy larvae bury themselves in the sediment to await their prey. The labium of the larva, with its palps deeply and irregularly toothed, is distinctive.

One genus, *Cordulegaster*, lives in North America. *Cordulegaster dorsalis* is the most widespread *Cordulegaster* west of the Rockies and is the only representative of the Cordulegastriidae in western Canadian grasslands. It is common on some coastal British Columbia streams, but it is also a rare inhabitant of running water, especially spring-fed streams, in the mountains of the Interior south of 51°N. The only grassland habitat currently known is Little Sand Creek near Jaffray (East Kootenay), which runs through dry, open coniferous forest and associated grassland patches (Cannings *et al.* 2000), although other occupied sites probably exist. Before Garry oak savannas on southern Vancouver Island were highly modified by humans, *C. dorsalis* likely flourished along some of the grassland streams there (e.g., Bowker Creek, Oak Bay) but, today, it is recorded only in nearby woodland. The eastern *Cordulegaster maculata* is rare at the western edge of its range in extreme southeastern Manitoba (e.g., Sandilands Provincial Forest) and has not been recorded on adjacent prairie, although presumably individuals could appear on small wooded streams there.

#### **Family MACROMIIDAE (Cruisers)**

North America: 9 species; Canada: 4 species; Canadian Grasslands: 2 species

The Macromiidae are large yellow and black dragonflies with the thorax encircled below the wings by a distinctive, oblique yellow band. They inhabit rivers and wave-washed shores of lakes, where the adults fly rapidly out over the water, but they also hunt along roads and railways, sometimes far from water. The larvae sprawl on the bottom silt

and sand. Their long spider-like legs and the horn-like projection between the eyes are characteristic. There are two North American genera, *Macromia* and *Didymops*, but only the former is recorded in Canadian grasslands. However, *Didymops transversa*, a common and widespread eastern forest species, occurs in extreme southeastern Manitoba and may venture out onto the prairies just to the west.

Three *Macromia* species may be found in or near Canadian grassland habitats, although only two are so far recorded. *Macromia magnifica* lives in a few of the southwestern valleys of mainland British Columbia. In the Okanagan Valley, most of the records at breeding sites are from Vaseux Lake, but it is often seen hunting along roads and abandoned railways in the hills above Okanagan Lake, 500 or 600 m above any potential breeding sites along the lakeshore below (Cannings *et al.* 1998). The nominate subspecies *M. m. magnifica* is the grassland form (Cannings *et al.* 2006). *Macromia taeniolata*, a large cruiser of the eastern United States, reaches Canada only along the rivers of extreme southwestern Ontario in Lambton and Essex counties (Catling and Brownell 2000) and was first recorded at Ojibway Prairie in 2004 (Pratt 2010). The most common and widespread eastern *Macromia*, *M. illinoensis*, is known from the forests of southeastern Manitoba, but has yet to be recorded at adjacent grassland sites. It is not known at Ojibway, although it ranges across southern Ontario and east to Nova Scotia.

### **Family CORDULIIDAE (Emeralds)**

North America: 50 species; Canada: 33 species; Canadian grasslands: 13 species

In most of Canada, the Corduliidae is a family best seen around lakes, boggy streams, and peatlands in the mountains or in northern forests. Many species are boreal in distribution. The adults are medium-sized dragonflies, usually with metallic blackish green or brassy green bodies; this and the bright green eyes of many species give the group its English name. The family is mainly found in forested habitats and only four genera are on the Canadian grassland list: *Cordulia*, *Dorocordulia*, *Epithea*, and *Somatochlora*.

*Cordulia shurtleffii* and *Dorocordulia libera* are generally forest species, but both occur in grassland habitats. *Cordulia shurtleffii* is a widespread boreal dragonfly, the most common species of the Corduliidae in Canada, typically inhabiting boggy lakes, fens, and beaver ponds. It enters grassland habitats all over British Columbia, but much less so in prairie habitats of the Great Plains, where it is mostly a species of the foothills (Bragg Creek) and northern fringes (Edmonton, Prince Albert). It is recorded from the Cypress Hills in both Alberta and Saskatchewan and is common in southern Manitoba (e.g., Treesbank; Walker and Corbet 1975), but is absent from Ojibway Prairie. *Dorocordulia libera* is normally a denizen of northeastern North American forest marshes and boggy habitats. It is uncommon in southeastern Manitoba, which is at the western edge of its range, but there are records for Winnipeg and Hansen Creek, both within grassland zones. It is rare and local in southwestern Ontario and has not been observed at Ojibway Prairie.

*Somatochlora* is the predominant genus of the Corduliidae in North America with 26 species, 20 of which are recorded in Canada. Most of these are not typical grassland species, but seven are known from grasslands. None are recorded at Ojibway Prairie in Ontario. *Somatochlora ensigera* (Fig. 17) develops in streams, often small ones, in scattered areas across the Prairies Ecozone (e.g., Maple Creek, Saskatchewan; Red, La Salle, Assiniboine, and Whitemud rivers in Manitoba) and in woodlands east to southern Ontario (single record) and Ohio. *Somatochlora semicircularis* is a western Cordilleran species that lives in sedge marshes. It is widespread in British Columbia and in and near the mountains of

Alberta (e.g., Sibbald Flats southwest of Calgary; Cypress Hills). In British Columbia, it is the most likely *Somatochlora* to appear in or at the edge of grasslands (e.g., Madeline Lake, Penticton; Cosens Bay, Vernon). A few others are marginal grassland species at best, but five more or less transcontinental boreal species are recorded from grassland zones (e.g., Aspen Parkland), usually in “forest islands” or at the grassland–woodland interface: *Somatochlora franklini* (e.g., Alberta: Red Deer, Wagner Natural Area near Edmonton; Saskatchewan: Saskatoon; Manitoba: Treesbank, Winnipeg, Victoria Beach), *Somatochlora hudsonica* (e.g., Alberta: Red Deer, Cypress Hills in fescue prairie), *Somatochlora kennedyi* (e.g., Manitoba: Winnipeg), *Somatochlora minor* (e.g., Alberta: Bragg Creek, Cypress Hills in fescue prairie); Manitoba: Treesbank, Onah), and *Somatochlora walshii* (e.g., Manitoba: Winnipeg).

*Epithea* species are dull emeralds, with mostly black and pale brown/yellow bodies and brown marks at the hind-wing bases. They fly in late spring and early summer. Females gather a cluster of eggs at the tip of the abdomen, supported by the long bifid subgenital plate (thus the English name, “baskettail”). Long strands of eggs are laid, sometimes communally, along lakeshores. *Epithea* species often feed in swarms. Two species on the grassland list are strictly eastern in distribution, ranging mostly from Ontario to Nova Scotia; they are both recorded at Ojibway Prairie but nowhere in grasslands to the west. *Epithea cynosura* is distributed westward to extreme eastern Manitoba but remains in the forests there, not extending west much from the Ontario border. *Epithea princeps* is an unusual baskettail in that it is large and darner-like, with strongly spotted wings. It has a distribution similar to that of *E. cynosura*; the only Manitoba records are recent (2004, 2009) from forest habitats in the extreme southeast (De Marsh and Taylor 2011). *Epithea canis* and *E. spinigera* are more or less transcontinental in the southern half of Canada. *Epithea canis* is weakly associated with the margins of the Prairies Ecozone in Saskatchewan (Cypress Hills, northern edge of Aspen Parkland) and Manitoba (Dauphin, Riding Mountain, Sandilands), while *E. spinigera* is more common and more likely to be seen in a variety of habitats, including grassland edges. It is common around lakes associated with Garry oak meadows on southern Vancouver Island, but uncommon at grassland sites in the dry Interior (e.g., Vaseux Lake, Penticton, Vernon). In the Prairie Provinces, it is common across southern Manitoba (e.g., Treesbank, Winnipeg) and in the boreal forests of Saskatchewan and Alberta, south to the Aspen Parkland (e.g., Edmonton).

### Family LIBELLULIDAE (Skimmers)

North America: 112 species; Canada: 45 species; Canadian grasslands: 37 species

The Libellulidae is the largest family of Odonata but is only slightly more diverse than the Gomphidae. The species are most common around ponds, marshy lakeshores, and sluggish streams where the adults, often colourful, dart about and spend much time perched horizontally in the sun. Females oviposit alone or in the company of guarding males by dipping the abdomen in the water, releasing the eggs. Many larvae, like those of the Corduliidae, move sluggishly or squat on the bottom mud; others are more active in vegetation.

The genus *Libellula* contains seven large, striking species in Canadian grasslands. Some have banded or spotted wings, and most mature males, especially, have extensive pale pruinosity (a white, gray, or pale blue powdery bloom that exudes from the cuticle) on the abdomen or entire body. *Libellula quadrimaculata* (Fig. 18), a widespread Holarctic species and one of the most common dragonflies worldwide, is nearly everywhere in

Canada, from northern bogs to alkaline grassland ponds. It lives in all areas covered by this study, from the Yukon to Ontario. *Libellula forensis* is strictly Cordilleran. It is most common on British Columbia's southern coast, where it is characteristic and abundant in ponds and marshes in Garry oak meadows, and in the Okanagan Valley, where it is common in grassland waters. It is rare in the Kootenays. *Libellula pulchella* is a large southern transcontinental species, often associated with grassland ponds, although it is rare in the Prairies Ecozone in Alberta and Saskatchewan. It ranges across the southern British Columbia Interior, with most records in the Okanagan Valley, where most of its habitat has been drained and filled in the past century. It is reported from Prairie grasslands in only the Cypress Hills (Hilton 1985), Medicine Hat (J. Acorn, pers. comm.) and Onefour (G. Hilchie and M. Buck, pers. comm.) in Alberta and from near Prince Albert in Saskatchewan (G. Hutchings, pers. comm.). However, it is common in southern Manitoba and at Ojibway Prairie. *Libellula luctuosa* is a southern transcontinental dragonfly that has shown up once in southern Manitoba at Winnipeg (Hughes and Duncan 2003), whereas it is common in Ontario and Québec. At Ojibway Prairie, it is the most common *Libellula* species (P. Pratt, pers. comm.). It has moved north in recent decades on the Pacific Coast (Paulson 2009) and may appear in British Columbia grasslands before long; this is perhaps a northward shift in distribution resulting from climate warming. Three eastern *Libellula* species recorded at Ojibway Prairie are *L. incesta*, *L. semifasciata*, and *L. vibrans*. In Canada, the latter is known from only extreme southwestern Ontario, while the other two range through southern Ontario and, to a limited extent, into the southern Maritimes.

The genera *Ladona* and *Plathemis*, which are closely related to *Libellula*, each contain one transcontinental species in Canadian grasslands. *Ladona julia* is decidedly more northern in distribution and is much less a grassland inhabitant than *Plathemis lydia*. *Ladona julia* is partial to montane, southern boreal, or Aspen Parkland lakes with peaty shores; it is absent from the prairie grasslands of Alberta and Saskatchewan but is common in southern Manitoba. It breeds uncommonly around northern grassland ponds in the Chilcotin region of central British Columbia (Cannings and Cannings 1987). In British Columbia, *Plathemis lydia* is recorded in southern British Columbia and from Manitoba eastward to Nova Scotia. In British Columbia, it likes muddy ponds in the warm lowlands of eastern Vancouver Island (Garry oak meadow remnants), the grasslands of the Okanagan, and (more rarely) the Kootenays in the Interior. Eastward, the northern limit of its range runs through central Montana and North Dakota in the United States (Paulson 2009), and so it is absent from the Canadian Great Plains except for the Winnipeg region, where it is rare, but apparently increasing in numbers (Hughes and Duncan 2003). It is common at Ojibway Prairie.

Two other genera, *Perithemis* and *Celithemis*, are mainly eastern. *Perithemis tenera* is a tiny, orange-winged dragonfly (clear with large brown marks in females), assumed to be a wasp mimic, at least away from water. It is widespread in the East, including much of the American Great Plains, but in Canada is mostly confined to southern Ontario. It is common at Ojibway Prairie. The eight species of *Celithemis* develop in marshy lakes and ponds and are more or less restricted to the eastern United States and Canada (four species). Two are recorded at Ojibway, *C. elisa* and *C. eponina*; both species have strongly coloured, patterned wings.

*Leucorrhinia* species (whitefaces) are small, black, white-faced dragonflies marked with red or yellow that are found around the marshy shores of lakes and ponds, often in peatlands, in the late spring or early summer. Whitefaces are most common in mountain or northern areas; they are largely absent from the dry grasslands of Alberta and Saskatchewan

but are more widespread in southern Manitoba. *Leucorrhinia intacta* is the anomaly in the genus, preferring ponds with water lilies in warm lowlands; it is the common species in the grassland valleys of southern British Columbia and over much of southern Ontario, including Ojibway Prairie, where it is abundant. Although it is absent from the driest parts of the Prairies, it lives in central Alberta and Saskatchewan and southern Manitoba. Despite its southern affinities, it is also recorded from northern Alberta and along the Mackenzie River in the Northwest Territories. *Leucorrhinia hudsonica* is one of the most wide-ranging dragonflies in Canada, from Yukon to Newfoundland. In grasslands, it is recorded in Yukon, British Columbia (e.g., Chilcotin region), the Aspen Parkland of Alberta and Saskatchewan, and throughout most of southern Manitoba. It is found in the Cypress Hills in both Alberta (where one of the sites is in a fescue prairie; Hilton 1985) and Saskatchewan. A close relative, *L. borealis* (Fig. 19), is a dragonfly of the western boreal forest and Cordillera, not ranging east of Hudson Bay. It is common over much of Yukon, Interior British Columbia, and the central forested areas of Saskatchewan and Alberta (also Cypress Hills at the same grassland locality as *L. hudsonica*), as well as over much of central and southern Manitoba. At some localities, especially in the Aspen Parkland and southern boreal forest, it can be strikingly abundant. On the other hand, *L. frigida* is eastern in distribution, ranging from the grassland interface of the southern interlake area of Manitoba to Nova Scotia. It is considered rare at Ojibway Prairie. *Leucorrhinia glacialis* and *L. proxima* are transcontinental but, at least in western Canada, *L. glacialis* ranges much less into the north than does *L. proxima*. In grasslands, neither is common in British Columbia, but *L. proxima*, especially, is widespread there (e.g., Penticton, Oyama). Both species are found in grassland-edge habitats across Alberta and Saskatchewan. They mainly occur in the Aspen Parkland in Alberta (e.g., Red Deer), although *L. glacialis* is rare in Saskatchewan. *Leucorrhinia proxima* lives in the Alberta and Saskatchewan Cypress Hills and, at least in Alberta, occurs at grassland sites there (Hilton 1985). Both species live across southern Manitoba, but only *L. proxima* is reported at Ojibway, where it is uncommon.

Although seven species of *Erythemis* live in North America north of Mexico, only two are found in Canada; these are the similar *E. collocata* and *E. simplicicollis*. Females and young males are green, and mature males are blue pruinose. In Canada, *E. collocata* lives in southwestern British Columbia, predominantly on the coast, where it is typical of ponds in Garry oak grasslands on Vancouver Island and the Gulf Islands. It is rare in South Okanagan grasslands at Osoyoos Lake. *Erythemis simplicicollis* in Canada ranges through southern Ontario and Québec; it is common at Ojibway Prairie. There is some evidence that *E. collocata* and *E. simplicicollis* may be conspecific (Paulson 2009).

*Sympetrum* (meadowhawks) is an important genus in Canadian grasslands, with 11 species recorded; both the diversity of species and the abundance of individuals in these habitats are notable. These are mostly small red dragonflies, which are usually abundant as adults in the late summer and fall. Females and young males are usually brown or yellow, although some females, at least those that are old, are red like the males. One species, *S. danae*, is black with yellow markings. Meadowhawks usually lay their eggs while male and female are in tandem or with a guarding male hovering near the female. Some species (e.g., *S. madidum*, *S. pallipes*, *S. internum*) breed in temporary ponds, and eggs are often laid in dry basins where they hatch in spring when the snow melts. Larval growth is rapid after the ponds fill with water. North America has 13 species, and all but one are recorded in Canada. They are especially common in marshy lowland habitats.

Three *Sympetrum* species on the grassland list are restricted to western North America. *Sympetrum illotum* (Fig. 20) ranges from the southern British Columbia coast south to



Panama. It is common and is an unusually early flyer for a *Sympetrum*, often appearing in April. With its relatively large size and broad scarlet abdomen, it is one of the most conspicuous dragonflies of ponds in the Garry oak meadows of southeastern Vancouver Island and the Gulf Islands. A closely related western species, *S. madidum*, ranges much more extensively in Canada, from southern British Columbia north to southeastern Yukon and Northwest Territories and east to Manitoba. The species is fairly common in southern British Columbia, including grassland sites (e.g., Aspen Grove, Osoyoos, Hat Creek, Athalmer) and ranges across the grasslands of Alberta (Lethbridge, Calgary) and Saskatchewan (Maple Creek, Battleford, Regina) to southwestern Manitoba (Aweme, Portage la Prairie). Cannings (1980, 1981) described the larva and presented ecological information on the species from studies in fescue grasslands of the eastern Chilcotin and Garry oak meadows near Victoria, British Columbia. *Sympetrum pallipes* is another western species but one that barely ranges east of the Rockies. It is common in the remnant savannas of southern Vancouver Island and the grasslands of the British Columbia Interior (Osoyoos, Oliver, Wasa, Douglas Lake) and is recorded from both the Alberta and Saskatchewan Cypress Hills (the single Alberta record there is from fescue prairie) but is rare in the Mixed Grassland Ecoregion in southern Alberta (e.g., Suffield).

Seven of the eight other meadowhawks recorded in grassland sites are transcontinental in distribution, with the lone species restricted to the East. The eastern species, *S. rubicundulum*, is the most common meadowhawk in open areas of Ojibway Prairie and almost reaches southern Manitoba at the extreme northwest extent of its range in the United States. A larval record in stormwater retention ponds in Winnipeg (Ackerman and Galloway 2003) needs to be confirmed, as there are no adult records, and Hughes and Duncan (2003) did not include the species on the Manitoba list. The related *S. internum* (Fig. 21) is characteristic of grassland marshes, ponds, and pools (especially those whose margins dry up) across the West from Yukon through British Columbia and east to Manitoba, but although it ranges east to Newfoundland, it is not known from Ojibway Prairie. Wing length in both sexes decreases northward (Cannings and Cannings 1997; Catling 2007) and colour patterns (the extent of amber on the hind-wing base) can vary between sexes and with latitude (Catling 2007). *Sympetrum obtrusum* does not range as far north as *S. internum* but, in the dry West, at least, it is more associated with woodland and is less common on the Prairies than *S. internum*. *Sympetrum obtrusum* is typical of sedge meadows and is often common in peatlands where *S. internum* is absent. In grasslands, it often inhabits temporary waters, for example, in British Columbia (Osoyoos, Vernon), Alberta (Claresholm, Devon), Saskatchewan (Manitou Lake), Manitoba (Westbourne, Swan River), and Ontario (uncommon at Ojibway). *Sympetrum costiferum* is common in many Canadian grasslands, at least from British Columbia to Manitoba. It occurs in many wetland types, but can be abundant at alkaline lakes in the British Columbia Interior and on the Great Plains. In Ontario, it is recorded from grassland-like ponds along Great Lakes beaches, although it is not reported from Ojibway Prairie. *Sympetrum danae* (Fig. 22) ranges around the northern parts of the globe and has wide ecological tolerances, being equally at home in mountain and northern peatlands, lowland marshes, and warm, shallow lake margins. It is a common grassland species from Yukon to Manitoba, but may be absent from the driest parts of the southern Prairies. *Sympetrum semicinctum* is a striking meadowhawk, with orange-brown coloration on the basal halves of the wings, which varies in intensity across its range (British Columbia to Nova Scotia). The western populations were considered separate (*S. occidentale* Bartenev) (Walker 1951) until recently (Catling *et al.* 2005). It is fairly common in southern British Columbia but less so

in Alberta, rare in Saskatchewan and Manitoba, and rare at Ojibway Prairie. Individuals or pairs often wander across grasslands well away from water, and although they are not restricted to grasslands, they can be common there. In Canada, *Sympetrum vicinum* ranges from the Atlantic to southeastern Manitoba. A disjunct western population lives from extreme southern British Columbia to northern California. Grassland populations occur at Ojibway Prairie (where it is common), in the Winnipeg area, and in British Columbia in the southern Okanagan grasslands at Vaseux Lake and on southern Vancouver Island. It flies late, well into November in mild autumns in British Columbia. *Sympetrum corruptum* is a transcontinental species, but is much more abundant in the West than east of the Mississippi River. Probably many of the individuals seen in eastern North America are migrants or wanderers (Paulson 2011). Breeding occurs in both spring and late summer in southern Canada. Spring breeding individuals apparently are migrants from the south, and their offspring, emerging in late summer and fall, often undertake impressive southward movements. The species is fairly common in grasslands of southern British Columbia east to Manitoba; it develops in shallow marshy lakes, saline ponds, and temporary pools.

*Pachydiplax longipennis* (Fig. 23) is a common southern transcontinental species that enters Canada only in southernmost areas of British Columbia, Manitoba, Ontario, Québec, and New Brunswick. There is a single Manitoba record at the forest–grassland interface at Lac du Bonnet, north of Winnipeg (Hughes and Duncan 2003). In Ontario it is common



**Fig. 21.** *Sympetrum internum* (Cherry-faced Meadowhawk), male. Photo: George Doerksen, Royal British Columbia Museum. **Fig. 22.** *Sympetrum danae* (Black Meadowhawk), male and female mating. Photo: George Doerksen, Royal British Columbia Museum. **Fig. 23.** *Pachydiplax longipennis* (Blue Dasher), male. Photo: Robert A. Cannings, Royal British Columbia Museum. **Fig. 24.** *Pantala hymenaea* (Spot-winged Glider), male. Photo: Dennis Paulson.

at Ojibway Prairie. In British Columbia, its distribution includes grassland habitats; it has a distribution almost exactly the same as that of *Erythemis collocata* (southwest coast, southern Okanagan) and the two are often found together.

*Tramea* species are called “saddlebags” because of the large dark marks at the base of the broad hind wings. It is a worldwide, but primarily tropical, genus, mainly found in southern Ontario in Canada. The two most common species, *Tramea lacerata* and *T. onusta*, range transcontinentally in the United States. These species and *T. carolina*, which is restricted to the East in North America, are all recorded at Ojibway Prairie. *Tramea lacerata* is common in southern Ontario and, since 1996, has been seen in British Columbia at Victoria in Garry oak grasslands (Cannings 1997), where it is known to mate, if not complete a life cycle. It also occurs at Parksville to the north.

The two species of *Pantala* are mainly tropical and subtropical in their worldwide distribution but wander widely, entering temperate regions. The hind wings are unusually broad, much like those of *Tramea*, which is likely closely related (Paulson 2011). Both are recorded in southern Canada, especially in Ontario, where both species breed, usually in lagoons and pools along Great Lakes beaches. There is a single record of *Pantala flavescens* in Alberta grasslands; it is rare in southern Manitoba and uncommon at Ojibway Prairie. *Pantala hymenaea* (Fig. 24) has wandered to coastal British Columbia at Victoria several times (Cannings 1988) and to southern Manitoba (e.g., Victoria Beach). It is common at Ojibway Prairie. Both *Pantala* species, *Tramea lacerata*, *Epithea princeps*, and *Anax junius* are conspicuous aerial hunters over Ojibway grasslands (P. Pratt, pers. comm.). Reports of northward wandering and migration of several species may increase in Canada as the climate warms.

### Biogeography and Faunal Elements

Species can be grouped with others that share similar distributions to form what can be termed faunal elements. The majority of the 124 species reported here from the Canadian grasslands are restricted to the Nearctic region, although five species, *Lestes dryas*, *Aeshna juncea*, *A. subarctica*, *Libellula quadrimaculata*, and *Sympetrum danae*, are Holarctic (defined here as species with transcontinental ranges in both North America and Eurasia). Two species (*Anax junius* and *Sympetrum corruptum*) are known from eastern Asia, but do not have Holarctic distributions. This section describes the Nearctic faunal elements (species with Holarctic distributions are also assigned to a North American faunal element). Those relevant to Canadian grassland Odonata are as follows:

1. Boreal (20 species). Species occurring in the northern spruce (*Picea*) forests, across the boreal zone from treeline to the southern margin. In general, these species range from the Atlantic Provinces across the northern New England states, Quebec, northern Ontario, parts of the northern tier of midwestern states, the Prairie Provinces north of the Great Plains, and northern British Columbia, often ranging considerably southward in the higher mountains and plateaus of the western Cordillera. These species can be further subdivided into the following:
  - i. Widespread Boreal (11 species). With ranges as described above.  
*Coenagrion resolutum*, *Enallagma annexum* *E. boreale*, *Aeshna eremita*, *A. juncea* (also Holarctic), *A. sitchensis*, *A. subarctica* (also Holarctic), *Cordulia shurtleffii*, *Somatochlora franklini*, *Leucorrhinia hudsonica*, *Sympetrum danae* (also Holarctic).
  - ii. Northern Boreal (2 species). Species that are common near the northern treeline, but that are virtually absent from the northern contiguous United States and from

- the southeastern Atlantic Provinces and do not extend far south into the Cordillera. *Coenagrion interrogatum*, *Aeshna septentrionalis*.
- iii. Southern Boreal (5 species). Species that are uncommon north of 60 °N in the West and absent near the arctic treeline in the East, but range far down the Cordillera and/or into the southeastern Atlantic Provinces and New England states. Some (e.g., *Aeshna interrupta*) are common on the Great Plains. *Aeshna interrupta*, *Somatochlora kennedyi*, *S. minor*, *S. walshii*, *Leucorrhinia proxima*.
  - iv. Western Boreal (2 species). Boreal species not found east of Hudson Bay. *Somatochlora hudsonica*, *Leucorrhinia borealis*.
2. Transition (17 species). Species generally most common in the southern boreal forests and adjacent montane forests in the West and mixed and deciduous forests in the East. *Calopteryx aequabilis*, *Enallagma ebrium*, *E. hageni*, *Nehalennia irene*, *Aeshna canadensis*, *A. constricta*, *A. umbrosa*, *Gomphus graslinellus*, *Epitheca canis*, *E. spinigera*, *Ladona julia*, *Leucorrhinia glacialis*, *L. intacta*, *Sympetrum costiferum*, *S. internum*, *S. obtrusum*, *S. semicinctum*.
  3. Cordilleran (12 species). Species mostly confined to the western mountains and their intervening valleys and plateaus but extending to various degrees into the Great Plains. *Argia emma*, *A. vivida*, *Ischnura cervula*, *Aeshna palmata*, *Rhionaeschna californica*, *Ophiogomphus occidentis*, *Stylurus olivaceus*, *Cordulegaster dorsalis*, *Macromia magnifica*, *Somatochlora semicircularis*, *Libellula forensis*, *Sympetrum illotum*.
  4. Pacific Coastal (1 species). Coastal species restricted to the lowlands and lower slopes of the mountains west of the Coast Mountains. *Ischnura erratica*.
  5. Western (10 species). Species confined to west of the 100th meridian, but otherwise ranging widely in North America. *Amphiagrion abbreviatum*, *Enallagma anna*, *E. clausum*, *Ischnura damula*, *I. perparva*, *Rhionaeschna multicolor*, *Ophiogomphus severus*, *Erythemis collocata*, *Sympetrum madidum*, *S. pallipes*.
  6. Great Plains (4 species). Species more or less confined to the Great Plains. *Coenagrion angulatum*, *Gomphus externus*, *Stylurus intricatus*, *Somatochlora ensigera*.
  7. Southern (16 species). Species ranging across the continent south of the boreal forests, often extending into transition areas, but with most of the range in the United States. *Archilestes grandis*, *Lestes forcipatus*, *Enallagma basidens*, *E. carunculatum*, *E. civile*, *Ischnura hastata*, *Anax junius*, *Libellula luctuosa*, *L. pulchella*, *Pachydiplax longipennis*, *Pantala flavescens*, *P. hymenaea*, *Plathemis lydia*, *Sympetrum vicinum*, *Tramea lacerata*, *T. onusta*.
  8. Eastern (38 species). Species ranging widely but mostly east of the 100th meridian. *Calopteryx maculata*, *Lestes rectangularis*, *Amphiagrion saucium*, *Argia fumipennis*, *Chromagrion conditum*, *Enallagma antennatum*, *E. aspersum*, *E. exsulans*, *E. geminatum*, *E. signatum*, *Ischnura posita*, *I. verticalis*, *Aeshna verticalis*, *Anax longipes*, *Epiaeschna heros*, *Arigomphus cornutus*, *A. villosipes*, *Dromogomphus spinosus*, *Gomphus fraternus*, *G. vastus*, *Ophiogomphus rupinsulensis*, *Progomphus obscurus*, *Stylurus amnicola*, *S. notatus*, *Macromia taeniolata*, *Dorocordulia libera*, *Epitheca cynosura*, *E. princeps*, *Celithemis elisa*, *C. eponina*, *Erythemis simplicicollis*, *Leucorrhinia frigida*, *Libellula incesta*, *L. semifasciata*, *L. vibrans*, *Perithemis tenera*, *Sympetrum rubicundulum*, *Tramea carolina*.
  9. Widespread (6 species). Species with broad distributions in North America, from north to south and east to west, overlapping several of the other elements listed. These species range into boreal regions to varying degrees. *Lestes congener*, *L. disjunctus*, *L. dryas* (also Holarctic), *L. unguiculatus*, *Libellula quadrimaculata* (also Holarctic), *Sympetrum corruptum*.

**Table 1.** Annotated list of the Odonata species of Canadian grasslands. The term following the English name of each species is the faunal element (range type as defined above). An “H” indicates a Holarctic species. Notes on distribution are necessarily general; provincial abbreviations indicate grassland occurrence (species may also occur widely in other habitats in other provinces and territories) and an additional “(int)” indicates the species more or less occurs at the forest interface of the grassland biome (or at higher elevations above grassland, including Cypress Hills) and is primarily a forest species. Yukon inclusion is restricted to occurrences at two grassland sites in the Takhini Valley and northwest of Lake Laberge as noted in the text. Ontario representation is from Ojibway Prairie only. Many eastern species recorded in the forests of extreme eastern Manitoba but not at grassland sites are excluded, although they occur close by. Other notes are given where necessary. See text for more clarification.

#### SUBORDER ZYGOPTERA (DAMSELFLIES)

##### FAMILY CALOPTERYGIDAE (JEWELWINGS)

*Calopteryx aequabilis* Say (River Jewelwing). Transition. BC (int), AB (int), SK, MB.

*Calopteryx maculata* Beauvois (Ebony Jewelwing). Eastern. ON.

##### FAMILY LESTIDAE (SPREADWINGS)

*Archilestes grandis* (Rambur) (Great Spreadwing). Southern. ON.

*Lestes congener* Hagen (Spotted Spreadwing). Widespread. BC, AB, SK, MB, ON.

*Lestes disjunctus* Selys (Northern Spreadwing). Widespread. YT, AB, SK, MB.

*Lestes dryas* Kirby (Emerald Spreadwing). Widespread (H). YT, BC, AB, SK, MB, ON.

*Lestes forcipatus* Rambur (Sweetflag Spreadwing). Southern. BC (int), SK (int), MB, ON.

*Lestes rectangularis* Say (Slender Spreadwing). Eastern. MB, ON.

*Lestes unguiculatus* Hagen (Lyre-tipped Spreadwing). Widespread. BC, AB, SK, MB, ON).

##### FAMILY COENAGRIONIDAE POND DAMSELS

*Amphiagrion abbreviatum* (Selys) (Western Red Damselfly). Western. BC, AB, SK, MB?

*Amphiagrion saucium* (Burmeister) (Eastern Red Damselfly). Eastern. MB?

*Argia emma* Kennedy (Emma’s Dancer). Cordilleran. BC, AB.

*Argia fumipennis* Burmeister (Variable Dancer). Eastern. SK.

*Argia vivida* Hagen (Vivid Dancer). Cordilleran. BC.

*Coenagrion angulatum* Walker (Prairie Bluet). Great Plains. BC, AB, SK, MB.

*Coenagrion resolutum* (Hagen) (Taiga Bluet). Widespread Boreal. YT, BC, AB, SK, MB, ON.

*Coenagrion interrogatum* (Hagen) (Subarctic Bluet). Northern Boreal. AB (int), SK (int)

*Chromagrion conditum* (Selys) (Aurora Damselfly). Eastern. MB.

*Enallagma anna* Williamson (River Bluet). Western. AB, SK.

*Enallagma annexum* (Hagen) (Northern Bluet). Widespread Boreal. YT, BC, AB, SK, MB.

*Enallagma antennatum* (Say) (Rainbow Bluet). Eastern. SK.

*Enallagma aspersum* (Hagen) (Azure Bluet). Eastern. ON.

*Enallagma basidens* Calvert (Double-striped Bluet). Southern. ON.

*Enallagma boreale* Selys (Boreal Bluet). Widespread Boreal. YT, BC, AB, SK, MB, ON.

*Enallagma carunculatum* Morse (Tule Bluet). Southern. BC, AB, SK, MB, ON.

*Enallagma civile* (Hagen) (Familiar Bluet). Southern. AB, SK, MB, ON.

*Enallagma clausum* Morse (Alkali Bluet). Western. BC, AB, SK, MB.

*Enallagma ebrium* (Hagen) (Marsh Bluet). Transition. BC, AB, SK, MB, ON.

*Enallagma exsulans* (Hagen) (Stream Bluet). Eastern. ON.

*Enallagma geminatum* Kellicott (Skimming Bluet). Eastern. ON.

*Enallagma hageni* (Walsh) (Hagen’s Bluet). Transition. BC (int), AB, SK, MB, ON.

*Enallagma signatum* (Hagen) (Orange Bluet). Eastern. ON.

*Ischnura cervula* Selys (Pacific Forktail). Cordilleran. BC, AB, SK.

*Ischnura erratica* Calvert (Swift Forktail). Pacific Coastal. BC.

*Ischnura damula* Calvert (Plains Forktail). Western. AB, SK, MB.

*Ischnura hastata* (Say) (Citrine Forktail). Southern. ON.

*Ischnura perparva* Selys (Western Forktail). Western. BC, AB, SK, MB.

*Ischnura posita* (Hagen) (Fragile Forktail). Eastern. MB, ON.

*Ischnura verticalis* (Say) (Eastern Forktail). Eastern. AB, SK, MB, ON.

*Nehalennia irene* (Hagen) (Sedge Sprite). Transition. BC, AB (int), SK (int), MB, ON.

**SUBORDER ANISOPTERA (DRAGONFLIES)****FAMILY AESHNIDAE (DARNERS)**

- Aeshna canadensis* Walker (Canada Darner). Transition. BC, AB (int), SK (int), MB.  
*Aeshna constricta* Say (Lance-tipped Darner). Transition. BC, AB, SK, MB, ON.  
*Aeshna eremita* Scudder (Lake Darner). Widespread Boreal. YT, BC, AB (int), SK (int), MB  
*Aeshna interrupta* Walker (Variable Darner). Southern Boreal. YT, BC, AB, SK, MB.  
*Aeshna juncea* (Linnaeus) (Sedge Darner). Widespread Boreal (H). YT, BC, AB (int), SK (int), MB (int).  
*Aeshna palmata* Hagen (Paddle-tailed Darner). Cordilleran BC, AB, SK (int).  
*Aeshna septentrionalis* Walker (Azure Darner). Northern Boreal. YT.  
*Aeshna sitchensis* Hagen (Zigzag Darner) Widespread Boreal. AB (int), SK (int), MB (int).  
*Aeshna subarctica* Walker (Subarctic Darner). Widespread Boreal (H). BC (int).  
*Aeshna verticalis* Hagen (Green-striped Darner). Eastern. MB.  
*Aeshna umbrosa* Walker (Shadow Darner). Transition. BC, AB (int), SK (int), MB, ON.  
*Anax junius* (Drury) (Common Green Darner). Southern. BC, AB, SK, MB, ON.  
*Anax longipes* Hagen (Comet Darner). Eastern. ON.  
*Epiaeschna heros* (Fabricius) (Swamp Darner). Eastern. ON.  
*Rhionaeschna californica* (Calvert) (California Darner). Cordilleran. BC.  
*Rhionaeschna multicolor* (Hagen) (Blue-eyed Darner). Western. BC, AB (int).

**FAMILY GOMPHIDAE (CLUBTAILS)**

- Argomphus cornutus* (Tough) (Horned Clubtail). Eastern. MB.  
*Argomphus villosipes* (Selys) (Unicorn Clubtail). Eastern. ON.  
*Dromogomphus spinosus* Selys (Black-shouldered Spinyleg). Eastern. MB (int).  
*Gomphus externus* Hagen (Plains Clubtail). Great Plains. MB.  
*Gomphus graslinellus* Walsh (Pronghorn Clubtail). Transition. BC, AB (int), SK (int), MB, ON.  
*Gomphus fraternus* (Say) (Midland Clubtail). Eastern. MB.  
*Gomphus vastus* (Walsh) (Cobra Clubtail). Eastern. ON.  
*Ophiogomphus occidentis* Hagen (Sinuous Snaketail). Cordilleran. BC.  
*Ophiogomphus rupinsulensis* (Walsh) (Rusty Snaketail) Eastern. SK, MB.  
*Ophiogomphus severus* Hagen (Pale Snaketail) Western. BC, AB, SK.  
*Progomphus obscurus* (Rambur) (Common Sanddragon) Eastern. ON.  
*Stylurus amnicola* (Walsh) (Riverine Clubtail) Eastern. MB.  
*Stylurus intricatus* (Hagen) (Brimstone Clubtail) Great Plains. AB, SK.  
*Stylurus notatus* (Rambur) (Elusive Clubtail) Eastern. SK, MB, ON.  
*Stylurus olivaceus* (Selys) (Olive Clubtail) Cordilleran. BC.

**FAMILY CORDULEGASTRIDAE (SPIKETAILS)**

- Cordulegaster dorsalis* Hagen (Pacific Spiketail). Cordilleran. BC.

**FAMILY MACROMIIDAE (CRUISERS)**

- Macromia magnifica* McLachlan (Western River Cruiser) Cordilleran. BC.  
*Macromia taeniolata* Rambur (Royal River Cruiser) Eastern. ON.

**FAMILY CORDULIIDAE (EMERALDS)**

- Cordulia shurtleffii* Scudder (American Emerald) Widespread Boreal. BC, AB (int), SK(int), MB.  
*Dorocordulia libera* (Selys) (Racket-tailed Emerald). Eastern. MB.  
*Epitheca canis* (McLachlan) (Beaverpond Baskettail). Transition. SK (int), MB (int).  
*Epitheca cynosura* (Say) (Common Baskettail). Eastern. ON.  
*Epitheca princeps* Hagen (Prince Baskettail). Eastern. ON.  
*Epitheca spinigera* (Selys) (Spiny Baskettail). Transition. BC, AB (int), SK (int), MB.  
*Somatochlora ensigera* Martin (Plains Emerald). Great Plains. SK, MB.  
*Somatochlora franklini* (Selys) (Delicate Emerald). Widespread Boreal. AB (int), SK(int), MB(N).  
*Somatochlora hudsonica* (Hagen) (Hudsonian Emerald). Western Boreal. YT, BC (int), AB(int).  
*Somatochlora kennedyi* Walker (Kennedy's Emerald). Southern Boreal. MB.  
*Somatochlora minor* Calvert (Ocellated Emerald). Southern Boreal. AB (int), MB.  
*Somatochlora semicircularis* (Selys) (Mountain Emerald). Cordilleran. BC, AB (int).  
*Somatochlora walshii* (Scudder) (Brush-tipped Emerald). Southern Boreal. MB.

**FAMILY LIBELLULIDAE (SKIMMERS)**

- Celithemis elisa* (Hagen) (Calico Pennant). Eastern. ON.  
*Celithemis eponina* (Drury) (Halloween Pennant). Eastern. ON.  
*Erythemis collocata* (Hagen) (Western Pondhawk). Western. BC.  
*Erythemis simplicicollis* (Say) (Eastern Pondhawk). Eastern. ON.  
*Ladona julia* (Uhler) (Chalk-fronted Corporal). Transition. MB (int).  
*Leucorrhinia borealis* Hagen (Boreal Whiteface). Western Boreal. YT, BC, AB (int), SK (int), MB.  
*Leucorrhinia frigida* Hagen (Frosted Whiteface). Eastern. MB (int), ON.  
*Leucorrhinia glacialis* Hagen (Crimson-ringed Whiteface). Transition. BC (int), AB (int), MB (int).  
*Leucorrhinia hudsonica* (Selys) (Hudsonian Whiteface). Widespread Boreal. BC, AB (int), SK (int), MB.  
*Leucorrhinia intacta* (Hagen) (Dot-tailed Whiteface). Transition. BC, AB (int), SK, MB, ON.  
*Leucorrhinia proxima* Calvert (Belted Whiteface). Southern Boreal. BC, AB (int), SK (int), MB, ON.  
*Libellula forensis* Hagen (Eight-spotted Skimmer). Cordilleran. BC.  
*Libellula incesta* Hagen (Slaty Skimmer). Eastern. ON.  
*Libellula luctuosa* Burmeister (Widow Skimmer). Southern. MB, ON.  
*Libellula pulchella* Drury (Twelve-spotted Skimmer). Southern. BC, AB, MB, ON.  
*Libellula quadrimaculata* Linnaeus (Four-spotted Skimmer). Widespread (H). YT, BC, AB, SK, MB, ON.  
*Libellula semifasciata* Burmeister (Painted Skimmer). Eastern. ON.  
*Libellula vibrans* Fabricius (Great Blue Skimmer). Eastern. ON.  
*Pachydiplax longipennis* (Burmeister) (Blue Dasher). Southern. BC, ON.  
*Pantala flavescens* (Fabricius) (Wandering Glider). Southern. AB (wanderer), MB (wanderer), ON.  
*Pantala hymenaea* (Say) (Spot-winged Glider). Southern. BC (wanderer), MB (wanderer), ON.  
*Perithemis tenera* (Say) (Eastern Amberwing). Eastern. ON.  
*Plathemis lydia* (Drury) (Common Whitetail). Southern. BC, MB, ON.  
*Sympetrum corruptum* (Hagen) (Variegated Meadowhawk). Widespread. BC, AB, SK, MB.  
*Sympetrum costiferum* (Hagen) (Saffron-winged Meadowhawk). Transition. BC, AB, SK, MB.  
*Sympetrum danae* (Sulzer) (Black Meadowhawk). Widespread Boreal (H). YT, BC, AB, SK, MB.  
*Sympetrum illotum* (Hagen) (Cardinal Meadowhawk). Cordilleran. BC.  
*Sympetrum internum* Montgomery (Cherry-faced Meadowhawk). Transition. YT, BC, AB, SK, MB.  
*Sympetrum madidum* (Hagen) (Red-veined Meadowhawk). Western. BC, AB, SK, MB.  
*Sympetrum obtrusum* (Hagen) (White-faced Meadowhawk). Transition. BC, AB (int), SK (int), MB, ON.  
*Sympetrum pallipes* (Hagen) (Striped Meadowhawk). Western. BC, AB, SK (int).  
*Sympetrum rubicundulum* (Say) (Ruby Meadowhawk). Eastern. ON.  
*Sympetrum semicinctum* (Say) (Band-winged Meadowhawk). Transition. BC, AB, SK, MB, ON.  
*Sympetrum vicinum* (Hagen) (Autumn Meadowhawk). Southern. BC, ON.  
*Tramea carolina* (Linnaeus) (Carolina Saddlebags). Eastern. ON.  
*Tramea lacerata* Hagen (Black Saddlebags). Southern. BC, ON.  
*Tramea onusta* Hagen (Red Saddlebags). Southern. ON.

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## Chapter 9

# Orthoptera of the Grasslands of British Columbia and the Yukon Territory

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**Abstract.** Of all the habitats available in British Columbia and the Yukon Territory, grasslands support by far the greatest diversity, 87 species, of Orthoptera. Although most of these species have broad distributions in western North America, 23 are not found in other provinces or territories and one is endemic to Yukon. The rarest and most restricted species are those that have their Canadian ranges limited to the arid shrub-steppe in southern British Columbia. Although most Orthoptera in British Columbia and Yukon grasslands are phytophagous, few cause economic damage to cultivated crops. The Orthoptera of British Columbia and Yukon are relatively well studied thanks to the work of a series of researchers over the last century. However, basic inventory and ecological study is needed throughout the region. Since 2005, Orthoptera in British Columbia and Yukon have received renewed attention in field collections and basic research.

**Résumé.** De tous les habitats disponibles en Colombie-Britannique et au Yukon, ceux des prairies présentent de loin la plus grande diversité d'orthoptères, soit 87 espèces. La plupart de ces espèces sont largement répandues dans l'ouest de l'Amérique du Nord, mais 23 d'entre elles sont inconnues dans les autres provinces et territoires, et une est endémique du Yukon. Les espèces les plus rares et les plus restreintes sont celles dont l'aire de répartition canadienne se limite à la steppe arbustive aride du sud de la Colombie-Britannique. Bien que la plupart des orthoptères des prairies de la Colombie-Britannique et du Yukon soient phytophages, rares sont ceux qui causent des dommages économiques aux cultures. Ces orthoptères sont relativement bien connus grâce au travail accompli par plusieurs chercheurs au cours du dernier siècle. Cependant, il reste nécessaire de procéder à des inventaires de base et à des études écologiques dans l'ensemble de cette région. Depuis 2005, les orthoptères de la Colombie-Britannique et du Yukon retiennent à nouveau l'attention des chercheurs qui effectuent des collectes sur le terrain et des travaux de recherche fondamentale.

### Introduction

The Orthoptera of British Columbia and Yukon comprise 108 species, two of which are represented by two subspecies (Vickery 1997; Miskelly 2012). These insects occur in virtually every habitat available in the region, including arctic tundra, mountain tops, wetlands, and forests of all descriptions. However, by far the greatest number of species can be found in grasslands. Fully 80% (87 species) of the regional orthopteran fauna occurs in grasslands. This includes generalist species that are found in a variety of open habitats, species more common in alpine areas or wetlands, and species that can be considered grassland obligates.

The first major contributions to the study of Orthoptera in British Columbia and Yukon came from E.R. Buckell. Buckell worked for the Dominion Entomological Branch, Canada Department of Agriculture, in Vernon and Kamloops from 1920 to 1949. During this time,

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he collected Orthoptera extensively throughout British Columbia and published many new species records, distribution notes, and other observations (e.g., Buckell 1925, 1929, 1930, 1945). Buckell's work provided the first basis for checklists of the Orthoptera of British Columbia and established a foundation for future researchers. A number of species collected by Buckell in the 1930s were not collected again in British Columbia until recent years. A few species are yet to be found again. Following the work of Buckell, the next major contributions to the study of the Orthoptera of British Columbia and Yukon were provided by V.R. Vickery. Vickery was an extension entomologist for the province of Nova Scotia from 1949 to 1961. From 1961 to 1986, he was a professor at McGill University and curator of the Lyman Entomological Museum, which contains the largest collection of Orthoptera in Canada. During his time in Montreal, Vickery collected widely and published on the Orthoptera across Canada (e.g., Vickery 1961, 1967; Vickery and Kevan 1967; Vickery and Nagy 1973). Although he conducted little field work in British Columbia or Yukon, Vickery made important contributions there, exemplified by the descriptions of two new species of Orthoptera that occur in Yukon grasslands, *Brunneria yukonensis* and *Xanthippus brooksi* (Vickery 1967, 1969). Most important, Vickery (together with D.K.McE. Kevan) authored an Agriculture Canada guide to the orthopteroid insects of Canada (Vickery and Kevan 1985). This monograph greatly facilitated the study of Orthoptera in Canada, for the first time providing a single source for the identification of all taxa and establishing a first checklist of the Orthoptera of Canada and of each of the provinces and territories. The next research of relevance to the Orthoptera of British Columbian grasslands began when G.G.E. Scudder initiated a research project surveying insects in the south Okanagan in the 1990s. More than 6,000 Orthoptera specimens were collected in pitfall traps over the course of 10 years (Royal BC Museum data), representing the most intensive Orthoptera sampling ever conducted in British Columbia. This study provided the first precise location information for many rare species that were previously known only from vague museum labels.

Since 2005, Orthoptera have increasingly been targeted in the field collections of the Royal BC Museum and have been collected in eight of British Columbia's nine terrestrial ecoregions (as listed in Demarchi 2011) and 14 of 16 biogeoclimatic zones (as listed in British Columbia Forest Service 2012). These collections and museum research by staff and volunteers at the Royal BC Museum and the BC Ministry of Environment have added several new species to the known fauna of British Columbia, corrected misidentifications of earlier specimens, accrued a great deal of new distributional data, and produced an updated checklist for British Columbia (Miskelly 2012). At the same time, workers in Yukon, led by NatureServe Yukon, have collected throughout the territory and produced a great deal of new distributional and ecological data. The Orthoptera of the grasslands of British Columbia and Yukon are presently being inventoried and researched more actively than at any time since the work of Buckell. The conservation status of Orthoptera has recently been ranked nationally and within British Columbia and Yukon (NatureServe 2012). Knowledge of the group is more complete than ever before, but significant gaps remain (see Research Priorities below).

### **Orthoptera of the Grasslands of British Columbia and Yukon**

The 87 Orthoptera species known from the grasslands of British Columbia and Yukon (Table 1) are spread among seven families and 14 subfamilies, though only two of these families and four subfamilies occur in Yukon. Most of the species diversity is found in the family Acrididae, with 57 species in British Columbia and 11 species in Yukon.

Feeding patterns in Orthoptera range from primarily phytophagous to including variable amounts of dead or live animal material in the diet. The majority of grassland Orthoptera species in British Columbia and Yukon are primarily phytophagous. A few species of generalist herbivores have adapted to agricultural habitats, where they are considered pests. The most notorious of these are *Melanoplus bivittatus*, *M. sanguinipes*, and *Camnula pellucida* (Buckell 1945; Vickery and Kevan 1985). A common belief is that all grasshoppers are pests, and most species occurring in Canada are described as occasional pests even in the absence of supporting evidence (Vickery and Kevan 1985). However, in this region at least, the diversity of Orthoptera in cultivated areas is very low and most species are rarely encountered outside of natural habitats. Grasshoppers generally do not cause economic damage to crops or range in British Columbia except when drought conditions have already stressed plants or reduced range productivity (British Columbia Ministry of Agriculture 2009). Many of the phytophagous Orthoptera feed preferentially on a select group of plants, such as graminoids, forbs, or shrubs (Vickery and Kevan 1985). Some species have narrow host-plant specificity. For example, *Melanoplus cinereus* feeds almost entirely on the shrub *Artemisia tridentata* Nuttall 1841, and *Hesperotettix viridis* feeds mainly on a small suite of species in the family Asteraceae (Sheldon and Rogers 1976). The most innocuous herbivores are the pygmy grasshoppers of the family Tetrigidae, which appear to feed mostly on algae that they scrape off soil particles (Vickery and Kevan 1985).

Many species of Orthoptera are omnivorous to a certain degree. The camel crickets of the family Rhaphidophoridae are scavengers of both plant and animal foods (JM, pers. obs.). Most members of the families Prophalangopsidae, Stenopelmatidae, and Tettigoniidae capture live prey in addition to feeding on plant material (Vickery and Kevan 1985; JM, pers. obs.). None of the Orthoptera of the grasslands of British Columbia and Yukon are primarily predaceous.

Recent collection data have also provided information on distribution patterns of British Columbia and Yukon Orthoptera. Forty-eight of the 87 species recorded in British Columbia and Yukon grasslands are found primarily or exclusively in these grasslands (Table 1) within this region. These species do not form a cohesive ecological group, but rather occur across different types of grasslands and in different parts of the region. The largest group within these primarily grassland species comprises those species associated with the most arid grasslands in British Columbia (Table 2). These shrub-dominated grasslands occur only in the hottest river valleys of the southern third of the province (Nicholson *et al.* 1991). Because of the uniqueness of this habitat, many of the species in these arid lands are highly restricted in both range and habitat. This group contains some of our rarest species, such as *Oedaleonotus enigma* and *Dissosteira spurcata*. Both species have been collected only a few times in British Columbia and only in the southern Okanagan Valley.

Species that are not restricted to grasslands are often associated with more widespread habitats that overlap with grasslands (Table 3). Wetlands of various descriptions support a number of species of Orthoptera, with the species assemblage changing somewhat when these wetlands occur in grassland settings. For example, all three species of *Tetrix* (Tetrigidae) in British Columbia are associated with sparsely vegetated mud or sand around wetlands. None of these are restricted to grassland settings. Riparian thickets support several species that are likewise not restricted to grasslands, such as *Oecanthus fultoni*, *O. rileyi*, and *Scudderella furcata*. Wet depressions dominated by grasses or sedges provide habitat for several species that are largely restricted to grasslands in British Columbia, such



**Table 1.** Orthoptera of the grasslands of British Columbia and Yukon. Bolded species are found only in grasslands within this region.

Family	Subfamily	Species
Stenopelmatidae	Stenopelmatinae	<b><i>Stenopelmatus fuscus</i> Haldeman 1852</b>
Rhaphidophoridae	Ceuthophilinae	<i>Ceuthophilus agassizii</i> (Scudder 1861) <i>Ceuthophilus alpinus</i> Scudder 1894 <i>Ceuthophilus vicinus</i> Hubbell 1936 <i>Pristoceuthophilus cercalis</i> Caudell 1916 <i>Pristoceuthophilus pacificus</i> (Thomas 1872)
Prophalangopsidae	Cyphoderrinae	<i>Cyphoderris buckelli</i> Hebard 1934
Tettigoniidae	Tettigoniinae	<b><i>Anabrus longipes</i> Caudell 1907</b> <b><i>Anabrus simplex</i> Haldeman 1852</b> <b><i>Apote robusta</i> Caudell 1907</b> <b><i>Peranabrus scabricollis</i> (Thomas 1872)</b> <b><i>Steiroxys</i> undescribed</b> <i>Steiroxys cf. trilineata</i> (Thomas 1870)
	Conocephalinae	<i>Conocephalus fasciatus</i> (DeGeer 1773) <i>Orchelimum gladiator</i> Bruner 1891
	Phaneropterinae	<i>Scudderia furcata</i> Bruner von Wattenwyl 1878
Gryllidae	Nemobiinae	<i>Allonemobius allardi</i> (Alexander and Thomas 1959) <b><i>Allonemobius fasciatus</i> (DeGeer 1773)</b>
	Gryllinae	<i>Gryllus pennsylvanicus</i> Burmeister 1838 <i>Gryllus veletis</i> (Alexander and Bigelow 1960)
	Oecanthinae	<b><i>Oecanthus argentinus</i> Saussure 1874</b> <b><i>Oecanthus californicus</i> Saussure 1874</b> <i>Oecanthus fultoni</i> Walker 1962 <b><i>Oecanthus quadripunctatus</i> Beutenmuller 1894</b> <i>Oecanthus rileyi</i> Baker 1905
Acrididae	Melanoplinae	<i>Asemoplus montanus</i> (Bruner 1885) <i>Bradynotes obesa</i> (Thomas 1872) <i>Buckellacris chilcotinae</i> (Hebard 1922) <b><i>Hesperotettix viridis</i> (Thomas 1872)</b> <i>Melanoplus alpinus</i> Scudder 1897 <i>Melanoplus bivittatus</i> (Say 1825) <i>Melanoplus borealis</i> (Fieber 1853) <i>Melanoplus bruneri</i> Scudder 1897 <b><i>Melanoplus cinereus</i> Scudder 1878</b> <b><i>Melanoplus confusus</i> Scudder 1897</b> <b><i>Melanoplus dawsoni</i> (Scudder 1875)</b> <i>Melanoplus femurrubrum</i> (DeGeer 1773) <b><i>Melanoplus foedus</i> Scudder 1878</b> <b><i>Melanoplus infantilis</i> Scudder 1878</b> <b><i>Melanoplus kennicotti</i> Scudder 1878</b> <b><i>Melanoplus occidentalis</i> (Thomas 1872)</b> <b><i>Melanoplus packardii</i> Scudder 1878</b>

		<i>Melanoplus rugglesi</i> Gurney 1949
		<i>Melanoplus sanguinipes</i> (Fabricius 1798)
		<i>Melanoplus washingtonius</i> (Bruner 1885)
		<b><i>Oedaleonotus enigma</i> (Scudder 1876)</b>
		<b><i>Phaetaliotes nebrascensis</i> (Thomas 1872)</b>
Oedipodinae		<i>Arphia conspersa</i> Scudder 1875
		<b><i>Arphia pseudonietana</i> (Thomas 1870)</b>
		<i>Camnula pellucida</i> (Scudder 1862)
		<b><i>Chortophaga viridifasciata</i> (DeGeer 1773)</b>
		<b><i>Circotettix carlinianus</i> (Thomas 1870)</b>
		<b><i>Circotettix rabula</i> Rehn and Hebard 1906</b>
		<b><i>Circotettix undulatus</i> (Thomas 1872)</b>
		<b><i>Conozoa sulcifrons</i> (Scudder 1876)</b>
		<b><i>Cratypedes lateritius</i> (Saussure 1884)</b>
		<b><i>Cratypedes neglectus</i> (Thomas 1870)</b>
		<i>Dissosteira carolina</i> (Linnaeus 1758)
		<b><i>Dissosteira spurcata</i> Saussure 1884</b>
		<b><i>Metator nevadensis</i> (Bruner 1905)</b>
		<b><i>Pardalophora apiculata</i> (Harris 1865)</b>
		<b><i>Spharagemon campestris</i> (McNeill 1901)</b>
		<b><i>Spharagemon equale</i> (Say 1825)</b>
		<i>Stethophyma gracile</i> (Scudder 1862)
		<b><i>Trachyrhachys kiowa</i> (Thomas 1872)</b>
		<b><i>Trimerotropis fontana</i> Thomas 1876</b>
		<b><i>Trimerotropis gracilis</i> (Thomas 1872)</b>
		<i>Trimerotropis pallidipennis</i> (Burmeister 1838)
		<i>Trimerotropis verruculata suffusa</i> Scudder 1876
		<i>Trimerotropis verruculata verruculata</i> (Kirby 1837)
		<i>Xanthippus brooksi</i> Vickery 1967
		<b><i>Xanthippus corallipes</i> (Haldeman 1852)</b>
Gomphocerinae		<i>Aeropedellus clavatus</i> (Thomas 1873)
		<b><i>Ageneotettix deorum</i> (Scudder 1876)</b>
		<b><i>Amphitornus coloradus</i> (Thomas 1873)</b>
		<b><i>Aulocara ellioti</i> (Thomas 1870)</b>
		<b><i>Brunneria brunnea</i> (Thomas 1871)</b>
		<b><i>Brunneria yukonensis</i> Vickery 1969</b>
		<i>Chloealtis abdominalis</i> (Thomas 1873)
		<i>Chloealtis conspersa</i> (Harris 1841)
		<b><i>Orphulella pelidna</i> (Burmeister 1838)</b>
		<i>Pseudochorthippus curtipennis</i> (Harris 1835)
		<b><i>Pseudopomala brachyptera</i> (Scudder 1862)</b>
		<b><i>Psoloessa delicatula</i> (Scudder 1876)</b>
Tetrigidae	Tetriginae	<i>Tetrix brunnerii</i> (Bolivar 1887)
		<i>Tetrix ornata</i> (Say 1834)
		<i>Tetrix subulata</i> (Linnaeus 1758)

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**Table 2.** Orthopteran species restricted to arid shrub-steppe within the British Columbia portion of their range.

Family	Subfamily	Species
Acrididae	Melanoplinae	<i>Hesperotettix viridis</i> (Thomas)
		<i>Melanoplus cinereus</i> (Scudder)
		<i>Melanoplus rugglesi</i> Gurney
		<i>Oedaleonotus enigma</i> (Scudder)
		<i>Phaetaliotes nebrascensis</i> (Thomas)
	Oedipodinae	<i>Dissosteira spurcata</i> Saussure
		<i>Trimerotropis gracilis</i> (Thomas)
Tettigoniidae	Tettigoniinae	<i>Apote robusta</i> Caudell
Stenopelmatidae	Stenopelmatinae	<i>Stenopelmatus fuscus</i> Haldeman

as *Orphulella pelidna* and *Allonemobius fasciatus*, but also support species that occur in a variety of moist, grassy habitats, including two species of meadow katydid, *Conocephalus fasciatus* and *Orchelimum gladiator*.

Mountain meadows support an orthopteran fauna that has a degree of overlap with grasslands. Species that occur from low-elevation grasslands all the way to alpine tundra include *Asemoplus montanus*, *Buckellacris chilcotinae*, *Melanoplus bruneri*, and *M. washingtonius*. Other species are absent from lower grasslands, but extend from the upper-elevation grasslands into subalpine or alpine regions. These include *Melanoplus alpinus* and *Steiroxys cf. trilineata*. A few species seem to be almost restricted to upper-elevation grasslands in British Columbia and are rarely found in either lower grasslands or higher mountain meadows. These include *Brunneria brunnea* (Fig. 1), *Pardalophora apiculata*, and *Peranabrus scabricollis*.

Some species of Orthoptera that are found in grasslands are associated more usually with wooded habitats. The camel crickets of the genera *Ceuthophilus* and *Pristoceuthophilus* are often found in heavily forested settings, but several species have also been found in grasslands, such as *Ceuthophilus vicinus*, *Pristoceuthophilus cercalis*, and *P. pacificus*. Open woodlands and forest edges support a diverse assemblage of orthopterans that overlaps with the grassland fauna. A small suite of species is found mainly in dry, open woodlands associated with grasslands. These species are more common in these semi-treed sites than they are in either open grassland or closed forest. Examples include *Cyphoderris buckelli*, *Chloealtis abdominalis*, and *C. conspersa*.

### Biogeographical Aspects

The biogeographical affinities of most orthopterans of British Columbia and Yukon were listed by Scudder and Vickery (1998). The majority of species are described as Cordilleran, Nearctic (excluding Beringia), or Western Nearctic (excluding Beringia). Thus, most of the fauna is made up of species that are relatively widespread, at least in western North America. Most Orthoptera species found in British Columbia and Yukon reach their northern limit in this region. A few range little, or not at all, to the south, whereas many have much larger ranges with the borders of the United States. Of the Orthoptera found in the grasslands of British Columbia and Yukon, 23 species are not found in other provinces or territories. Of

**Table 3.** General habitat associations of species found partially in grasslands of British Columbia and Yukon.

Species	Wetland/ Riparian	Woodland/ Forest	Montane/ Alpine	Disturbed/ Generalist	Arctic Tundra
<i>Ceuthophilus agassizii</i>		X			
<i>Ceuthophilus alpinus</i>		X			
<i>Ceuthophilus vicinus</i>		X			
<i>Pristoceuthophilus cercalis</i>		X			
<i>Pristoceuthophilus pacificus</i>		X			
<i>Cyphoderris buckelli</i>		X			
<i>Steiroxys cf. trilineata</i>			X		
<i>Conocephalus fasciatus</i>	X				
<i>Orchelimum gladiator</i>	X				
<i>Scudderia furcata</i>	X				
<i>Allonemobius allardi</i>	X				
<i>Gryllus pennsylvanicus</i>				X	
<i>Gryllus veletis</i>				X	
<i>Oecanthus fultoni</i>	X				
<i>Oecanthus rileyi</i>	X				
<i>Asemoplus montanus</i>			X		
<i>Bradynotes obesa</i>			X		
<i>Buckellacris chilcotinae</i>			X		
<i>Melanoplus alpinus</i>			X		
<i>Melanoplus bivittatus</i>	X				
<i>Melanoplus borealis</i>			X		
<i>Melanoplus bruneri</i>			X		
<i>Melanoplus femurrubrum</i>				X	
<i>Melanoplus sanguinipes</i>				X	
<i>Melanoplus washingtonius</i>			X		
<i>Camnula pellucida</i>				X	
<i>Dissosteira carolina</i>				X	
<i>Stethophyma gracile</i>	X				
<i>Trimerotropis pallidipennis</i>				X	
<i>Trimerotropis verruculata suffusa</i>		X			
<i>Trimerotropis verruculata verruculata</i>		X			
<i>Xanthippus brooksi</i>					X
<i>Aeropedellus clavatus</i>			X		
<i>Chloealtis abdominalis</i>		X			
<i>Chloealtis conspersa</i>		X			
<i>Pseudochorthippus curtipennis</i>				X	
<i>Tetrix brunnerii</i>	X				
<i>Tetrix ornata</i>	X				
<i>Tetrix subulata</i>	X				

these, 22 have their Canadian distribution limited to British Columbia, and one (*Brunneria yukonensis*) is endemic to Yukon. None of those species that have their Canadian range limited to British Columbia are endemic. Many are typical of the arid lands of the Great Basin, such as *Melanoplus rugglesi*, *Dissosteira spurcata*, and *Metator nevadensis*.

A large degree of overlap occurs between the orthopteran faunas of British Columbia and Yukon grasslands and those of the Canadian prairie grasslands. Of the 87 species recorded from British Columbia and Yukon grasslands, at least 50 also occur in the prairies (Vickery and Kevan 1985). The Orthoptera of Canadian prairie grasslands are slightly more diverse, with approximately 100 species recorded (Vickery and Kevan 1985). The similarity in the species richness of the two regions is remarkable, given the comparatively small area that grasslands occupy in British Columbia and Yukon. Several species that occur in British Columbia are more typical of prairie grasslands and range into British Columbia only on the periphery of a range that is more extensive east of the Rocky Mountains. These species may occur in British Columbia in the East Kootenays or the Peace River region (Vickery and Kevan 1985; Royal British Columbia Museum data). Examples include *Anabrus simplex*, *Melanoplus packardii*, and *Chortophaga viridifasciata*. Two other species have a similar distribution pattern, but also extend west over the northern edge of the Rocky Mountains into the southern Yukon and northwestern British Columbia. *Arphia conspersa* and *Melanoplus kennicotti* (Fig. 2) follow this pattern. Both have restricted ranges in British Columbia grasslands, but are characteristic members of the fauna of Yukon grasslands (Royal BC Museum data). Two species found in Yukon grasslands have Beringian distributions and are not known to occur south of the territory (Vickery 1997). *Brunneria yukonensis* has been recorded only in the grasslands of the southern Yukon. *Xanthippus brooksi* has been recorded through much of Yukon and western Northwest Territories in a variety of habitats, including grassland, dry tundra, and sparsely vegetated south-facing slopes (Vickery 1997; Royal BC Museum data).

### Research Priorities

Although the legacy of previous researchers has provided an important base from which to build knowledge on the Orthoptera of British Columbia and Yukon, much remains to be learned about the ecology, habits, and distribution of all species. Most historic specimens are labelled with only vague location information, and these should be refined through ongoing fieldwork. Basic inventory data are needed throughout the region. In particular, additional species are expected to occur in northwestern British Columbia, the Kootenays, and the Peace Region (Miskelly 2012). Even in the most heavily sampled areas (i.e., British Columbia's Lower Mainland and Okanagan Valley), significant new records are obtained regularly and several historic records have not been replicated. Orthoptera are known for extreme fluctuations in abundance from year to year, with slight changes in weather patterns causing great changes in the relative abundance of different species (Mulkern 1980). Regular monitoring in well-studied areas and repeated sampling in poorly studied areas are important for the documentation of these fluctuations and detection of overlooked species.

Several species that occur in grasslands within British Columbia and Yukon have been identified as potentially rare (Scudder 1994) or ranked as "at risk" (NatureServe 2012). It is important that more field work be devoted to these species to describe their habitat requirements, assess whether they are truly rare, and determine whether they are in need of conservation measures. The status of many species is likely to change as more complete information is obtained about their distributions and habitat associations.



**Fig. 1.** *Brunneria brunnea* (Thomas) is found mainly in upper-elevation grasslands in southern British Columbia. A congener is endemic to grasslands of the southern Yukon. Photo by the author.



**Fig. 2.** *Melanoplus kennicotti* Scudder is found in the grasslands of northeastern British Columbia and southwestern Yukon. Photo by the author.

Although the Orthoptera of Canada are relatively well resolved taxonomically, a few areas of uncertainty exist where revisions are needed, particularly in the family Tettigoniidae. The genus *Steiroxys*, in particular, has baffled taxonomists for more than a century (Caudell 1907; Rentz and Birchim 1968). At present, three species are believed to occur in British Columbia, but none can be identified to species with certainty and one is likely undescribed (Miskelly 2012). Other taxonomic problems in the family relate to possible synonymies within the genera *Apote* and *Anabrus*.

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## Chapter 10

# The Heteroptera (Hemiptera) of the Prairies Ecozone of Canada

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**Abstract.** Five hundred eighty-two Heteroptera taxa are listed for the Prairies Ecozone in Canada. This number represents 40.7% of the taxa reported for Canada and 79.2% of the taxa recorded from the three Prairie Provinces. The dominant components are species with a Nearctic distribution, excluding Beringia. However, the Great Basin-Prairies element is the most distinctive.

### Introduction

Maw *et al.* (2000) listed the Heteroptera recorded from the three Prairie Provinces in Canada. Brooks and Kelton (1967) considered the aquatic and semi-aquatic Heteroptera of Alberta, Saskatchewan, and Manitoba, while Scudder *et al.* (2010) documented the aquatic Hemiptera recorded from the prairie grasslands and parkland. In the terrestrial Heteroptera, Kelton (1980) treated the plant bugs of the Prairie Provinces, and subsequent individual taxonomic papers have advanced the knowledge of many of the genera. Matsuda (1977) included prairie species in his consideration for the Aradidae of Canada, and Kelton (1978) did likewise for the Anthocoridae (*s.l.*).

The only detailed annotated provincial list of Heteroptera available is that of Strickland (1953) for the province of Alberta, but this is now somewhat out of date. There are no published annotated lists for the provinces of Manitoba or Saskatchewan.

### Data Sources

All species of Heteroptera listed from the provinces of Alberta, Manitoba, and Saskatchewan in Maw *et al.* (2000) were examined, as well as additional species listed from these provinces since 1999, and detailed distributional data for all of these species were assembled (Tables 1–3). These data were obtained from published papers and from an examination of specimens in the various collections across Canada, with special emphasis placed on specimens in the Canadian National Collection of Insects, Arachnids, and Nematodes in Ottawa. All species with specimen localities within the Prairies Ecozone as defined by the Ecological Stratification Working Group (1996) are included in this chapter. Species recorded from the Cypress Upland Ecoregion are included (Table 1, Geographical Pattern No. 8), although this is an outlier of the montane vegetation zone that occurs on the lower slopes of the Rocky

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Mountains. However, it is included in the Prairies Ecozone by the Ecological Stratification Working Group (1996). In the following text, only relevant references to taxonomic papers published since 1999 are included. Maw *et al.* (2000) provide references to the rest of the relevant taxonomic literature. The systematic arrangement follows Maw *et al.* (2000), except that the Ischnorhynchidae and Orsillidae are recognized following Sweet (2000).

## Heteroptera of the Prairies Ecozone

### *General Biology*

All of the aquatic and semi-aquatic Heteroptera are predators. All have species adapted to living either in or on water and some are especially adapted to living in extremely saline inland waters (Scudder 1976).

**Table 1.** Geographical patterns recognized in the Heteroptera of the Prairies Ecozone and number of taxa in each.

Geographical Pattern	Comments	Number of Taxa
1. Nearctic, including Beringia	Species with a wide Nearctic distribution and which also occur in the unglaciated areas of northwestern North America, as well as the Western Cordillera	56
2. Nearctic, excluding Beringia	Species with a wide Nearctic distribution, including the Western Cordillera, but which are absent from the unglaciated areas of northwestern North America	205
3. Nearctic, excluding the Western Cordillera and Beringia	Species with a wide Nearctic distribution, but which are absent from both the Western Cordillera and unglaciated areas of northwestern North America	52
4. Western Nearctic, including Beringia	Species that are usually confined to western North America, west of about the 100 <sup>th</sup> meridian, and which also occur in the unglaciated areas of northwestern North America	14
5. Western Nearctic, excluding Beringia	Species that are usually confined to western North America, west of about the 100 <sup>th</sup> meridian, and which are absent from the unglaciated areas of northwestern North America	100
6. Eastern Nearctic	Species that are usually confined to the eastern part of North America, east of about the 100 <sup>th</sup> meridian	36
7. Western Cordilleran, including Beringia	Species that in North America are usually confined to the mountainous Cordilleran area in the west, sometimes including the Cypress Uplands, and which are also present in the unglaciated areas of northwestern North America	1
8. Western Cordilleran, excluding Beringia	Species that in North America are usually confined to the mountainous Cordilleran area in the west, sometimes including the Cypress Uplands, and which are absent in the unglaciated areas of northwestern North America	10
9. Great Plains-Prairies	Species confined to the Great Plains and/or Prairies Ecozone in Canada	23
10. Nearctic-Neotropical	Species widely distributed in North America and with a range that extends well into the Neotropical region	22
11. Holarctic	Species widely distributed in both the Palearctic and Nearctic	51
12. Cosmopolitan	Species widely distributed in the world, occurring in several zoogeographical realms	2
13. Introduced	Species not native to North America, having been accidentally or intentionally introduced	10

Most terrestrial Heteroptera are phytophagous, and some are pests of crops (Beirne 1972). However, some terrestrial taxa, such as the ambush bugs (Phymatidae), assassin bugs (Reduviidae), damsel bugs (Nabidae), minute pirate bugs (Anthocoridae, *s.l.*), some plant bugs (Miridae), and some stink bugs (Pentatomidae) are predaceous. Even some normally phytophagous species are at times predaceous (Wheeler 2001). As a result, a number of Heteroptera species are of economic importance (Schaefer and Panizzi 2000).

### ***Systematic Review***

To date, 582 taxa of Heteroptera have been recorded from the Prairies Ecozone (Table 3). These represent 79.2% of the 735 taxa so far reported from the three Prairie Provinces. In the Prairies Ecozone, 51 (8.8%) of the species of Heteroptera are aquatic, 14 (2.4%) are semi-aquatic, and the remaining 517 (88.8%) taxa are terrestrial.

### ***Infraorder Nepomorpha***

This infraorder includes five aquatic families. The giant water bug family, Belostomatidae, is represented by three species. *Lethocerus americanus* (Leidy) is widely distributed, but both *Belostoma flumineum* Say and *L. griseus* (Say) occur only in the southeastern part of Manitoba. The single species of water scorpion, *Ranatra fusca* Palisot (Nepidae), has long been known from southeastern Manitoba (Brooks and Kelton 1967), but has recently been reported from both Alberta and Saskatchewan (Parker and Phillips 2007; Farris and Gotceitas 2011). Farris and Gotceitas (2011) report the species in the Spruce Coulee Reservoir in the Cypress Hills Interprovincial Park in Alberta. The water boatmen (Corixidae) are represented by 10 genera and 38 species. Most of these are widely distributed and many have colonized man-made water bodies, but *Cenocorixa expleta* (Uhler) and *Dasycorixa rawsoni* Hungerford seem to be confined to saline lakes and ponds (Scudder *et al.* 2010). Two genera and eight species of backswimmers (Notonectidae) are recorded from the ecozone, with *Buenoa margaritacea* Torre Bueno, *Notonecta insulata* Kirby, and *N. irrorata* Uhler occurring only in the southeastern part of Manitoba. The single species of pygmy backswimmer (Pleidae), *Neoplea striola* (Fieber), is common in the southeastern part of Manitoba and was recently reported from Saskatchewan (Parker and Phillips 2007).

### ***Infraorder Gerromorpha***

This infraorder includes five semi-aquatic families of Heteroptera. There is just one species of water treader (Mesoveliidae), *Mesovelia mulsanti* White, which is widely distributed. The two species of velvet water bugs (Hebridae), *Hebrus burmeisteri* Lethierry & Severin and *Merragata hebroides* White, also appear to be widely distributed. The single marsh treader (Hydrometridae), *Hydrometra martini* Kirkaldy, occurs widely in Manitoba (Brooks and Kelton 1967) and recently was recorded from Saskatchewan (Parker and Phillips 2007). The only species of small water strider (Veliidae), *Microvelia buenoi* Drake, seems to be widely distributed in the ecozone. To date, nine species of water strider (Gerridae) involving five genera have been recorded, with *Aquarius nyctalis* (Drake & Hottes) and *Limnoporus notabilis* (Drake & Hottes) confined to the western area of the ecozone. *Aquarius remigis* (Say), *Metrobates hesperius* Uhler, and *Rheumatobates palosi* Blatchley are usually found on flowing water, with *M. hesperius* so far only known from southeastern Manitoba (Brooks and Kelton 1967). Although Spence and Scudder (1980) noted that *Gerris buenoi* Kirkaldy was common on small ponds in British Columbia and *G. pingreensis* Drake & Hottes was most common on large lakes, Spence (1981) found that *G. pingreensis* tended to seek out emergent cover when available, whereas *G. buenoi* is a habitat generalist with a distribution

affected by a tendency to avoid other *Gerris* species. However, Spence and Cárcamo (1991) found that *G. buenoi* and *G. pingreensis* can co-occur in emergent zones of lakes in Alberta, but that the dominance of *G. pingreensis* on permanent lakes related primarily to life history traits and was not principally the result of differences in intraguild predation.

### ***Infraorder Leptodomorpha***

The shore bugs (Saldidae) are the only family in this infraorder in the ecozone. This family is represented by five genera and 20 species, many of which are Holarctic species (Table 2).

### ***Infraorder Cimicomorpha***

Eight families in this infraorder are present in the ecozone. There are three species of bed bugs (Cimicidae), with *Cimex lectularius* Linnaeus the most recognizable and now a common pest. Six species of minute pirate bugs (Anthocoridae) are present, representing six genera. The family Lyctocoridae, until recently considered part of the Anthocoridae (Kelton 1978), is represented by the cosmopolitan *Lyctocoris campestris* (Fabricius). There are 12 species of damsel bugs (Nabidae) in three genera, with *Nabicula americolimbata* (Carayon) and *N. flavomarginata* (Scholtz) being Holarctic. Kerzhner (1993) raised *Pagasa nigripes* Harris to specific status and recorded it from Alberta and Winnipeg. Scudder (2008) reported this species also from British Columbia and the Northwest Territories and noted that earlier records of *P. fusca* (Stein) from the Yukon (Scudder 1997; Maw *et al.* 2000) actually refer to *P. nigripes*.

By far the largest family of Heteroptera in the ecozone is the Miridae, the plant bugs. They have been considered in detail by Kelton (1980), and considerable updates have been made since by Cassis (1984), Forero (2008), Henry (1982, 1983, 1991, 2006), Henry and Kim (1984), Rosenzweig (1997), Schuh (2000, 2001, 2004), Schuh and Schwartz (1988, 2004, 2005), Schuh *et al.* (1995), Schwartz (1984, 1989, 1994, 1998, 2008, 2011), Schwartz and Footitt (1992a, 1998), Schwartz and Schuh (1999), Schwartz and Scudder (2000, 2003), Schwartz *et al.* (1991), Schwartz and Stonedahl (2004), Scudder (2000, 2004), Scudder and Schwartz (2001, 2012), Stonedahl (1990), Stonedahl and Schwartz (1986), and Yasunaga *et al.* (2002).

To date, 82 genera and 280 species of Miridae have been detected in the ecozone. A number of these are noteworthy agricultural pests. Best known is the alien alfalfa plant bug, *Adelphocoris lineolatus* (Goeze) (Beirne 1972), and several species of *Lygus* (Beirne 1972; Schwartz and Footitt 1992b), which have been the subject of detailed studies (Otani and Cárcamo 2011). At least 25 mirids are eastern species that just enter the ecozone in Manitoba (Table 2). Strickland (1953) reported *Stenodema virens* (L.) from Alberta, but this species does not occur in North America (Kelton 1961). Specimens determined as this species by Strickland in the University of Alberta Strickland Museum (UASM) from Lethbridge are *S. pilosipes* Kelton, and those from Wetaskiwin are *S. vicinum* Provancher. Two female specimens in the UASM from Medicine Hat collected by E.H. Strickland on 7.viii.1939, originally determined by Strickland as *Hadronema bispinosa* but subsequently labelled as *Hadronema* sp. prob. *picta* Uhler by E.H.N. Smith in 1951 and recorded as *H. picta* by Strickland (1953), are actually *H. bispinosum* Knight: The Alberta record of *H. pictum* Uhler was queried by Maw *et al.* (2000), as noted by Forero (2008). *Hadronema pictum* was not reported from Alberta by either Kelton (1980) or Forero (2008). *Aoplonema rubrum* Forero was recorded from Drumheller as *H. uhleri* Van Duzee by Strickland (1953), and this record was accepted by Maw *et al.* (2000). A male specimen in the UASM from Drumheller collected by W.R.M. Mason on 14.vi.1946 was correctly identified by Strickland, although Forero (2008) did not report *A. rubrum* from Alberta. Strickland (1953) recorded *Orthotylus viridis* Van Duzee from Edmonton on *Salix*, but this is an eastern North

American species that was not included in Kelton (1980), and the Alberta record was queried by Maw *et al.* (2000). A male specimen in the UASM from Edmonton, collected on *Salix* by E.H. Strickland on 19.vi.1937 and determined by Strickland as *O. viridis*, is actually *O. fuscicornis* Knight. Finally, the species from Waterton reported as *Melanotrichus insignis* Van Duzee in Strickland (1953) and determined as this species by E.H.N. Smith is actually *Ilnacorella sulcata* Knight. However, this species is only known from Waterton in Alberta, which is the type locality. It has so far not been collected in the open prairie grasslands.

The lace bugs (Tingidae), with nine genera and 21 species, are well distributed in the ecozone, with *Corythucha arcuata* (Say) and *C. bellula* Gibson found only in the east and *C. distincta* Osborn & Drake restricted to the west. *Corythaica acuta* (Drake) (Fig. 1) has recently been found at the Suffield Canadian Forces Base (Scudder 2013). The assassin bugs (Reduviidae) are represented by six genera and six species, most of which are widely distributed in the Nearctic. Two species of ambush bugs (Phymatidae) are present, *Phymata americana americana* Melin and *P. vicina vicina* Handlirsch.



**Figs. 1–6.** 1. *Corythaica acuta*, male; 2. *Nisoscolopocerus apiculatus*, female; 3. *Chelinidea vittiger*, female; 4. *Ischnodemus hesperus*, male; 5. *Melacoryphus admirabilis*, female; 6. *Uhleriola floralis*, female.

### ***Infraorder Pentatomomorpha***

So far, 17 families in this infraorder have been recorded from the ecozone. The flat bugs (Aradidae) are represented by two genera and 13 species. The family in Canada has been monographed by Matsuda (1977), but the genus *Aneuris* was revised by Picchi (1977).

Within the superfamily Coreoidea, the Alydidae, or broad-headed bugs, are represented by five genera and eight species. *Alydus scutellatus* Van Duzee is confined to the west, having been recorded from Elkwater, while *Stachyocnemus apicalis* (Dallas) is rare and in Canada known so far only from Alberta. Six genera and six species of squash bugs and allies (Coreidae) are present, *Nisoscolopocerus apiculatus* Barber (Fig. 2) being confined to the ecozone in Canada and evidently quite rare. *Chelinidea vittiger* Uhler (Fig. 3) is also known only from the Prairies Ecozone in Canada and is associated with *Opuntia* cacti (De Vol and Goeden 1973; Acorn 2011). The scentless plant bugs (Rhopalidae) are quite common, being represented by four genera and five species. The boxelder bug *Boisea trivittata* (Say) can be abundant and a nuisance when it moves to the warmth of houses in autumn (Schaefer and Kotulski 2000).

Within the superfamily Lygaeoidea, the introduced *Chilacis typhae* (Perris) is the only representative of the Artheneidae, occurring on common cattail or common bulrush (*Typha latifolia* Linnaeus), now recognized as widely distributed in North America (Wheeler and Fetter 1987; Wheeler and Stoops 1999; Scudder 2000; Wheeler 2002; Scudder and Footitt 2006; Roch 2008). It has recently been reported from both Alberta and Saskatchewan (Scudder 2010). Only two species of stilt bugs (Berytidae) are present, both widely distributed. Chinch bugs (Blissidae) are represented by three species, *Ischnodemus hesperus* Parshley (Fig. 4) being confined to the tallgrass prairie areas of Manitoba. There are three species of Cymidae and six species of big-eyed bugs (Geocoridae), but further research may show that more species of the latter are actually present. Four genera and seven taxa are noted at present in the Lygaeidae (*s.s.*), with *Melacoryphus admirabilis* (Uhler) (Fig. 5) recently identified from the Grasslands National Park in Saskatchewan (Scudder 2010). The suture-zone between the western *Lygaeus kalmii kalmii* Stål and the eastern *L. kalmii angustomarginatus* Parshley occurs in Manitoba (Parshley 1923; Slater and Knop 1969). In the Orsillidae, further bar-coding research on the species of *Nysius* is needed to clarify the identity of some of the species in the ecozone. However, *N. niger* Baker (= *N. ericae* Amer. auct.) is reported to be a common agricultural pest (Beirne 1972). Three species of *Crophius* (Oxycarenidae) are recorded, with *Crophius bohemanni* (Stål) so far only known from Cypress Hills in Saskatchewan (Scudder 2010). Seed bugs in the family Rhyparochromidae are well represented, with 20 genera and 26 species so far recognized. *Uhleriola floralis* (Uhler) (Fig. 6) is a typical inhabitant of sand hills (Acorn 2011). Recent additions to the prairie fauna include *Antilocoris minutus* (Bergroth), *Eremocoris ferus* (Say), *Megalonotus sabulicola* (Thomson), *Neosuris castanea* (Barber), *Perigenes constrictus* (Say), *Sisamnes claviger* (Uhler), *Stygnocoris rusticus* (Fallén), and *Zeridoneus petersoni* Reichert (Scudder 2008, 2010). The family includes three introduced alien species, namely, *Megalonotus sabulicola*, *Stygnocoris rusticus*, and *S. sabulosus* (Schilling) (Table 2). As reported in the *Calgary Herald* (page A8) on August 4, 2003, Dr. D.L. Johnson recorded that the Holarctic seed bug *Spragisticus nebulosus* (Fallén) occurred in the “millions” attracted to light at 2200 hours in a shopping centre at Medicine Hat in Alberta. The exceptionally high number of these bugs forced the closure of a McDonald’s restaurant and the employment of a Bobcat to clean the parking lot (D.L. Johnson, pers. comm.). As far as is known, this population explosion has not reoccurred since, and the factors responsible for the vast numbers have not been determined.

Within the superfamily Piesmatoidea, four species of Piesmatidae have been recognized in the ecozone. In the superfamily Pentatomoidea, five families are present, there being two species of acanthosomatids (Acanthosomatidae) and two species of burrowing bugs (Cydnidae). Stink bugs in the family Pentatomidae are represented by 20 genera and 40 species, with *Coenus delius* (Say) (Fig. 7) being a typical sand hill species (Acorn 2011). *Chlorochroa belfragei* (Stål), *C. faceta* (Say) (Fig. 8), *C. opuntiae* Esselbaugh (Fig. 9), and *C. viridicata* (Walker) (Fig. 10) are evidently rare and found only on the Prairies in Canada. The more common *C. uhleri* (Stål) can be an agricultural pest, although this was incorrectly cited as *C. sayi* Stål in Beirne (1972): *C. sayi* does not occur in Canada as far as is known (Scudder and Thomas 1987). There are nine species of shield bugs (Scutelleridae), with *Euptychodera corrugata* (Van Duzee) (Fig. 11) and *Fokkeria producta* (Van Duzee) (Fig. 12) being rare. Only five species of negro bugs (Thyreocoridae) are reported from the ecozone, with *Corimelaena nigra* Dallas being a typical sand hill inhabitant (Acorn 2011).



**Figs. 7–12.** 7. *Coenus delius*, male (genital capsule exserted); 8. *Chlorochroa faceta*, female; 9. *C. opuntiae*, male; 10. *C. viridicata*, male; 11. *Euptychodera corrugata*, female; 12. *Fokkeria producta*, female.



### ***Biogeographical Aspects***

The 582 Heteroptera taxa so far reported from the Prairies Ecozone represent 40.7% of the 1,429 true bug taxa currently recorded from Canada. Only the Ceratocombidae, Gelastocoridae, Ochtenidae, Naucoridae, Lasiochilidae, Microphysidae, Heterogastridae, and Pachygronthidae are not represented in the ecozone biota.

The ecozone Heteroptera can be assigned to 13 geographical patterns (Tables 1 and 2). Some species are not categorized as in Scudder (2011), owing to more recent information available on their distribution. In the following categories, the Western Cordillera region is taken to be the mountainous areas of northwestern North America, in addition to the western United States considered in the Mountain Provinces by Bailey (1995). Similarly, the Great Basin-Prairies coincide with the Prairies Ecozone as defined by the Ecological Stratification Working Group (1996), in addition to the Great Plains in the Temperate Steppe Division by Bailey (1995): The Prairies Ecozone is the most northern extension of the Great Plains (Shorthouse 2010). The 100<sup>th</sup> meridian is generally taken to separate the east and west Nearctic area. Table 1 details the geographical patterns and number of taxa present in each, while Table 2 lists the species or subspecies placed in these categories.

The 205 taxa in the Nearctic, excluding the Beringia category, constituting 35.2% of the heteropteran fauna in the ecozone, is the dominant component. The second largest element with 100 taxa, constituting 17.2% of the fauna, is the Western Nearctic, excluding the Beringia category. The 56 species in the Nearctic, including the Beringia category, constituting 9.6% of the fauna, is the third largest element. The Nearctic, excluding the Western Cordillera and Beringia category, with 52 species constituting 8.9% of the fauna, and the Holarctic element with 51 species, amounting to 8.8% of the total fauna, are almost as common. The Western Cordillera, excluding the Beringia category with 10 species (1.7%), includes *Irbisia nigripes* Knight, with specimens known from Twin Butte in Alberta, and *Phyllopiidea montana* Knight, which also occurs in the Elkwater area of the Cypress Uplands. Likewise, the single species in the Western Cordillera, including the Beringia category, namely, *Tupiocoris confusus* (Kelton), is also known from Elkwater. The 36 species (6.3%) in the Eastern Nearctic component are typically confined to southeastern Manitoba and are usually found east of the 100<sup>th</sup> meridian. There are only two cosmopolitan species and 10 introduced species. As might be expected, the most distinctive category in the ecozone is the Great Basin-Prairies component, consisting of 23 species, constituting 4.0% of the heteropteran fauna, with some of these evidently quite rare.

### ***Research Priorities***

As in other ecozones (Scudder 2011), there are few data to indicate any definite trends in species occurrence and abundance. Although most of the grasslands have been cultivated and those that remain have been altered by grazing or severely fragmented by roads, conduits for energy, or urbanization (Williams *et al.* 2011), there seem to be no studies that have assessed the impacts on the heteropteran fauna. Undoubtedly some true bugs have been put at risk, although none are listed by Hall *et al.* (2011). However, because today less than 1% of the tallgrass prairie remains (Shorthouse and Larson 2010), and much of what is left is threatened, species confined to this type of grassland may be at risk.

Although loss of natural wetland habitat on the prairies has created a great challenge for biodiversity (Gibbs 2000), most of the aquatic Hemiptera have managed to colonize and breed in man-made water bodies (Scudder *et al.* 2010). However, species such as *Cenocorixa expleta* and *Dasyxorixa rawsoni* that are restricted to saline lakes and ponds may be highly impacted by the anticipated drying trend associated with climate change in the next few decades (Williams *et al.* 1988). Clearly, a number of research projects are required to assess the status and conservation of the Heteroptera of the Prairies Ecozone.

**Table 2.** Geographical patterns and species composition in the Heteroptera of the Prairies Ecozone.

1. NEARCTIC, INCLUDING BERINGIA	Family ARADIDAE
Family CORIXIDAE	<i>Aradus abbas</i> Bergroth
<i>Callicorixa alaskensis</i> Hungerford	<i>A. tuberculifer</i> Kirby
<i>C. audeni</i> Hungerford	<i>A. uniannulatus</i> Parshley
<i>Cymatia americana</i> Hussey	Family ALYDIDAE
<i>Sigara decoratella</i> (Hungerford)	<i>Alydus eurinus</i> (Say)
Family VELIIDAE	Family COREIDAE
<i>Microvelia buenoi</i> Drake	<i>Coriomeris humilis</i> (Uhler)
Family GERRIDAE	Family RHOPALIDAE
<i>Gerris buenoi</i> Kirkaldy	<i>Stictopleurus punctiventris</i> (Dallas)
<i>G. pingreensis</i> Drake & Hottes	Family GEOCORIDAE
Family SALDIDAE	<i>Geocoris bullatus</i> (Say)
<i>Salda obscura</i> Provancher	<i>G. discopterus</i> Stål
<i>S. provancheri</i> Kelton & Lattin	<i>G. howardi</i> Montandon
<i>Saldula nigrita</i> Parshley	Family OXYCARENIDAE
Family ANTHOCORIDAE	<i>Crophius disconotus</i> (Say)
<i>Anthocoris antevolens</i> White	Family RHYPAROCHROMIDAE
<i>A. dimorphicus</i> Anderson & Kelton	<i>Eremocoris borealis</i> (Dallas)
<i>A. musculus</i> (Say)	<i>Ligyrocoris diffusus</i> (Uhler)
<i>Tetraphleps canadensis</i> Provancher	<i>Slaterobius insignis</i> (Uhler)
<i>T. furvus</i> Van Duzee	Family ACANTHOSOMATIDAE
Family NABIDAE	<i>Elasmucha lateralis</i> (Say)
<i>Nabicula nigrovittata nearctica</i> Kerzhner	Family PENTATOMIDAE
<i>Nabis americanoferus</i> Carayon	<i>Aelia americana</i> Dallas
<i>Pagasa nigripes</i> Harris	<i>Neottiglossa trilineata</i> (Kirby)
Family MIRIDAE	<i>N. undata</i> (Say)
<i>Chlamydatus keltoni</i> Schuh & Schwartz	Family THYREOCORIDAE
<i>Dicyphus discrepans</i> Knight	<i>Corimelaena nigra</i> Dallas
<i>Labops hesperius</i> Uhler	2. NEARCTIC, EXCLUDING BERINGIA
<i>Lygidea annexa</i> (Uhler)	Family BELOSTOMATIDAE
<i>Lygus borealis</i> (Kelton)	<i>Belostoma flumineum</i> Say
<i>L. potentillae</i> Kelton	<i>Lethocerus americanus</i> (Leidy)
<i>L. rubrosignatus</i> Knight	Family NEPIDAE
<i>L. shulli</i> Knight	<i>Ranatra fusca</i> Palisot
<i>Mecomma angustatum</i> (Uhler)	Family CORIXIDAE
<i>M. gilvipes</i> (Stål)	<i>Arctocorisa sutilis</i> (Uhler)
<i>Mimoceps insignis</i> Uhler	<i>Cenocorixa dakotensis</i> (Hungerford)
<i>Neolygus communis</i> (Knight)	<i>C. utahensis</i> (Hungerford)
<i>Orthotylus neglectus</i> Knight	<i>Dasycorixa hybrida</i> (Hungerford)
<i>Orectoderus obliquus</i> Uhler	<i>D. johanseni</i> (Walley)
<i>Pinalitus rostratus</i> Kelton	<i>D. rawsoni</i> Hungerford
<i>Plagiognathus brunneus</i> (Provancher)	
<i>P. parshleyi</i> (Knight)	
<i>P. suffuscipennis</i> Knight	
<i>Salignus tahoensis</i> (Knight)	
<i>Tupiocoris similis</i> (Kelton)	

*Hesperocorixa atopodonta* (Hungerford)  
*H. laevigata* (Uhler)  
*H. michiganensis* (Hungerford)  
*H. minorella* (Hungerford)  
*H. vulgaris* (Hungerford)  
*Sigara alternata* (Say)  
*S. bicoloripennis* (Walley)  
*S. conocephala* (Hungerford)  
*S. grossolineata* Hungerford  
*S. mullettensis* (Hungerford)  
*S. penniensis* (Hungerford)  
*S. solensis* (Hungerford)  
*Trichocorixa borealis* Sailer

Family NOTONECTIDAE

*Buenoa confusa* Truxal  
*B. macrotibialis* Hungerford  
*Notonecta borealis* Hussey  
*N. undulata* Say

Family PLEIDAE

*Neoplea striola* (Fieber)

Family MESOVELIIDAE

*Mesovelgia mulsanti* White

Family HEBRIDAE

*Merragata hebroides* White

Family HYDROMETRIDAE

*Hydrometra martini* Kirkaldy

Family GERRIDAE

*Aquarius nyctalis* (Drake & Hottes)  
*A. remigis* (Say)  
*Gerris comatus* Drake & Hottes  
*Limnoporus dissortis* (Drake & Hottes)

Family SALDIDAE

*Lampracanthia crassicornis* (Uhler)  
*Salda buenoi* (McDunnough)  
*Saldula bouchervillei* (Provancher)  
*S. confluenta* (Say)  
*S. laticollis* (Reuter)

Family CIMICIDAE

*Oeciacus vicarius* Horváth

Family ANTHOCORIDAE

*Cardiastethus borealis* Kelton  
*Macrotrachiella nigra* Parshley

Family NABIDAE

*Nabidula propinqua* (Reuter)  
*N. subcoleoprata* (Kirby)  
*Nabis alternatus* Parshley

*N. roseipennis* Reuter

*N. rufusculus* Reuter

Family MIRIDAE

*Adelphocoris rapidus* (Say)  
*Agnocoris pulverulentus* (Uhler)  
*Atractotomus atricolor* (Knight)  
*Blepharidopterus provancheri* (Burque)  
*Collaria meilleurii* Provancher  
*Ceratocapsus nigricephalus* Knight  
*Chlamydatus associatus* (Uhler)  
*Clivinema villosum* Reuter  
*Criocoris saliens* (Reuter)  
*Deraeocoris albigulus* Knight  
*D. fasciolus* Knight  
*D. histrio* (Reuter)  
*D. triannulipes* Knight  
*Dicyphus hesperus* Knight  
*Fulvius slateri* Wheeler  
*Hadronema militare* Uhler  
*Henrilygus ultranubilus* (Knight)  
*Hyaliodes harti* Knight  
*Ilmacora albifrons* Knight  
*I. stalii* Reuter  
*Labops brooksi* Slater  
*L. hirtus* Knight  
*Leptopterna amoena* Uhler  
*Litomiris debilis* (Uhler)  
*Lopidea confluenta* (Say)  
*L. media* (Say)  
*L. minor* Knight  
*L. teton* Knight  
*Lygidea rosacea* Reuter  
*L. salicis* Knight  
*Lygus lineolaris* (Palisot)  
*L. rubroclarus* Knight  
*L. rufidorsus* (Kelton)  
*L. solidaginis* (Kelton)  
*L. unctuosus* (Kelton)  
*Melanotrichus brindleyi* Knight  
*M. leviculus* Knight  
*Neolygus atritylus* (Knight)  
*Neurocolpus nubilus* (Say)  
*Noctuocoris fumidus* (Van Duzee)  
*Orthops scutellatus* Uhler  
*Orthotylus candidatus* Van Duzee  
*O. dorsalis* (Provancher)  
*O. notabilis* Knight  
*O. nyctalis* Knight  
*O. ornatus* Van Duzee  
*Phoenicocoris rostratus* (Knight)  
*Phytocoris conspersipes* Reuter  
*P. conspurcatus* Reuter  
*P. lasiomeris* Reuter  
*P. neglectus* Knight  
*P. pallidicornis* Reuter

*Piceophylus keltoni* Schwartz & Schuh  
*Pilophorus neoclavatus* Schuh & Schwartz  
*P. uhleri* Knight  
*Plagiognathus albatus* (Van Duzee)  
*P. alboradialis* Knight  
*P. davisii* Knight  
*P. dispar* Knight  
*P. flavidus* Knight  
*P. fuscipes* Knight  
*P. fuscus* (Provancher)  
*P. guttatipes* (Uhler)  
*P. laricicola* Knight  
*P. maculipennis* (Knight)  
*P. modestus* (Reuter)  
*P. negundinus* Knight  
*P. nigronitens* Knight  
*Polymerus breviostris* Knight  
*P. chrysopsis* Knight  
*P. venaticus* (Uhler)  
*Prepops bivittis* (Stål)  
*P. borealis* (Knight)  
*P. nigripilus* (Knight)  
*P. rubellicollis* (Knight)  
*Psallovirus piceicola* (Knight)  
*Schaffneria pilophoroides* (Knight)  
*Sericophanes heidemanni* Poppius  
*Slaterocoris atritibialis* (Knight)  
*S. breviatus* (Knight)  
*S. pallidicornis* (Knight)  
*S. stygicus* (Say)  
*Stenodema vicina* (Provancher)  
*Teratocoris discolor* Uhler

## Family TINGIDAE

*Corythucha cydoniae* (Fitch)  
*C. elegans* Drake  
*C. hewitti* Drake  
*C. marmorata* (Uhler)  
*C. mollicula* Osborn & Drake  
*C. pallipes* Parshley  
*Hesperotingis antennata* Parshley  
*Melanorhopala clavata* (Stål)  
*Physatocheila plexa* (Say)  
*P. variegata* Parshley

## Family REDUVIIDAE

*Barce fraterna* (Say)  
*Pygolampis pectoralis* (Say)  
*Rhynocoris ventralis* (Say)  
*Sinea diadema* (Fabricius)

## Family PHYMATIDAE

*Phymata americana americana* Melin  
*P. vicina vicina* Handlirsch

## Family ARADIDAE

*Aneurus simplex* Uhler  
*Aradus acutus* Say  
*A. finestus* Bergroth  
*A. kormilevi* Heiss  
*A. persimilis* Van Duzee  
*A. proboscideus* Walker  
*A. quadrilineatus* Say

## Family ALYDIDAE

*Alydus conspersus conspersus* Montandon  
*A. conspersus infuscatus* Fracker  
*Megalotomus quinquespinosus* (Say)  
*Protenor belfragei* Haglund  
*Tollius curtulus* (Stål)

## Family COREIDAE

*Leptoglossus occidentalis* Heidemann

## Family RHOPALIDAE

*Strictopleurus viridicatus* (Uhler)

## Family BERYTIDAE

*Jalysus wickhami* Van Duzee  
*Neoneides muticus* (Say)

## Family CYMIDAE

*Cymus luridus* Stål

## Family GEOCORIDAE

*Geocoris limbatus* Stål

## Family ISCHNORHYNCHIDAE

*Kleidocerys ovalis* Barber

## Family LYGAEIDAE

*Melacoryphus lateralis* (Dallas)

## Family ORSILLIDAE

*Nysius angustatus* Uhler  
*N. niger* Baker

## Family RHYPAROCHROMIDAE

*Eremocoris ferus* (Say)  
*Perigenes constrictus* (Say)  
*Peritrechus fraternus* Uhler  
*Plinthisus americanus* Van Duzee  
*Sisamnes claviger* (Uhler)  
*Uhleriola floralis* (Uhler)  
*Zeridoneus costalis* (Van Duzee)

## Family ACANTHOSOMATIDAE

*Elasmostethus cruciatus* (Say)

## Family CYDNIDAE

*Microporus obliquus* Uhler  
*Sehirus cinctus albonotatus* Dallas

## Family PENTATOMIDAE

*Apoecilus bracteatus* (Fitch)  
*A. cynicus* (Say)  
*Banasa dimidiata* (Say)  
*Brochymena quadripustulata* (Fabricius)  
*Chlorochroa uhleri* (Stål)  
*Coenus delius* (Say)  
*Cosmopepla lintneriana* Kirkaldy  
*Euschistus servus euschistoides* (Vollenhoven)  
*E. tristigmus luridus* Dallas  
*Holcostethus limbolarius* (Stål)  
*H. macdonaldi* Rider & Rolston  
*Perillus bioculatus* (Fabricius)  
*P. circumcinctus* Stål  
*P. exaptus* (Say)  
*Podisus brevispinus* Phillips  
*P. maculiventris* (Say)  
*P. placidus* Uhler  
*P. serieventris* Uhler  
*Rhacognathus americanus* Stål  
*Trichopepla atricornis* Stål

## Family SCUTELLERIDAE

*Eurygaster alternata* (Say)  
*E. amerinda* Bliven  
*Homaemus bijugis* Uhler

## Family THYREOCORIDAE

*Corimelaena pulicaria* (Germar)  
*Galgupha nitiduloides* (Wolff)  
*G. ovalis* Hussey

3. NEARCTIC, EXCLUDING THE WESTERN  
CORDILLERA AND BERINGIA

## Family CORIXIDAE

*Cenocorixa bifida bifida* (Hungerford)  
*Corisella tarsalis* (Fieber)  
*Hesperocorixa scabricula* (Walley)  
*Palmacorixa buenoi* Abbott  
*P. gillettei* Abbott  
*Sigara decorata* (Abbott)  
*S. lineata* (Forster)  
*S. mathesoni* Hungerford  
*S. trilineata* (Provancher)  
*Trichocorixa verticalis interiors* Sailer

## Family HEBRIDAE

*Hebrus burmeisteri* Lethierry & Severin

## Family GERRIDAE

*Rheumatobates palosi* Blatchley

## Family SALDIDAE

*Pentacora signoreti* (Guérin-Méneville)

## Family ANTHOCORIDAE

*Xylocoris hirtus* Kelton

## Family MIRIDAE

*Ceratocapsus modestus* (Uhler)  
*Deraeocoris aphidophagus* Knight  
*D. nitenatus* Knight  
*D. ornatus* Knight  
*D. quercicola* Knight  
*Halticus intermedius* Uhler  
*Lopidea lathyri* Knight  
*Lygus plagiatus* Uhler  
*L. vanduzeei* Knight  
*Metriorrhynchomiris dislocatus* (Say)  
*Microphyllellus fuscicornis* Knight  
*Orthotylus basicornis* Knight  
*O. pennsylvanicus* Henry  
*Phytocoris brimleyi* Knight  
*P. erectus* Van Duzee  
*P. salicis* Knight  
*Plagiognathus tumidifrons* (Knight)  
*Poecilocapsus lineatus* (Fabricius)  
*Polymerus severini* Knight  
*Prepops zonatus* (Knight)  
*Pseudatomoscelis seriatus* (Reuter)  
*Taedia pallidula* (McAtee)  
*Trigonotylus tarsalis* (Reuter)  
*Tropidostepes amoenus* Reuter  
*T. brooksi* Kelton  
*T. palmeri* (Reuter)

## Family TINGIDAE

*Leptoypa mutica* (Say)

## Family ALYDIDAE

*Stachyocnemus apicalis* (Dallas)

## Family COREIDAE

*Chelinidea vittiger* Uhler  
*Merocoris distinctus* Dallas

## Family RHOPALIDAE

*Boisea trivittata* (Say)

## Family LYGAEIDAE

*Lygaeopilus tripunctatus* (Dallas)  
*Melacoryphus admirabilis* (Uhler)

## Family RHYPAROCHROMIDAE

*Drymus unus* (Say)

## Family PENTATOMIDAE

*Menedes insertus* (Say)  
*Neottiglossa sulcifrons* Stål  
*Thyanta accerra* McAtee

Family THYREOCORIDAE  
*Galgupha atra* Amyot & Serville

## 4. WESTERN NEARCTIC, INCLUDING BERINGIA

Family CORIXIDAE  
*Sigara fallenoidea* (Hungerford)

Family ANTHOCORIDAE  
*Anthocoris tomentosus* Péricart

Family MIRIDAE  
*Brooksetta viridicata* (Uhler)  
*Deraeocoris brevis* (Uhler)  
*Lopidea dakota* Knight  
*L. nigridea serica* Knight  
*Lygus elisus* Van Duzee  
*Pilophorus vicarius* Poppius  
*Stenodema pilosipes* Kelton

Family OXYCARENIDAE  
*Crophius bohemani* (Stål)  
*C. ramosus* Barber

Family PENTATOMIDAE  
*Chlorochroa granulosa* (Uhler)

Family SCUTELLERIDAE  
*Homaemus aeneifrons consors* Uhler  
*Phimodera binotata* (Van Duzee)

## 5. WESTERN NEARCTIC, EXCLUDING BERINGIA

Family CORIXIDAE  
*Cenocorixa expleta* (Uhler)  
*Sigara washingtonensis* Hungerford

Family NOTONECTIDAE  
*Notonecta kirbyi* Hungerford

Family GERRIDAE  
*Limnopus notabilis* (Drake & Hottes)

Family SALDIDAE  
*Saldula comatula* Parshley  
*S. explanata* (Uhler)  
*S. opiparia* Drake & Hottes

Family ANTHOCORIDAE  
*Xylocoris californicus* (Reuter)

Family NABIDAE  
*Nabicula vanduzeei* (Kirkaldy)

Family MIRIDAE  
*Aoplonema princeps* (Uhler)  
*A. rubrum* Forero  
*Brooksetta chelifera* (Knight)

*B. inconspicua* (Uhler)  
*B. incurva* (Knight)  
*Ceratocapsus geminatus* Knight  
*Conostethus americanus* Knight  
*Coquillettia schwartzi* Wyniger  
*Dacota hesperia* Uhler  
*Dichroscytus ruberellus* Knight  
*Europiella angulata* (Uhler)  
*E. consors* (Uhler)  
*E. pilosellus* (Uhler)  
*Hadronema bispinosum* Knight  
*H. breviatum* Knight  
*H. simplex* Knight  
*Hoplomachus affiguratus* (Uhler)  
*Irbisia brachycera* (Uhler)  
*I. elongata* Knight  
*I. fuscipubescens* Knight  
*Labopidea pallida* Knight  
*Labops tumidifrons* Knight  
*Lopidea confraterna* (Gibson)  
*Lygus atritibialis* Knight  
*L. convexicollis* Reuter  
*L. keltoni* Schwartz  
*L. robustus* (Uhler)  
*L. striatus* Knight  
*Megalopsallus femoralis* Kelton  
*M. nigrofemoratus* (Knight)  
*M. rubropictipes* Knight  
*M. sparsus* (Van Duzee)  
*Melanotrichus albocostatus* (Van Duzee)  
*M. atriplicis* Knight  
*M. coagulatus* (Uhler)  
*Orthotylus fuscicornis* Knight  
*O. ute* Knight  
*Phoenicocoris longirostris* (Knight)  
*Phytocoris laevis* (Uhler)  
*P. listi* Knight  
*P. validus* Reuter  
*Pilophorus salicis* Knight  
*Plagiognathus annulatus* Uhler  
*P. shoshonea* Knight  
*Polymerus basivittis* (Reuter)  
*P. diffusus* (Uhler)  
*P. hirtus* Knight  
*P. rufipes* Knight  
*P. sculleni* Knight  
*Prepops eremicola* (Knight)  
*Pseudopsallus anograe* Knight  
*P. demensus* (Van Duzee)  
*P. sericatus* (Uhler)  
*Sixeonotus rostratus* Knight  
*Trigonotylus americanus* Carvalho  
*T. antennatus* Kelton  
*T. brooksi* Kelton  
*T. flavicornis* Kelton  
*Tupiocoris tibialis* (Kelton)

## Family TINGIDAE

*Corythaica acuta* Drake  
*C. venusta* (Champion)  
*Corythucha salicata* (Uhler)  
*Dictyla labeculata* (Uhler)  
*Hesperotingis fuscata* Parshley  
*H. occidentalis* Drake

## Family REDUVIIDAE

*Fitchia spinosula* Stål

## Family ARADIDAE

*Aradus compressus* Heidemann  
*A. insolitus* Van Duzee  
*A. intectus* Parshley  
*A. parshleyi* Van Duzee

## Family ALYDIDAE

*Alydus scutellatus* Van Duzee

## Family COREIDAE

*Nisoscolopocerus apiculatus* Barber

## Family RHOPALIDAE

*Arhyssus scutatus* (Stål)

## Family BLISSIDAE

*Blissus occiduus* Barber

## Family CYMIDAE

*Cymus coriacipennis* (Stål)

## Family GEOCORIDAE

*Geocoris atricolor* Montandon

## Family LYGAEIDAE

*Lygaeus kalmii kalmii* Stål  
*Melanopleurus perplexus* Scudder

## Family PIESMATIDAE

*Parapiesma explanatum* (McAtee)  
*Piesma costatum* (Uhler)  
*P. patrule* McAtee

## Family PENTATOMIDAE

*Chlorochroa faceta* (Say)  
*C. ligata* (Say)  
*C. opuntiae* Esselbaugh  
*Codophila remota* (Horváth)  
*Cosmopela integressus* (Uhler)  
*Holcostethus abbreviatus* Uhler  
*H. tristis* (Van Duzee)  
*Tepa rugulosa* (Say)

## Family SCUTELLERIDAE

*Euptychodera corrugata* (Van Duzee)  
*Vanduzeeina balli* (Van Duzee)

## 6. EASTERN NEARCTIC

## Family NOTONECTIDAE

*Buenoa margaritacea* Torre Bueno  
*Notonecta insulata* Kirby  
*N. irrorata* Uhler

## Family MIRIDAE

*Americodema nigrolineatum* (Knight)  
*Ceratocapsus digitulus* Knight  
*C. pilosulus* Knight  
*Neolygus belfragei* (Reuter)  
*N. canadensis* (Knight)  
*N. omnivagus* (Knight)  
*N. quercalbae* (Knight)  
*N. viticollis* (Reuter)  
*Opistheurista cladestina* (Van Duzee)  
*Phytocoris onustus* Van Duzee  
*Pilophorus amoenus* Uhler  
*P. furvus* Knight  
*P. piceicola* Knight  
*P. setiger* Knight  
*Plagiognathus blatchleyi* Reuter  
*P. longirostris* (Knight)  
*Polymerus flavocostatus* Knight  
*Prepops fraternus* (Knight)  
*Reuteria querci* (Say)  
*Schaffneria davisii* (Knight)  
*Tropidostepes canadensis* Van Duzee  
*T. commisuralis* (Reuter)  
*T. pettiti* Reuter  
*T. pubescens* (Knight)

## Family TINGIDAE

*Corythucha arcuata* (Say)  
*C. bellula* Gibson

## Family BLISSIDAE

*Ischnodemus hesperius* Parshley

## Family CYMIDAE

*Cymus angustatus* Stål

## Family LYGAEIDAE

*Lygaeus kalmii angustomarginatus* Parshley

## Family RHYPAROCHROMIDAE

*Antilocoris minutus* (Bergroth)

## Family PENTATOMIDAE

*Chlorochroa belfragei* (Stål)  
*C. persimilis* Horváth

## Family SCUTELLERIDAE

*Homaemus aeneifrons aeneifrons* (Say)7. WESTERN CORDILLERAN, INCLUDING  
BERINGIA

## Family MIRIDAE

*Tupiocoris confusus* (Kelton)8. WESTERN CORDILLERAN, EXCLUDING  
BERINGIA

## Family CIMICIDAE

*Cimex pilosellus* (Horváth)

## Family MIRIDAE

*Chlamydatus obliquus* (Uhler)*C. pallidicornis* Knight*Europiella unipuncta* Knight*Irbisia nigripes* Knight*Lopidea picta* Knight*Phylloidea montana* Knight*Pilophorus americanus* Poppius

## Family TINGIDAE

*Corythucha distincta* Osborn & Drake

## Family RHYPAROCHROMIDAE

*Neosuris castanea* (Barber)

## 9. GREAT PLAINS-PRAIRIES

## Family CORIXIDAE

*Palmacorixa janeae* Brooks

## Family MIRIDAE

*Chlamydatus artemisiae* Kelton*C. ruficornis* Knight*Coquillettia albertae* Kelton*Ilnacora vittifrons* Knight*Labopidea brooksi* Kelton*L. planifrons* Knight*Lopidea balli* Knight*Melanotrichus leonardi* (Kerzhner & Schuh)*M. wallisi* Kelton*Orectoderus montanus* Knight*O. salicis* Knight*Orthotylus angulatus* (Uhler)*Parthenicus brooksi* Kelton*Phytocoris brooksi* Kelton*Polymerus balli* Knight*P. rubrocuneatus* Knight*Trigonotylus canadensis* Kelton

## Family BLISSIDAE

*Blissus canadensis* Leonard

## Family RHYPAROCHROMIDAE

*Plinthisus indentatus* Barber*Zeridoneus petersoni* Reichert

## Family PENTATOMIDAE

*Chlorochroa viridicata* (Walker)

## Family SCUTELLERIDAE

*Fokkeria producta* (Van Duzee)

## 10. NEARCTIC-NEOTROPICAL

## Family BELOSTOMATIDAE

*Lethocerus griseus* (Say)

## Family CORIXIDAE

*Trichocorixa sexcincta* (Champion)

## Family GERRIDAE

*Metrobates hesperius* Uhler

## Family SALDIDAE

*Saldula orbiculata* (Uhler)

## Family ANTHOCORIDIAE

*Orius insidiosus* (Say)*O. tristicolor* (White)*Xylocoris galactinus* (Fieber)

## Family NABIDAE

*Pagasa fusca* (Stein)

## Family REDUVIIDAE

*Zelus tetracanthus* Stål

## Family COREIDAE

*Catorhintha mendica* Stål

## Family RHOPALIDAE

*Arhyssus lateralis* (Say)*Harmostes reflexulus* (Say)

## Family GEOCORIDAE

*Geocoris pallens* Stål

## Family LYGAEIDAE

*Melanopleurus pyrrhopteris* (Stål)

## Family ORSILLIDAE

*Neortholomus scolopax* (Say)*Nysius raphanus* Howard*N. tenellus* Barber*Xyonysius californicus* (Stål)



## Family RHYPAROCHROMIDAE

*Atrazonotus umbrosus* (Distant)  
*Emblethis vicarius* Horváth  
*Kolenetrus plenus* (Distant)

## Family PIESMATIDAE

*Parapiesma cinereum* (Say)

## 11. HOLARCTIC

## Family SALDIDAE

*Micracanthia bergrothi* (Jakovlev)  
*M. fennica* (Reuter)  
*Saldula opacula* (Zetterstedt)  
*S. pallipes* (Fabricius)  
*S. palustris* (Douglas)  
*S. saltatoria* (Linnaeus)  
*Teloleuca bifasciata* (Thomson)  
*T. pellucens* (Fabricius)

## Family NABIDAE

*Nabicula americolimbata* (Carayon)  
*N. flavomarginata* (Scholtz)

## Family MIRIDAE

*Anocoris rubicundus* (Fallén)  
*Atomoscelis onustus* (Fieber)  
*Blepharidopterus diaphanous* (Kirschbaum)  
*Capsus cinctus* (Kolenati)  
*Chlamydatus pulicarius* (Fallén)  
*Cyrtorhinus caricis* (Fallén)  
*Europiella artemisiae* (Becker)  
*E. decolor* (Uhler)  
*Fieberocapsus flaveolus* (Reuter)  
*Labopidea lenensis* (Lindberg)  
*Labops burmeisteri* Stål  
*Lygocoris pabulinus* (Linnaeus)  
*L. rugicollis* (Fallén)  
*Lygus punctatus* (Zetterstedt)  
*L. rugulipennis* Poppius  
*Monosynamma bohemanni* (Fallén)  
*Pilophorus clavatus* (Linnaeus)  
*Pithanus hrabei* Stehlik  
*Polymerus cognatus* (Fieber)  
*P. unifasciatus* (Fabricius)  
*Psallus aethiops* (Zetterstedt)  
*P. falleni* Reuter  
*Stenodema trispinosa* Reuter  
*Teratocoris caricis* Kirkaldy  
*T. paludum* Sahlberg  
*Trigonotylus caelestialium* (Kirkaldy)  
*T. viridis* (Provancher)  
*Tytthus pubescens* (Knight)

## Family TINGIDAE

*Acalypta elegans* Horváth  
*Galeatus spinifrons* (Fallén)

## Family ARADIDAE

*Aradus lugubris* Fallén

## Family ALYDIDAE

*Alydus calcaratus* (Linnaeus)

## Family ISCHNORHYNCHIDAE

*Kleidocerys resedae* (Panzer)

## Family ORSILLIDAE

*Nysius thymi* (Wolff)

## Family RHYPAROCHROMIDAE

*Ligyrocorys sylvestris* (Linnaeus)  
*Peritrechus convivus* (Stål)  
*Scolopostethus thomsoni* Reuter  
*Sphragisticus nebulosus* (Fallén)  
*Trapezonotus arenarius* (Linnaeus)

## Family PENTATOMIDAE

*Sciocoris microphthalmus* Flor  
*Zicrona caerulea* (Linnaeus)

## 12. COSMOPOLITAN

## Family CIMICIDAE

*Cimex lectularius* Linnaeus

## Family LYCTOCORIDAE

*Lyctocoris campestris* (Fabricius)

## 13. INTRODUCED

## Family MIRIDAE

*Adelphocoris lineolatus* (Goeze)  
*Leptopterna dolabrata* (Linnaeus)  
*Melanotrichus flavosparsus* (Sahlberg)  
*Phytocoris populi* (Linnaeus)  
*Pithanus maerkeli* (Herrich-Schaeffer)  
*Plagiognathus chrysanthemi* (Wolff)

## Family ARTHENEIDAE

*Chilacis typhae* (Perris)

## Family RHYPAROCHROMIDAE

*Megalonotus sabulicola* (Thomason)  
*Stygnocoris rusticus* (Fallén)  
*S. sabulosus* (Schilling)

**Table 3.** Systematic list of the Heteroptera of the Prairies Ecozone. *Species checklist available at:* <http://dx.doi.org/10.5886/1hqp8r1s>

Infraorder NEPOMORPHA	Superfamily NOTONECTOIDEA
Superfamily NEPOIDEA	Family NOTONECTIDAE
Family BELOSTOMATIDAE	Subfamily ANISOPINAE
<i>Belostoma flumineum</i> Say	<i>Buenoa confusa</i> Truxal
<i>Lethocerus americanus</i> (Leidy)	<i>B. macrotibialis</i> Hungerford
<i>L. griseus</i> (Say)	<i>B. margaritacea</i> Torre Bueno
Family NEPIDAE	Subfamily NOTONECTINAE
<i>Ranatra fusca</i> Palisot	<i>Notonecta borealis</i> Hussey
Superfamily CORIXOIDEA	<i>N. insulata</i> Kirby
Family CORIXIDAE	<i>N. irrorata</i> Uhler
Subfamily CORIXINAE	<i>N. kirbyi</i> Hungerford
Tribe CORIXINI	<i>N. undulata</i> Say
<i>Arctocorisa sutilis</i> (Uhler)	Family PLEIDAE
<i>Callicorixa alaskensis</i> Hungerford	<i>Neoplea striola</i> (Fieber)
<i>C. audeni</i> Hungerford	Infraorder GERROMORPHA
<i>Cenocorixa bifida bifida</i> (Hungerford)	Superfamily MESOVELOIDEA
<i>C. dakotensis</i> (Hungerford)	Family MESOVELIIDAE
<i>C. expleta</i> (Uhler)	<i>Mesovelia mulsanti</i> White
<i>C. utahensis</i> (Hungerford)	Superfamily HEBROIDEA
<i>Corisella tarsalis</i> (Fieber)	Family HEBRIDAE
<i>Hesperocorixa atopodonta</i> (Hungerford)	<i>Hebrus burmeisteri</i> Lethierry & Severin
<i>H. laevigata</i> (Uhler)	<i>Merragata hebroides</i> White
<i>H. michiganensis</i> (Hungerford)	Superfamily HYDROMETROIDEA
<i>H. minorella</i> (Hungerford)	Family HYDROMETRIDAE
<i>H. scabricula</i> (Walley)	<i>Hydrometra martini</i> Kirkaldy
<i>H. vulgaris</i> (Hungerford)	Superfamily GERROIDEA
<i>Palmacorixa buenoi</i> Abbott	Family VELIIDAE
<i>P. gillettei gillettei</i> Abbot	Subfamily MICROVELIIDAE
<i>P. janeae</i> Brooks	<i>Microvelia buenoi</i> Drake
<i>Sigara alternata</i> (Say)	Family GERRIDAE
<i>S. bicoloripennis</i> (Walley)	Subfamily GERRINAE
<i>S. conocephala</i> (Hungerford)	<i>Aquarius nyctalis</i> (Drake & Hottes)
<i>S. decorata</i> (Abbott)	<i>A. remigis</i> (Say)
<i>S. decoratella</i> (Hungerford)	<i>Gerris buenoi</i> Kirkaldy
<i>S. fallenoidea</i> (Hungerford)	<i>G. comatus</i> Drake & Hottes
<i>S. grossolineata</i> Hungerford	<i>G. pingreensis</i> Drake & Hottes
<i>S. lineata</i> (Forster)	<i>Limnoporus dissortis</i> (Drake & Hottes)
<i>S. mathesoni</i> Hungerford	<i>L. notabilis</i> (Drake & Hottes)
<i>S. mullattensis</i> (Hungerford)	Subfamily RHAGODOTARSINAE
<i>S. penniensis</i> (Hungerford)	<i>Rheumatobates palosi</i> Blatchley
<i>S. solensis</i> (Hungerford)	Subfamily TREPOBATINAE
<i>S. trilineata</i> (Provancher)	<i>Metrobates hesperius</i> Uhler
<i>S. washingtonensis</i> Hungerford	Infraorder LEPTOPODOMORPHA
<i>Trichocorixa borealis</i> Sailer	Family SALDIDAE
<i>T. sexcincta</i> (Champion)	Subfamily CHILOXANTHINAE
<i>T. verticalis interiors</i> Sailer	<i>Pentacora signoreti</i> (Guérin-Méneville)
Tribe GLAENOCORISINI	
<i>Dasycorixa hybrida</i> (Hungerford)	
<i>D. johanseni</i> (Walley)	
<i>D. rawsoni</i> Hungerford	
Subfamily CYMATINAE	
<i>Cymatia americana</i> Hussey	

## Subfamily SALDINAE

## Tribe SALDINI

- Lampracanthia crassicornis* (Uhler)  
*Salda buenoi* (McDunnough)  
*S. obscura* Provancher  
*S. provancheri* Kelton & Lattin  
*Teloleuca bifasciata* (Thomson)  
*T. pellucens* (Fabricius)

## Tribe SALDOIDINI

- Micranthia bergrothi* Jakovlev  
*M. fennica* (Reuter)  
*Saldula bouchervillei* (Provancher)  
*S. comatula* Parshley  
*S. confluenta* (Say)  
*S. explanata* (Uhler)  
*S. laticollis* (Reuter)  
*S. nigrita* Parshley  
*S. opacula* (Zetterstedt)  
*S. opiparia* Drake & Hottes  
*S. orbiculata* (Uhler)  
*S. pallipes* (Fabricius)  
*S. palustris* (Douglas)  
*S. saltatoria* (Linnaeus)

## Infraorder CIMICOMORPHA

## Superfamily CIMICOIDEA

## Family CIMICIDAE

- Cimex lectularius* Linnaeus  
*C. pilosellus* (Horváth)  
*Oeciacus vicarius* Horváth

## Family ANTHOCORIDAE

## Tribe ANTHOCORINI

- Anthocoris antevolens* White  
*A. dimorphicus* Anderson & Kelton  
*A. musculus* (Say)  
*A. tomentosus* Péricart  
*Tetraphleps canadensis* Provancher  
*T. furvus* Van Duzee

## Tribe ORIINI

- Macrotracheliella nigra* Parshley  
*Orius insidiosus* (Say)  
*O. tricolor* (White)

## Tribe DUFOURIELLINI

- Cardiastethus borealis* Kelton

## Tribe XYOLCORINI

- Xylocoris californicus* (Reuter)  
*X. galactinus* (Fieber)  
*X. hirtus* Kelton

## Family LYCTOCORIDAE

- Lycetocoris campestris* (Fabricius)

## Family NABIDAE

## Subfamily NABINAE

## Tribe NABINI

- Nabicula americolimbata* (Carayon)  
*N. flavomarginata* (Scholtz)  
*N. nigrovittata nearctica* Kerzhner  
*N. propinqua* (Reuter)  
*N. subcoleoprata* Kirby  
*N. vanduzeei* (Kirkaldy)  
*Nabis alternatus* Parshley  
*N. americanoferus* Carayon  
*N. roseipennis* Reuter  
*N. rufusculus* Reuter

## Subfamily PROSTEMMATINAE

## Tribe PROSTEMMATINI

- Pagasa fusca* (Stein)  
*P. nigripes* Harris

## Superfamily MIROIDEA

## Family MIRIDAE

## Subfamily BRYOCORINAE

## Tribe DICYPHINI

- Dicyphus discrepans* Knight  
*D. hesperus* Knight  
*Tupiocoris confusus* (Kelton)  
*T. similis* (Kelton)  
*T. tibialis* (Kelton)

## Tribe ECCRITOTARSINI

- Sixeonotus rostratus* Knight

## Subfamily CYLAPINAE

## Tribe CYLAPINI

- Fulvius slateri* Wheeler

## Subfamily DERAEOCORINAE

## Tribe CLIVENEMATINI

- Clivinema villosum* Reuter

## Tribe DERAEOCORINI

- Deraeocoris albigulus* Knight  
*D. aphidophagus* Knight  
*D. brevis* (Uhler)  
*D. fasciolus* Knight  
*D. histrio* (Reuter)  
*D. nitenatus* Knight  
*D. ornatus* Knight  
*D. quercicola* Knight  
*D. triannulipes* Knight

## Tribe HYALIODINI

- Hyaliodes harti* Knight

## Subfamily MIRINAE

## Tribe MIRINI

- Adelphocoris lineolatus* (Goeze)  
*A. rapidus* (Say)  
*Agnocoris pulverulentus* (Uhler)

- A. rubicundus* (Fallén)  
*Capsus cinctus* (Kolenati)  
*Dichrooscytus ruberellus* Knight  
*Henrilygus ultranubilus* (Knight)  
*Irbisia brachycera* (Uhler)  
*I. elongata* Knight  
*I. fuscipubescentes* Knight  
*I. nigripes* Knight  
*Lygidea annexa* (Uhler)  
*L. rosacea* Reuter  
*L. salicis* Knight  
*Lygocoris pabulinus* (Linnaeus)  
*L. rugicollis* (Fallén)  
*Lygus atritibialis* Knight  
*L. borealis* (Kelton)  
*L. convexicollis* Reuter  
*L. elisus* Van Duzee  
*L. keltoni* Schwartz  
*L. lineolaris* (Palisot)  
*L. plagiatus* Uhler  
*L. potentillae* Kelton  
*L. punctatus* (Zetterstedt)  
*L. robustus* (Uhler)  
*L. rubroclarus* Knight  
*L. rubrosignatus* Knight  
*L. rufidorsus* (Kelton)  
*L. rugulipennis* Poppius  
*L. shulli* Knight  
*L. solidaginis* (Kelton)  
*L. striatus* Knight  
*L. unctuosus* (Kelton)  
*L. vanduzeei* Knight  
*Metriorrhynchomiris dislocatus* (Say)  
*Neolygus atritylus* (Knight)  
*N. belfragei* (Reuter)  
*N. canadensis* (Knight)  
*N. communis* (Knight)  
*N. omnivagus* (Knight)  
*N. quercalbae* (Knight)  
*N. viticollis* (Reuter)  
*Neurocolpus nubilus* (Say)  
*Orthops scutellatus* Uhler  
*Phytocoris brimleyi* Knight  
*P. brooksi* Kelton  
*P. conspersipes* Reuter  
*P. conspurcatus* Knight  
*P. erectus* Van Duzee  
*P. laevis* (Uhler)  
*P. lasiomeris* Reuter  
*P. listi* Knight  
*P. neglectus* Knight  
*P. onustus* Van Duzee  
*P. pallidicornis* Reuter  
*P. populi* (Linnaeus)  
*P. salicis* Knight  
*P. validus* Reuter  
*Pinalitus rostratus* Kelton  
*Poecilocapsus lineatus* (Fabricius)  
*Polymerus balli* Knight  
*P. basivittis* (Reuter)  
*P. brevirostris* Knight  
*P. chrysopsis* Knight  
*P. cognatus* (Fieber)  
*P. diffusus* (Uhler)  
*P. flavocostatus* Knight  
*P. hirtus* Knight  
*P. rubrocuneatus* Knight  
*P. rufipes* Knight  
*P. sculleni* Knight  
*P. severini* Knight  
*P. unifasciatus* (Fabricius)  
*P. venaticus* (Uhler)  
*Salignus tahoenis* (Knight)  
*Taedia pallidula* (McAtee)  
*Tropidosteptes amoenus* Reuter  
*T. brooksi* Kelton  
*T. canadensis* Van Duzee  
*T. commisuralis* (Reuter)  
*T. palmeri* (Reuter)  
*T. pettiti* Reuter  
*T. pubescens* (Knight)
- Tribe RESTHENINI
- Opistheurista cladestina* (Van Duzee)  
*Prepops bivittis* (Stål)  
*P. borealis* (Knight)  
*P. eremicola* (Knight)  
*P. fraternus* (Knight)  
*P. nigripilus* (Knight)  
*P. rubellicollis* (Knight)  
*P. zonatus* (Knight)
- Tribe STENODEMINI
- Collaria meillearii* Provancher  
*Leptopterna amoena* Uhler  
*L. dolobrata* (Linnaeus)  
*Litomiris debilis* (Uhler)  
*Mimoceps insignis* Uhler  
*Pithanus hrabei* Stehlik  
*P. maerkeli* (Herrich-Schaeffer)  
*Stenodema pilosipes* Kelton  
*S. trispinosa* Reuter  
*S. vicinum* (Provancher)  
*Teratocoris caricis* Kirkaldy  
*T. discolor* Uhler  
*T. paludum* Sahlberg  
*Trigonotylus americanus* Carvalho  
*T. antennatus* Kelton  
*T. brooksi* Kelton  
*T. caelestialium* (Kirkaldy)  
*T. canadensis* Kelton  
*T. flavicornis* Kelton  
*T. tarsalis* (Reuter)  
*T. viridis* (Provancher)

## Subfamily ORTHOTYLINAE

## Tribe HALTICINI

*Halticus intermedius* Uhler  
*Labops brooksi* Slater  
*L. burmeisteri* Stål  
*L. hesperius* Uhler  
*L. hirtus* Knight  
*L. tumidifrons* Knight

## Tribe ORTHOTYLINI

*Aoplonema princeps* Uhler  
*A. rubrum* Forero  
*Blepharidopterus diaphanus* (Kirshbaum)  
*B. provancheri* (Burque)  
*Brooksetta chelifera* (Knight)  
*B. inconspicua* (Uhler)  
*B. incurva* (Knight)  
*B. viridicata* (Uhler)  
*Ceratocapsus digitulus* Knight  
*C. geminatus* Knight  
*C. modestus* (Uhler)  
*C. nigricephalus* Knight  
*C. pilosulus* Knight  
*Cyrtorhinus caricis* (Fallén)  
*Fieberocapsus flaveolus* (Reuter)  
*Hadronema bispinosum* Knight  
*H. breviatum* Knight  
*H. militare* Uhler  
*H. simplex* Knight  
*Ilnacora albifrons* Knight  
*I. stalii* Reuter  
*I. vittifrons* Knight  
*Labopidea brooksi* Kelton  
*L. lenensis* (Lindberg)  
*L. pallida* Knight  
*L. planifrons* Knight  
*Lopidea balli* Knight  
*L. confluenta* (Say)  
*L. confraterna* (Gibson)  
*L. dakota* Knight  
*L. lathyri* Knight  
*L. media* (Say)  
*L. minor* Knight  
*L. nigridea serica* Knight  
*L. picta* Knight  
*L. teton* Knight  
*Mecomma angustatum* (Uhler)  
*M. gilvipes* (Stål)  
*Melanotrichus albocostatus* (Van Duzee)  
*M. atriplicis* Knight  
*M. brindleyi* Knight  
*M. coagulatus* (Uhler)  
*M. flavosparsus* (Sahlberg)  
*M. leonardi* (Kerzhner & Schuh)  
*M. leviculus* Knight  
*M. wallisi* Kelton  
*Noctuocoris fumidus* (Van Duzee)  
*Orthotylus angulatus* (Uhler)  
*O. basicornis* Knight  
*O. candidatus* Van Duzee

*O. dorsalis* (Provancher)  
*O. fuscicornis* Knight  
*O. neglectus* Knight  
*O. notabilis* Knight  
*O. nyctalis* Knight  
*O. ornatus* Van Duzee  
*O. pennsylvanicus* Henry  
*O. ute* Knight  
*Parthenicus brooksi* Kelton  
*Pseudopsallus anograe* Knight  
*P. demensus* (Van Duzee)  
*P. sericatus* (Uhler)  
*Reuteria querci* (Say)  
*Schaffneria davisii* (Knight)  
*S. pilophoroides* (Knight)  
*Sericophanes heidemanni* Poppius  
*Slaterocoris atritibialis* (Knight)  
*S. breviatus* (Knight)  
*S. pallidicornis* (Knight)  
*S. stygicus* (Say)

## Subfamily PHYLINAE

## Tribe PRONOTOCREPINI

*Coquillettia albertae* Kelton  
*C. schwartzi* Wyniger  
*Orectoderus montanus* Knight  
*O. obliquus* Uhler  
*O. salicis* Knight

## Tribe LEUCOPHOROPTERINI

*Tytthus pubescens* (Knight)

## Tribe PHYLINI

*Americodema nigrolineatum* (Knight)  
*Atomoscelis onustus* (Fieber)  
*Atractotomus atricolor* (Knight)  
*Chlamydatum artemisiae* Kelton  
*C. associatus* (Uhler)  
*C. keltoni* Schuh & Schwartz  
*C. obliquus* (Uhler)  
*C. pallidicornis* Knight  
*C. pulcarius* (Fallén)  
*C. ruficornis* Knight  
*Conostethus americanus* Knight  
*Criocoris saliens* (Reuter)  
*Dacota hesperia* (Uhler)  
*Europiella angulata* (Uhler)  
*E. artemisiae* (Becker)  
*E. consors* (Uhler)  
*E. decolor* (Uhler)  
*E. pilosellus* (Uhler)  
*E. unipuncta* Knight  
*Hoplomachus affiguratus* (Uhler)  
*Megalopsallus femoralis* Kelton  
*M. nigrofemoratus* (Knight)  
*M. rubropictipes* Knight  
*M. sparsus* (Van Duzee)  
*Microphyllellus fuscicornis* Knight  
*Monosynamma bohemani* (Fallén)  
*Phoenicocoris longirostris* (Knight)

*P. rostratus* (Knight)  
*Phyllophidea montana* Knight  
*Piceophylus keltoni* Schwartz & Schuh  
*Plagiognathus albatus* (Van Duzee)  
*P. alboradialis* Knight  
*P. annulatus* Uhler  
*P. blatchleyi* Reuter  
*P. brunneus* (Provancher)  
*P. chrysanthemii* (Wolff)  
*P. davisii* Knight  
*P. dispar* Knight  
*P. flavidus* Knight  
*P. fuscipes* Knight  
*P. fuscus* (Provancher)  
*P. guttatipes* (Uhler)  
*P. laricicola* Knight  
*P. longirostris* (Knight)  
*P. maculipennis* (Knight)  
*P. modestus* (Reuter)  
*P. negundinus* Knight  
*P. nigronitens* Knight  
*P. parshleyi* (Knight)  
*P. shoshonea* Knight  
*P. suffuscipennis* Knight  
*P. tumidifrons* (Knight)  
*Psallivius piceicola* (Knight)  
*Psallus aethiops* (Zetterstedt)  
*P. falleni* Reuter  
*Pseudatomoscelis seriatus* (Reuter)

## Tribe PILOPHORINI

*Pilophorus americanus* Poppius  
*P. amoenus* Uhler  
*P. clavatus* (Linnaeus)  
*P. furvus* Knight  
*P. neoclavatus* Schuh & Schwartz  
*P. piceicola* Knight  
*P. salicis* Knight  
*P. setiger* Knight  
*P. uhleri* Knight  
*P. vicarius* Poppius

## Superfamily TINGOIDEA

## Family TINGIDAE

## Tribe TINGINI

*Acalypta elegans* Horváth  
*Corythaica acuta* (Drake)  
*C. venusta* (Champion)  
*Corythucha arcuata* (Say)  
*C. bellula* Gibson  
*C. cydoniae* (Fitch)  
*C. distincta* Osborn & Drake  
*C. elegans* Drake  
*C. hewitti* Drake  
*C. marmorata* (Uhler)  
*C. mollicula* Osborn & Drake  
*C. pallipes* Parshley  
*C. salicata* Gibson  
*Dictyla labeculata* (Uhler)  
*Galeatus spinifrons* (Fallén)  
*Hesperotingis antennata* Parshley

*H. fuscata* Parshley  
*H. occidentalis* Drake  
*Leptoypa mutica* (Say)  
*Melanorhopala clavata* (Stål)  
*Physatocheila plexa* (Say)  
*P. variegata* Parshley

## Superfamily REDUVIOIDEA

## Family REDUVIIDAE

## Subfamily EMESINAE

## Tribe METAPTERINI

*Barce fraterna* (Say)

## Subfamily HARPACTORINAE

*Fitchia spinosula* Stål

*Rhynocoris ventralis* (Say)

*Sinea diadema* (Fabricius)

*Zelus tetracanthus* Stål

## Subfamily STENOPODAINAE

*Pygolampis pectoralis* (Say)

## Family PHYMATIDAE

## Subfamily PHYMATINAE

*Phymata americana americana* Melin

*P. vicina vicina* Handlirsch

## Infraorder PENTATOMOMORPHA

## Superfamily ARADOIDEA

## Family ARADIDAE

## Subfamily ANEURINAE

*Aneurus simplex* Uhler

## Subfamily ARADINAE

*Aradus abbas* Bergroth

*A. acutus* Say

*A. compressus* Heidemann

*A. funestus* Bergroth

*A. insolitus* Van Duzee

*A. intectus* Parshley

*A. kormilevi* Heiss

*A. lugubris* Fallén

*A. parshleyi* Van Duzee

*A. persimilis* Van Duzee

*A. proboscideus* Walker

*A. quadrilineatus* Say

*A. tuberculifer* Kirby

*A. uniannulatus* Parshley

## Superfamily COREOIDEA

## Family ALYDIDAE

## Subfamily ALYDINAE

*Alydus calcaratus* (Linnaeus)

*A. conspersus conspersus* Montandon

*A. conspersus infuscatus* Fracker

*A. eurinus* (Say)

*A. scutellatus* Van Duzee

*Megalotomus quinquespinosus* (Say)

*Stachyocnemus apicalis* (Dallas)

*Tollius curtulus* (Stål)

## Subfamily MICROELYTRINAE

*Protenor belfragei* Haglund

## Family COREIDAE

## Subfamily COREINAE

## Tribe ANISOSCELIDINI

*Leptoglossus occidentalis* Heidemann

## Subfamily CHELINIDEINI

*Chelinidea vittiger* Uhler

## Tribe COREINI

*Catorhintha mendica* Stål*Nisoscolopocerus apiculatus* Barber

## Subfamily MEROPACHYDINAE

## Tribe MEROCORINI

*Merocoris distinctus* Dallas

## Subfamily PSEUDOPHLOEINAE

*Coriomeris humilis* (Uhler)

## Family RHOPALIDAE

## Subfamily RHOPALINAE

## Tribe HARMOSTINI

*Harmostes reflexulus* (Say)

## Tribe NEISTHREINI

*Arhyssus lateralis* (Say)*A. scutatus* (Stål)

## Tribe RHOPALINI

*Stictopleurus punctiventris* (Dallas)*S. viridicatus* (Uhler)

## Subfamily SERINETHINAE

*Boisea trivittata* (Say)

## Superfamily LYGAEOIDEA

## Family ARTHENEIDAE

*Chilacis typhae* (Perris)

## Family BERYTIDAE

## Subfamily BERYTINAE

*Neoneides muticus* (Say)

## Subfamily METACANTHINAE

*Jalysus wickhami* Van Duzee

## Family BLISSIDAE

*Blissus canadensis* Leonard*B. occidius* Barber*Ischnodemus hesperius* Parshley

## Family CYMIDAE

*Cymus angustatus* Stål*C. coriacipennis* (Stål)*C. luridus* Stål

## Family GEOCORIDAE

*Geocoris atricolor* Montandon*G. bullatus* (Say)*G. discopterus* Stål*G. howardi* Montandon*G. limbatus* Stål*G. pallens* Stål

## Family ISCHNORHYNCHIDAE

*Kleidocerys ovalis* Barber*K. resedae* (Panzer)

## Family LYGAEIDAE

*Lygaeospilus tripunctatus* (Dallas)*Lygaeus kalmii angustomarginatus* Parshley*L. kalmii kalmii* Stål*Melacoryphus admirabilis* (Uhler)*M. lateralis* (Dallas)*Melanopleurus perplexus* Scudder*M. pyrrhopterus* (Stål)

## Family ORSILLIDAE

## Tribe METRARGINI

*Xyonysius californicus* (Stål)

## Tribe NYSIINI

*Nysius angustatus* Uhler*N. niger* Baker*N. raphanus* Howard*N. tenellus* Barber*N. thymi* (Wolff)

## Tribe ORSILLINI

*Neortholomus scolopax* (Say)

## Family OXYCARENIDAE

*Crophius bohemani* (Stål)*C. disconotus* (Say)*C. ramosus* Barber

## Family RHYPAROCHROMIDAE

## Subfamily PLINTHISINAE

*Plinthisus americanus* Van Duzee*P. indentatus* Barber

## Subfamily RHYPAROCHROMINAE

## Tribe ANTILLOCORINI

*Antillocoris minutus* (Bergroth)

## Tribe DRYMINI

*Drymus unus* (Say)*Eremocoris borealis* (Dallas)*E. ferus* (Say)*Scolopostethus thomsoni* Reuter

## Tribe GONIANOTINI

*Atrazonotus umbrosus* (Distant)*Emblethis vicarius* Horváth*Trapezonotus arenarius* (Linnaeus)

## Tribe MEGALONOTINI

*Megalonotus sabulicola* (Thomson)  
*Sphragisticus nebulosus* (Fallén)

## Tribe MYODOCHINI

*Kolenetrus plenus* (Distant)  
*Ligyrocoris diffusus* (Uhler)  
*L. sylvestris* (Linnaeus)  
*Perigenes constrictus* (Say)  
*Sisamnes claviger* (Uhler)  
*Slaterobius insignis* (Uhler)  
*Zeridoneus costalis* (Van Duzee)  
*Z. petersoni* Reichart

## Tribe RHYPAROCHROMINI

*Peritrechus convivus* (Stål)  
*P. fraternus* Uhler  
*Uhleriola floralis* (Uhler)

## Tribe STYGNOCORINI

*Stygnocoris rusticus* (Fallén)  
*S. sabulosus* (Schilling)

## Tribe UDEOCORINI

*Neosuris castanea* (Barber)

## Superfamily PIESMATOIDEA

## Family PIESMATIDAE

*Parapiesma cinereum* (Say)  
*P. explanatum* (McAtee)  
*Piesma costatum* (Uhler)  
*P. patruela* McAtee

## Superfamily PENTATOMOIDEA

## Family ACANTHOSOMATIDAE

*Elasmotethus cruciatus* (Say)  
*Elasmucha lateralis* (Say)

## Family CYDNIDAE

## Subfamily CYDNINAE

*Microporus obliquus* Uhler

## Subfamily SEHIRINAE

*Sehirus cinctus albonotatus* Dallas

## Family PENTATOMIDAE

## Subfamily ASOPINAE

*Apoecilus bracteatus* (Fitch)  
*A. cynicus* (Say)  
*Perillus bioculatus* (Fabricius)  
*P. circumcinctus* Stål  
*P. exaptus* (Say)  
*Podisus brevispinus* Phillips  
*P. maculiventris* (Say)  
*P. placidus* Uhler  
*P. serieiventris* Uhler  
*Rhacognathus americanus* Stål  
*Zicrona caerulea* (Linnaeus)

## Subfamily PENTATOMIDAE

## Tribe HYALINI

*Brochymena quadripustulata* (Fabricius)

## Tribe PENTATOMINI

*Aelia americana* Dallas  
*Banasa dimidiata* (Say)  
*Chlorochroa belfragei* (Stål)  
*C. faceta* (Say)  
*C. granulosa* (Uhler)  
*C. ligata* (Say)  
*C. opuntiae* Esselbaugh  
*C. persimilis* Horváth  
*C. uhleri* (Stål)  
*C. viridicata* (Walker)  
*Codophila remota* (Horváth)  
*Coenus delius* (Say)  
*Cosmopepla intergressus* (Uhler)  
*C. lintneriana* Kirkaldy  
*Euschistus servus euschistoides* (Vollenhoven)  
*E. tristigma luridus* Dallas  
*Holcostethus abbreviatus* Uhler  
*H. limbolarius* (Stål)  
*H. macdonaldi* Rider & Rolston  
*H. tristis* (Van Duzee)  
*Meneclis insertus* (Say)  
*Neottiglossa sulcifrons* Stål  
*N. trilineata* (Kirby)  
*N. undata* (Say)  
*Tepa rugulosa* (Say)  
*Thyanta accerra* McAtee  
*Trichopepla atricornis* Stål

## Tribe SCIOCORINI

*Sciocoris microphthalmus* Flor

## Family SCUTELLERIDAE

## Subfamily EURYGASTRINAE

*Euptychodera corrugata* (Van Duzee)  
*Eurygaster alternata* (Say)  
*E. amerinda* Bliven  
*Fokkeria producta* (Van Duzee)  
*Phimodera binotata* (Say)  
*Vanduzeeina balli* (Van Duzee)

## Subfamily PACHYCORINAE

*Homaemus aeneifrons aeneifrons* Uhler  
*Homaemus aeneifrons consors* Uhler  
*H. bijugis* (Uhler)

## Family THYREOCORIDAE

*Corimelaena nigra* Dallas  
*C. pulicaria* (Germar)  
*Galgupha atra* Amyot & Serville  
*G. nitiduloides* (Wolff)  
*G. ovalis* Hussey



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## Chapter 11

# Canadian Grasslands and Their Endemic Leafhoppers (Hemiptera: Auchenorrhyncha: Cicadellidae)

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**Abstract.** The greatest numbers of leafhopper species endemic to Canada are those of grasslands, 33 of which are known. A far larger number, 263 species, are more broadly endemic to Nearctic grasslands. All 296 demonstrate strong regional differences not widely recognized in ecoregional classifications. Most endemics come from the open prairies (174 species). Second most numerous are the various faunas on comparatively tiny intermontane grasslands of southern British Columbia with 126 endemics, including the newly recorded *Dikrella nevadensis* (Lawson), here reinstated from synonymy. Of these endemics, 96 are found in the Okanagan-Similkameen valley system, 43 belong to the East Kootenays, and another 43 are found near Victoria and Vancouver, with numerous overlaps. One is known only from North Beach on the Haida Gwaii (Queen Charlotte) Islands and this is related to an endemic on Vancouver Island and the adjacent mainland. The fauna of the isolated, more northerly fescue grasslands have 80 endemics (39 in the Peace River district, 25 in the Thompson valley system and 43 in the lower Fraser River valley and its lesser tributaries), and these are similar to the fauna of aspen parkland. An additional 58 endemics are characteristic of the Prairie Peninsula, of which 21 are found on the tallgrass prairie of southernmost Ontario, as contrasted to 23 from alkaline fens, 21 from beaches, 16 from alvars, and 4 from sand plains, many of which are shared with oak savanna. Beringian grasslands have 24 grassland endemics, two of which inhabit arctic areas of the Yukon. Each of these isolated grasslands and their subdivisions have their own endemics and unique histories, many traceable to separate glacial-age refugia. Understanding the rich endemic biota of the many distinctive grassland types in Canada is essential in characterizing their ecology and in setting conservation priorities.

**Résumé.** Les prairies canadiennes renferment le plus grand nombre d'espèces endémiques de cicadelles du pays, dont 33 sont connues. Le nombre d'espèces généralement endémiques aux prairies néarctiques est beaucoup plus considérable, s'établissant à 263. Toutes ces 296 espèces laissent constater d'importantes différences régionales qui ne sont pas largement reconnues dans le système de classification des écorégions. La plupart des espèces endémiques habitent des prairies dégagées (174). Au second rang viennent les diverses entomofaunes vivant dans les prairies intermontagneuses de superficie comparativement plus petite du sud de la Colombie-Britannique, où l'on trouve 126 espèces endémiques, y compris une nouvelle mention avec *Dikrella nevadensis* (Lawson), ici rétabli comme espèce valide. De toutes ces espèces endémiques, 96 se trouvent dans le système de vallées Okanagan-Similkameen, 43 se trouvent dans la portion orientale du bassin de la Kootenay, et 43 autres se trouvent près de Victoria et de Vancouver, plusieurs coexistant dans le même habitat. Une des espèces n'est connue qu'à North Beach, dans l'archipel Haida Gwaii (Îles de la Reine-Charlotte), et s'apparente à une espèce endémique de l'île de Vancouver et de la zone continentale adjacente. La faune de la prairie à fétuque, isolée et plus nordique, compte 80 espèces endémiques (39 dans le district de Peace River, 25 dans la vallée de la rivière Thompson et 43 dans la vallée du bas Fraser et de ses affluents), et ressemble à la faune de la tremblaie-parc. Cinquante-huit autres espèces endémiques sont caractéristiques de la péninsule de Prairie, parmi lesquelles 21 s'observent dans la prairie à herbes hautes de l'extrême-sud de l'Ontario, alors qu'on en trouve 23 dans les tourbières alcalines, 21 sur les plages, 16 dans les alvars et 4 sur les deltas d'eskers, dont plusieurs se trouvent également dans les chênaies-parcs. Les prairies béringiennes renferment 24 espèces endémiques des prairies, dont deux habitent

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les régions arctiques du Yukon. Chacune de ces prairies isolées et de leurs subdivisions possèdent leurs propres espèces endémiques et présentent une histoire qui leur est propre et qui remonte souvent à des refuges distincts de l'âge glaciaire. Il est essentiel de bien connaître les riches biotes endémiques des nombreux types distinctifs de prairies du Canada pour pouvoir en caractériser l'écologie et établir les priorités en matière de conservation.

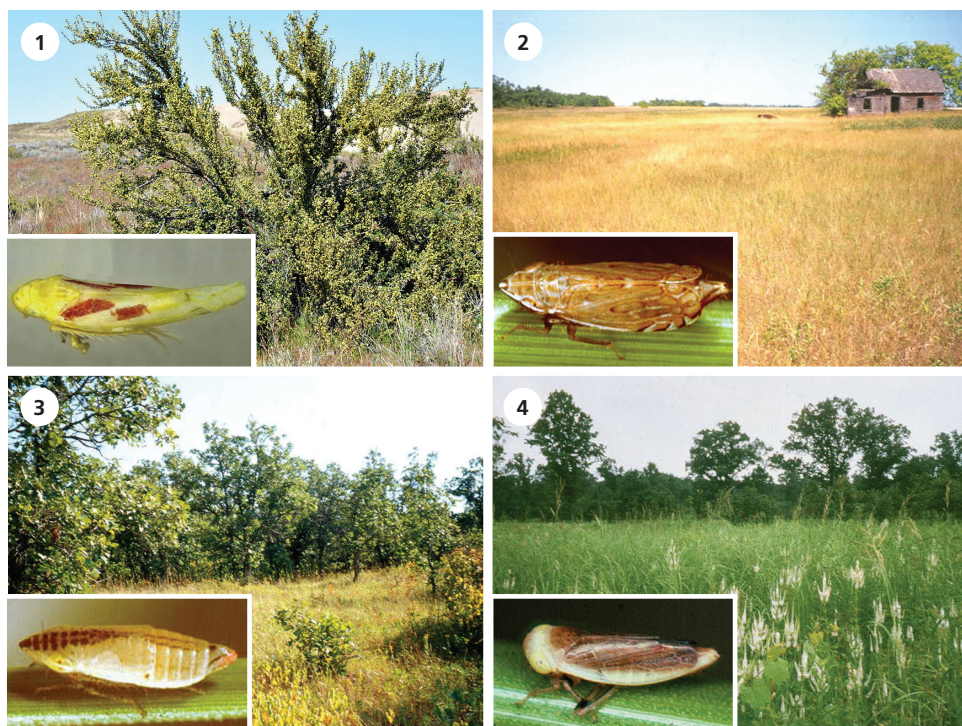
## Introduction

Grasslands in Canada include some of the most endangered habitats in the country. They are usually in prime agricultural areas and are also easily converted to other uses. Conserving the remaining areas and their endemic insects is an urgent, ever-growing problem. Unfortunately, grasslands are usually described in ecological generalizations that have little value to conservation priorities. The oldest such classification system differentiates eastern from western prairies according to the height of dominant grass species. This is simple, convenient, and still often cited (e.g., Anderson 2006). Such generalizations are misleading, however, because they are subject to extreme variation. For example, in Manitoba, big bluestem (the most prominent tall grass of the eastern grasslands) grows more than 1 m tall immediately after a burn, or when summer temperatures are higher than usual; otherwise, it may grow prostrate like crab grass (pers. obs.).

Biogeographical regions of the North American prairies are more accurately represented by the species of dominant and subdominant plants (Coupland 1952; Munroe 1956; Küchler 1964). This system, in turn, has been replaced in Canada by an Ecozone classification according to substrate type (Smith *et al.* 1996; Shorthouse 2010; Shorthouse and Larson 2010), which is designed to give a long-term perspective to ecology. The Prairies Ecozone can be subdivided into ecoprovinces, ecoregions, and ecodistricts. This classification system has been adapted and further extended to embrace endemic organisms (Ricketts *et al.* 1999) as a criterion for delimiting ecoregions with ancient roots. Unfortunately, this ecoregional classification of the Prairies Ecozone does not consider the important contribution made by the numerous endemic leafhoppers to the biodiversity found there (Hamilton 2005a).

Leafhoppers (Hemiptera: Cicadellidae) are many and varied, often being easy to collect. There are more than 20,000 species of leafhoppers described worldwide (Oman *et al.* 1990), of which some 1,200 occur in Canada (Maw *et al.* 2000). Grassland leafhoppers (Figs. 1–4) are so common that, at any one spot, they usually comprise about 50% of the contents of a sweep net. Their numbers can be so great that 100 sweeps are considered to be an adequate representation of their fauna for a particular site: two historical records from 1920 of *Xerophloea* in Nebraska reported swarming in such great numbers that their dead bodies gathered under street lights in drifts up to 5 cm thick (Lawson 1931).

The first regional list of a grassland leafhopper fauna in Canada, from Alberta, was issued 60 years ago (Strickland 1953). It contained 124 dubiously identified species, of which perhaps as many as 40 valid species were from grasslands and represented only about 9% of the leafhoppers now known from the province (Maw *et al.* 2000). Some very common species that are prominent among those 40 species are not limited to the Prairies, for example, *Draeculacephala* feeding on sedges in sloughs as well as in northern fens; the widespread northern leafhoppers *Cuerna septentrionalis* (Walker), *Diplocolenus configuratus* (Uhler), and *D. evansi* (Ashmead); the generalist *Driotura gammaroides* (Van Duzee); and the southern migrant or “tramp” species *Endria inimica* (Say) and *Exitianus exitiosus* (Uhler). Two common species that are absent from the list came as invasives to Alberta only in recent years: *Athysanus argentarius* Metcalf and *Doratura stylata*



**Figs. 1–4.** Leafhoppers associated with Canadian grasslands, west to east: 1, *Dikrella nevadensis* on *Purshia tridentata* on Cordilleran grasslands; 2, *Flexamia graminea* on true tallgrass prairie in western Manitoba (this site is dominated by needlegrass and little bluestem on glacial till with big bluestem on the more mesic periphery); 3, *Aflexia rubranura* on oak savanna of Manitoba; 4, *Limotettix* (*Dryola*) *elegans* on low spikerush in “tallgrass” oak openings at Windsor, Ontario (dominated by big bluestem and cordgrass in mesic areas, little bluestem on sandy uplands). Photograph of *Purshia*, taken in Washington by Robert Carr, and of insects by J. Elsaesser (1) and Chris Dietrich (2–4).

(Boheman). The failure to discover more leafhoppers from an area that was at the time largely resilient native grassland may be attributed in part to the difficulties of accessing sites. Road maps from the early 1950s show only four paved roads of any extent anywhere on the Canadian Prairies, supplemented by a broken grid work of gravel roads spaced an average of 60 km apart. The majority of early collections were taken along these primitive roads (Fig. 5). Collecting leafhoppers has become much easier since those days (Fig. 6) with the development of extensive paved road networks, especially on the Prairies. Unfortunately, these same roads have also divided native areas, opening up more land to crops and destroying remaining native grasslands. For example, many of the extensive tracts of grassland recorded by Coupland (1973) have vanished or been reduced to small holdings of varying quality, making assessment of the remainder a daunting task.

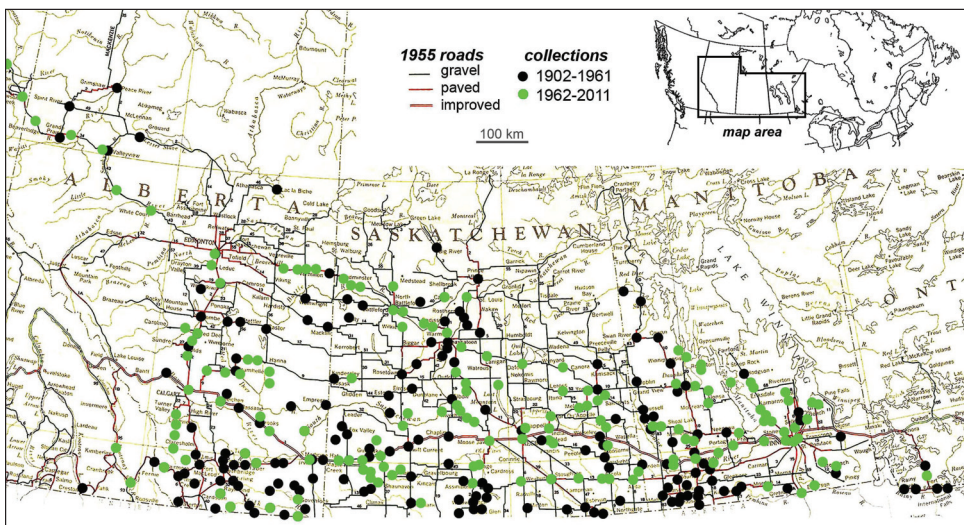
The first summary of the Canadian leafhopper fauna was compiled by the Irish lepidopterist B.P. Beirne (1956). He did little collecting personally and his summary of 480 Canadian leafhoppers was based almost entirely on specimens in the Canadian National Collection of Insects (CNCI). He did note, however, that 11 of the 70 genera were grass feeders and another 29 genera probably included grass feeders.



The first survey of grassland leafhoppers in Canada was taken over a 10-year period by A.R. Brooks (Fig. 7, yellow sites). He sampled relatively few prairie remnants each year, and the summer of 1960 was devoted almost entirely to repeated surveying of the area around Elbow, Saskatchewan, a site he had visited twice in earlier years. The impetus for a whole collecting season devoted to this one area was almost certainly two dams that were being built in 1958 to flood the valley of the South Saskatchewan River valley to form Lake Diefenbaker. After this last survey of Saskatchewan, his only subsequent collecting trips were a 1961 tour of the Athabasca and Peace River districts of Alberta and a revisit to Elbow in May of 1964.

The first intensive leafhopper transect across Canada was organized in 1968 by H.H. Ross of the Illinois Natural History Survey. Collecting began in Saskatchewan on the way to the Alaska Highway (Fig. 7, purple sites). This survey made many notable finds, with sampling targeted to grasses in the Peace River district of Alberta and points farther north. Subsequent taxonomic work based on these samples (Ross 1970; Ross and Hamilton 1970; Hamilton and Ross 1972, 1975) revealed the importance of highly localized grasslands outside the boundaries of the Prairies as reservoirs of relict grassland faunas (Fig. 8) and generated evidence that prairie leafhoppers survived Pleistocene glaciation in two main habitats: the high plains of Texas and the unglaciated valleys of Beringia.

Subsequent studies of leafhoppers in Manitoba during the summer of 1963 (Hamilton 1972) and surveys conducted in the Yukon (1979–1988), Grasslands National Park (1995) and adjacent grasslands of Saskatchewan (1994–1995), the grasslands of Ontario (Hamilton 1994a, 1997, 2002a, 2002b, 2005a; Skevington *et al.* 2001; Bouchard *et al.* 2002; Paiero *et al.* 2003), and tallgrass prairie in Winnipeg (Wade and Roughley 2010) were complemented by similar studies in the United States (Whitcomb *et al.* 1994; Hamilton 1995, 2012). This recent collecting shows that approximately 300 Canadian leafhopper species are



**Fig. 5.** Collecting localities for leafhoppers of Canadian grasslands mapped against main roads extant in 1955 (base map @Department of Natural Resources Canada). Early sites (to 1961, indicated by black circles) were less precisely indicated than those of later collections (green circles) and lacked data on host plants and habitats. CNCI data is supplemented by records from Manitoba (Hamilton 1972).

probably endemic to grasslands, or 25% of all Canadian species. These represent 40% of all leafhopper species that occur west of Ontario (Maw *et al.* 2000). All common but regionalized grassland-endemic leafhoppers are restricted to dominant or subdominant plants (Hamilton and Whitcomb 2010). These intimate insect–host relationships are the basis of biogeographical analysis (Hamilton 2002*b*, 2005*a*, 2005*b*, 2009), and particularly those leafhoppers with flightless females (Hamilton 1994*a*; Hamilton and Zack 1999) suggest additional refugia once existed in periglacial areas south of the ice front (Marie-Victorin 1938) and on the Gulf coast of the southeastern United States (Hamilton 2012). The historical roots of the biota can be assessed by analyzing which endemic species have ranges adjacent to such probable glacial-age refugia (Table 1).

The numbers of grassland-endemic leafhoppers in Canada seem surprising in light of the fact that most of the grasslands, including those of adjacent states, were glaciated during the Pleistocene. Furthermore, such northern grasslands have been reported as having a depauperate fauna compared with those of the southern prairies (e.g., Whitcomb

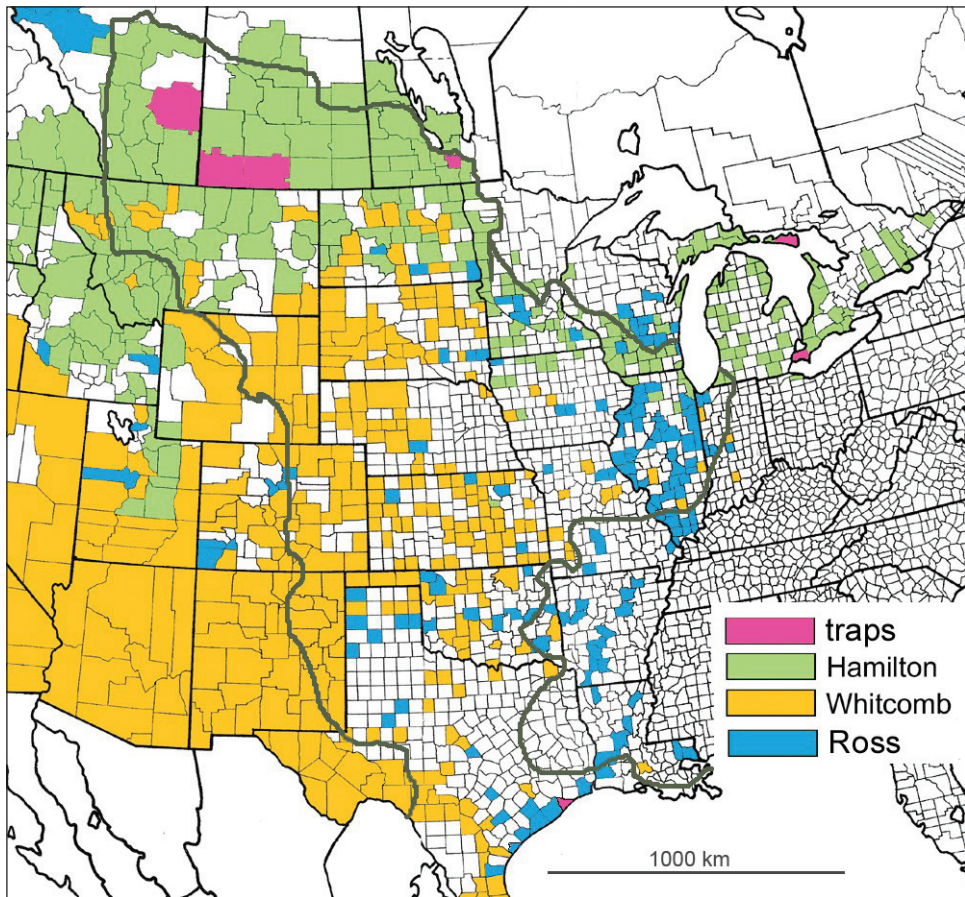


Fig. 6. Sampling coverage for the prairies and adjacent grasslands 1962–2006 (for 2008 season in New England, see Hamilton 2012, and for Beringian collections, see Ross 1970 and Hamilton 1997). Counties (or, in western Canada, census districts) sampled by most recent surveys, as indicated by colour scheme. Bold outline indicates area traditionally associated with prairies in Canada and the United States.

**Table 1.** Probable glacial-age refugia of grassland-endemic leafhopper species in Canada (based on present distributions derived from CNCI material and notes and maps by R.F. Whitcomb). “Other” grasslands may not necessarily be periglacial refugia. Genera appearing under only one such list are boldfaced; numbers of species are in parentheses (for species names, see Table 2) and total number of species in Canada from each source are boldfaced.

Source	Leafhoppers
Gulf coast (7)	<i>Chlorotettix</i> (1), <b><i>Dorydiella</i></b> (1), <i>Flexamia</i> (1), <i>Gypona</i> (1), <i>Limotettix</i> (1), <i>Neohecalus</i> (1), <i>Polyamia</i> (1)
Beringia (10)	<i>Athysanella</i> (2), <b><i>Chlorita</i></b> (1), <b><i>Diplocolenus</i></b> (2), <i>Hebecephalus</i> (3), <i>Limotettix</i> (1), <i>Mocuellus</i> (1)
South-western grasslands (62)	<i>Aligia</i> (1), <i>Athysanella</i> (1), <b><i>Aplanus</i></b> (1), <i>Auridius</i> (1), <i>Ballana</i> (2), <b><i>Caladonus</i></b> (1), <i>Calanana</i> (1), <b><i>Carsonus</i></b> (1), <i>Ceratagallia</i> (3), <i>Chlorotettix</i> (1), <i>Colladonus</i> (6), <b><i>Dicyphonia</i></b> (1), <b><i>Dikraneura</i></b> (4), <b><i>Dikrella</i></b> (1), <i>Empoasca</i> (4), <b><i>Endrila</i></b> (1), <b><i>Eutettix</i></b> (1), <b><i>Forcipata</i></b> (1), <i>Gypona</i> (1), <i>Gyponana</i> (1), <i>Hecalus</i> (1), <i>Idiocerus</i> (7), <b><i>Koebelia</i></b> (1), <b><i>Lebradea</i></b> (1), <i>Limotettix</i> (3), <i>Norvellina</i> (1), <i>Paraphlepsius</i> (1), <i>Psammotettix</i> (2), <b><i>Scaphytopius</i></b> (2), <b><i>Stragania</i></b> (2), <i>Texananus</i> (3), <b><i>Twiningia</i></b> (2), <i>Xerophloea</i> (1), <b><i>Xyphon</i></b> (1)
Texas high plains (87)	<b><i>Acinopterus</i></b> (1), <i>Amblysellus</i> (3), <i>Athysanella</i> (5), <i>Attenuipyga</i> (3), <i>Auridius</i> (3), <b><i>Balclutha</i></b> (1), <i>Ballana</i> (2), <i>Ceratagallia</i> (6), <b><i>Cicadula</i></b> (2), <i>Commellus</i> (2), <i>Cuerna</i> (1), <i>Deltocephalus</i> (2), <b><i>Driotura</i></b> (1), <i>Empoasca</i> (5), <i>Erythroneura</i> (1), <b><i>Euscelis</i></b> (1), <i>Flexamia</i> (7), <i>Graminella</i> (1), <b><i>Hardya</i></b> (1), <i>Hecalus</i> (1), <i>Idiocerus</i> (3), <i>Laeviccephalus</i> (5), <i>Latalus</i> (1), <i>Limotettix</i> (4), <i>Lonatura</i> (2), <i>Macropsis</i> (3), <i>Memnonia</i> (3), <b><i>Mesamia</i></b> (4), <i>Mocuellus</i> (1), <b><i>Neokolla</i></b> (1), <i>Norvellina</i> (2), <i>Paraphlepsius</i> (3), <b><i>Pendarus</i></b> (1), <i>Polyamia</i> (1), <b><i>Stirellus</i></b> (1), <i>Texananus</i> (1), <i>Unoka</i> (1), <i>Xerophloea</i> (1)
Pacific Northwest periglacial grasslands (43)	<i>Aligia</i> (1), <i>Attenuipyga</i> (1), <i>Ceratagallia</i> (1), <i>Colladonus</i> (1), <i>Cuerna</i> (1), <i>Elymana</i> (1), <i>Empoasca</i> (7), <i>Erythroneura</i> (1), <b><i>Errhomus</i></b> (1), <i>Hebecephalus</i> (4), <b><i>Helochara</i></b> (1), <i>Idiocerus</i> (4), <i>Latalus</i> (2), <i>Mocuellus</i> (1), <i>Norvellina</i> (1), <i>Oncopsis</i> (1), <i>Orocastus</i> (4), <b><i>Pinumius</i></b> (1), <i>Psammotettix</i> (4), <i>Rosenus</i> (1), <b><i>Sorhoanus</i></b> (2), <i>Texananus</i> (1), <i>Unoka</i> (1)
Other grasslands (87)	<b><i>Aflexia</i></b> (1), <i>Amblysellus</i> (2), <i>Athysanella</i> (5), <i>Attenuipyga</i> (1), <i>Auridius</i> (1), <i>Ceratagallia</i> (2), <i>Chlorotettix</i> (1), <i>Colladonus</i> (1), <i>Commellus</i> (2), <i>Cuerna</i> (3), <b><i>Davidsonia</i></b> (2), <i>Deltocephalus</i> (3), <b><i>Destria</i></b> (1), <i>Elymana</i> (1), <i>Empoasca</i> (3), <i>Erythroneura</i> (1), <b><i>Extrusanus</i></b> (1), <i>Flexamia</i> (6), <i>Graminella</i> (3), <i>Gyponana</i> (1), <i>Hecalus</i> (1), <i>Idiocerus</i> (6), <i>Laeviccephalus</i> (3), <i>Latalus</i> (1), <i>Limotettix</i> (7), <i>Lonatura</i> (2), <i>Macropsis</i> (2), <b><i>Macrosteles</i></b> (2), <i>Memnonia</i> (3), <i>Mocuellus</i> (1), <b><i>Neocoelidia</i></b> (1), <i>Neohecalus</i> (1), <i>Oncopsis</i> (3), <i>Orocastus</i> (1), <i>Paraphlepsius</i> (3), <b><i>Prairiana</i></b> (3), <i>Rosenus</i> (1), <b><i>Stenometopiellus</i></b> (1), <b><i>Telusius</i></b> (1), <i>Texananus</i> (2)

*et al.* 1987). The underutilization of grassland leafhopper data in Canada (Hamilton 2004) is partly a reflection of historical events. Many entomologists were taking occasional leafhopper specimens before 1950 but few of these specimens were identified, as their critically important male genital characters were only just becoming studied (DeLong and Slesman 1929; Oman 1933), and authoritative identifications were not possible until after comprehensive keys became available (DeLong 1948; Oman 1949).

The purpose of this chapter is to provide a critical analysis of the evidence for endemic Canadian grassland leafhoppers (Figs. 1–4). First, before discussing “endemism” and “grasslands,” it is necessary to define such terms. Second, the known records from collections over the years must be analyzed for completeness (Figs. 5 and 6) and identifications checked to verify that they represent accurate and unbiased lists (Tables 1 and 2). Finally, placing evidence of endemics in their Canadian distribution patterns (Figs. 7–9) and in the wider context of North American grasslands (Figs. 10 and 11), together with evidence of postglacial dispersals from refugia, should reveal what these insects can

tell us about the extent of our grasslands and the glacial-age events that shaped the fauna. It is postulated that this information may prove critical in determining conservation strategies for ecosystems, as well as for specific sites (Fig. 12), and may affect monitoring protocols judged most appropriate to the situations in these, our most threatened ecosystems.

Previously recorded plant hosts are listed by scientific and common names in a previous volume of this series (Hamilton and Whitcomb 2010); in the subsequent text only the common names of such plants are mentioned.

## Definitions

Leafhoppers feeding on grasses may be found in many different habitats, ranging from open plains to wet areas in woodlands. Conversely, grasslands range from those dominated by grasses to shrublands with few if any grasses, particularly if they are overgrazed. Since leafhoppers can inhabit tiny remnants of grasslands (Hamilton and Whitcomb 2010), a clear definition is needed of what constitutes a “grassland endemic.”

*Grasslands* are here defined as areas where trees appear to be normally absent or sparse and where the historically dominant seed plants (phanerogams) are grasses inhabited by native leafhoppers that are specifically different from those found in adjacent woodlands and disturbed habitats. Such a definition excludes most tundra and alpine habitats where sedges or forbs are dominant, differentiates transitory habitats from prehistoric habitats, and covers such localized grasslands as alvars (limestone plains: Brownell and Riley 2000) and sand ridges, or prairie grass patches growing on alkaline fens (Bess and Hamilton 1999). Grasses growing in tidal areas of James Bay and the Maritime Provinces may also support host-dependent leafhoppers, but as these are discussed elsewhere (Hamilton 2010, 2012), they are not included in this analysis, although their ranges are noted.

*Grassland insects* are here defined as either those that are widespread on major grassland areas, or those that have an observed association with a plant that is associated with grassland habitats, such as wolf willow or sagebrush.

*Grassland endemism* is here defined as an association of insects with grasslands that is intense enough that 85% or more of the insect populations occur only on grasslands, or only on a particular plant that is considered to be a dominant or subdominant of grasslands. This is aligned with the definition of endemism in ecoregional classifications (e.g., Ricketts *et al.* 1999). The definition of grassland endemic is a narrower definition than grassland insect and is the group of leafhoppers used to define grasslands. For example, the presence of a single leafhopper characteristic of grasslands can be enough to differentiate its habitat from neighbouring woodlands, but that leafhopper may fail to satisfy the definition of an endemic by being common in other ecological areas in non-contiguous sites. In addition, if an endemic co-occurs with other leafhoppers, those leafhoppers are not necessarily grassland endemics.

Grassland leafhoppers may fall into three categories, depending on how well they match the measures of endemism:

1. Grassland-dependent = species reported only from Canadian grasslands, or more widely distributed species represented by numerous samples showing restriction to grassland-associated plants
2. Grassland-associated = geographically associated, but not restricted to Canada or known to have hosts characteristic of grasslands
3. Putative = association with grasslands not clearly demonstrated through lack of sufficient information

Ecoregional terms used in this discussion are those appropriate to leafhopper distributions and are defined and diagrammed elsewhere (Hamilton 2009). In general terms, steppe represents the northern half of the mixedgrass prairies of North America, where cool-season grasses are dominant and “true prairie” extends from western Manitoba into eastern Saskatchewan, with oak savanna east of the Red River Valley and around Lake Manitoba.

### Collecting Coverage

The CNCI contains an estimated 13,500 specimens of grassland leafhoppers. Together with other collections examined (Hamilton 1972, 2004), these include 296 species that are probably grassland-endemic (Table 2), of which two are restricted to tidal grasslands: *Elymana pacifica* on the eastern coast of Vancouver Island and *Neohecalus lineatus*, which is widespread on the Atlantic coast. These 296 species represent more than a quarter of some 1,100 grassland-endemic leafhoppers found throughout North America (R.F. Whitcomb 2005, unpublished data<sup>1</sup>).

To assess the sampling coverage, both the overall number of locations sampled (Figs. 5–7) and the efficiency of sampling must be considered. Random sampling is known to be inefficient, and targeted collecting on specific plant types and habitats is necessary to ensure an adequate sample. Little-known sites are best located and accessed with the assistance of local experts, such as those working with conservation agencies. Accordingly, samples from targeted collecting (generally studies from after 1962) are postulated to be more representative of the fauna than earlier collections. The present faunal list (Table 2) is divided by an estimate of the relative numbers of specimens collected before 1962 and after that time, when targeted collecting became more common. These subsets of collections each represent approximately half a century, given that practically no specimens were collected before 1912. Thus, it is valid to compare them in assessing any improvements in our knowledge.

Comparing the early collections to the later collections allowed a comprehensive tracking of grassland-endemic leafhoppers over the years in the three westernmost provinces (British Columbia to Saskatchewan). Most of the grassland-endemic species were sampled in the first 50 years, though few were correctly named in that period, and almost as many specimens of each species were taken in this period as in the later collections. This first half century covered the period of mostly random collecting and almost all of the massive collection of leafhoppers by Brooks and associates.

The latter 50 years (1962–2011) includes all of the pan and pitfall trapping and most collecting on targeted hosts, with more precise information on sites and habitats sampled, recorded either in field notes or in publications. This collecting resulted in 53 species (18% of the endemics) being considerably more commonly collected than in the first half century (numbers boldfaced in Table 2). Large numbers of specimens of some grassland-endemic leafhoppers that were rarely or not sampled in the early period came in particular from Manitoba and farther east (Fig. 7, green sites). One striking case is *Flexamia prairiana*, a specialist on big bluestem that was represented by more than 300 specimens in the later collections. Only a single literature record (Hamilton 1972) and 10 other CNCI specimens of this species come from the earlier period. Similarly, the

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<sup>1</sup> R.F. Whitcomb projects: leafhopper diversity and evolution in North American prairies (<http://www.canacoll.org/Hemip/Staff/Hamilton/Hamilton.htm#Projects>)

leafhoppers specializing on little bluestem (the dominant grass of prairies in Manitoba and around Lake Huron (Fig. 9)) are most commonly *Flexamia delongi*, *F. graminea*, and *Stirellus bicolor*, each represented by 90–400 specimens from the later collections but 0–10 from the earlier period.

## Identification

The baseline for a prairie fauna is represented by those from the “Great Plain states” (Oman 1949). Knowledge of the Canadian grassland leafhopper fauna and their strong host associations has increased substantially over the past several decades (Hamilton and Whitcomb 2010) because of increased sampling and taxonomic efforts. A huge portion of the continent has now been fairly uniformly sampled (Fig. 6). During the same time, a considerable taxonomic effort has gone into other leafhopper studies as well. The known fauna covering all Nearctic ecological areas has grown by an estimated 450 additional species (new species minus synonymies) since 1949, for a total exceeding 3,800 species. Species names cited below are those in the latest checklist of Canadian Hemiptera (Maw *et al.* 2000), except as noted below.

The taxonomy of Canadian leafhopper species that could possibly be grassland endemics was checked by DNA bar-coding genes (658–664 DNA base pairs of mitochondrial cytochrome oxidase I) using specimens collected in grasslands over the previous 60 years (KGAH, unpublished data). To date, more than 2,000 specimens of leafhoppers have been bar-coded in an attempt to include all of the relevant grassland species where suitable specimens were found in the CNCI. An average of 2.5 specimens per species was used to cover geographical variation and different life stages and to test for uniformity within a series taken at the same time on the same host. More specimens were used if the specimens available were taken before 1980, as initial trials indicated that the probability of a successful result diminishes significantly beyond 30 years. All specimens bar-coded in this study are deposited in the CNCI, and genetic records are available in the Barcode of Life Database at <http://www.boldsystems.org>.

Additional highly regionalized new species were discovered or confirmed through bar-coding. These included a series that is morphologically similar to *Laevicephalus exiguus*, but came from sand reed grass on dunes at one site (Sauble Beach, Ontario), a short series of unidentifiable female *Mocuellus* from one site in British Columbia, and a single female *Flexamia* from Manitoba with an unusual facial pattern. Likewise, *Auridius ordinatus crocatus* Hamilton bar-coded as a distinct species and, conversely, a series of female *Laevicephalus* from Manitoba thought to be undescribed proved to be *L. saskatchewanensis* Hamilton. Bar-coding also confirmed that *Davidsonia major* and *D. snowi* do not belong to *Macrosteles* Fieber, as currently thought (Oman 1949; Beirne 1956), and that *Endria inimica* belongs in that genus rather than in *Amplicephalus*.

Three dubious records from Canadian grasslands (Maw *et al.* 2000) could not be checked and are here excluded from the analysis: *Destria fumida* (Sanders & DeLong) from Saskatchewan and Manitoba, *Extrusanus ovatus* (Sanders & DeLong) from Saskatchewan, and *Rosenus obliquus* (DeLong & Davidson) from British Columbia. The following name changes for archived specimens from the same checklist are reported:

1. “*Ballana chelata*” and “*B. hebea*” from British Columbia were corrected to *B. velosa* and *B. venditaria* following examination of type material (KGAH, unpublished data).
2. *Dikrella nevadensis* (Fig. 1), a distinctive species previously known only from Nevada, is newly reported in Canada, where it feeds only on antelope brush, *Purshia*

*tridentata* (Pursh) in grasslands, and is here removed from synonymy with *D. cruentata* (Gillette), an inhabitant of woodlands.

3. “*Mesamia frigida*” bar-coded differently from specimens of that species collected from Arizona; the British Columbia record is here corrected to *M. diana*.
4. “*Ollarianus insanus*” is here corrected to *Aplanus albidus* after comparison to specimens of *Ollarianus* from Arizona.

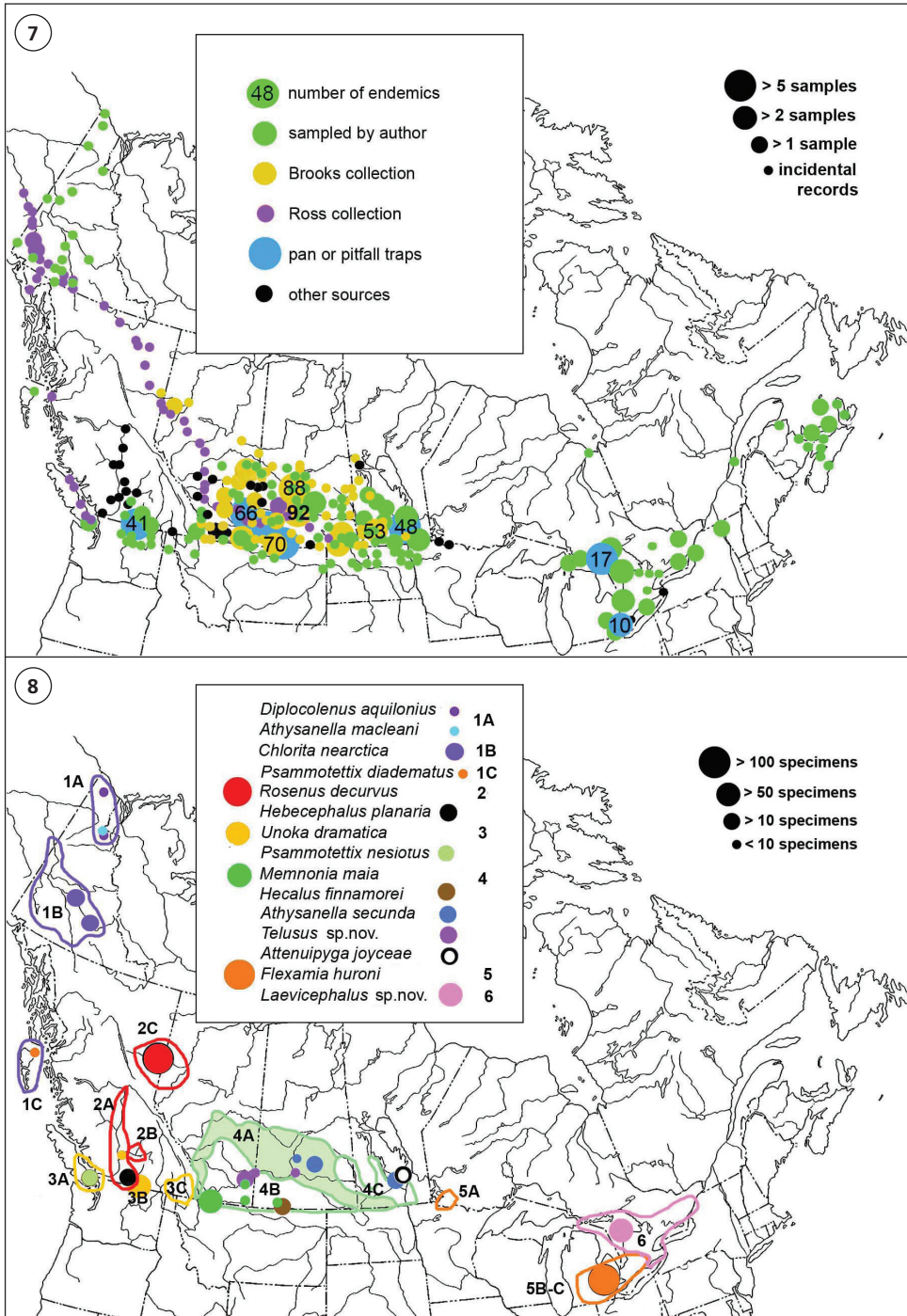
### Reliability of Data

The majority of Canadian grassland leafhoppers were collected in more than 300 sites widely distributed across the Prairies (Fig. 5), but were also found in numerous remote locations (Figs. 7 and 8) from the Haida Gwaii Islands on the Pacific Coast eastward to Cape Breton and from the arctic slopes of the Yukon down to southernmost Ontario. The individual distributions of the 15 most restricted endemic species are also widely dispersed from the Pacific Coast to southern Ontario (Fig. 8) and are found in most grassland types, including the Peace River district of British Columbia, which is farthest from any unglaciated area. All grasslands have been adequately sampled except for limited data from the Rainy River district of western Ontario (Fig. 8, district 5A), where only two grassland species have been found. All grasslands have been revisited since 1962 except those of the Cariboo District in British Columbia north of the junction of the Fraser and Thompson rivers, but results in the southern portion of the Fraser drainage system are consistent with what is known from farther north.

Host-targeted collecting has been effective in finding representatives of the largely destroyed and highly localized eastern grasslands. It is also important for establishing host associations and tracking seasonality and dispersal while enhancing our knowledge of rare species or life stages. Pan and pitfall traps were effective in documenting biodiversity most quickly and effectively at particular sites and also led to new insights in biology. One such study was a multi-year comparison of a relict prairie outside Winnipeg, Manitoba (Wade and Roughley 2010) after a burn off. It documented by pitfall trapping that usually three years are required for univoltine leafhoppers to recover to pre-burn populations. It also yielded mostly adults and nymphs of the introduced European genus *Anoscopus* (approximately 3,000 specimens each) that feeds at ground level. The same traps turned up an equal number of adults of the ant-guest leafhopper genus *Xestocephalus*, but only three mature specimens of its extremely rare nymphs were taken. From this evidence, it is apparent that nymphs of *Xestocephalus* are rarely found because they leave ant nests only to moult to adults.

Only one notable Canadian record comes from a pan trap. The discovery of a single individual of the flightless, stick-like leafhopper *Attenuipyga balli* in a pan trap in southern Saskatchewan (Hamilton 2000), many hundreds of kilometres north of its known range in Kansas and adjacent counties of Nebraska, shows that these insects must be vigorous walkers to have come so far in postglacial times. Particularly interesting was the fact that the pan trap was set in a stand of the non-native crested wheat grass, *Agropyron cristatum* (L.), which could not possibly be the host of any such leafhopper. The trapped specimen was probably caught because it was migrating in search of its normal host.

Only 43 of 296 probable grassland-endemic species (15%) are putative grassland species whose association with grasslands is not clearly demonstrated, but their affinities to grasslands are supported by the known behaviour of their congeners. Of the remainder, 118 are grassland-associated, based on numerous records but not demonstrated to have grassland hosts. Additional collecting will almost certainly decrease this category and



**Figs. 7 and 8.** Grassland leafhopper sampling in Canada and within 100 km of Canadian soil. 7, All sites, ranked by intensity and method of collecting; 8, most restricted endemism in grassland sites, ranked by scarcity of sites and number of specimens found in each and grouped according to adjacent areas (see the Distribution of Endemics section in text for a description of alphanumeric distribution codes).



increase the number of grassland-dependent species, currently standing at 134 leafhoppers (45% of the 296 possible grassland endemics). For example, *Commellus comma* and *Flexamia dakota* are known presently from isolated localities, but will probably be found more widely with intensive searching.

### Regional Context

Grassland leafhoppers from Canada must be placed in a wider context in any discussion of endemism. Their records were compared with an unpublished list of all such leafhoppers in North America that was compiled by the late R.F. Whitcomb (R.F. Whitcomb 2005, unpublished data<sup>1</sup>), and compared with his published (Whitcomb and Hicks 1988; Whitcomb *et al.* 1994) and unpublished maps of species distributions. Records of his collection sites and those of H.H. Ross (Figs. 6 and 7) were abstracted from their collection notes, which are preserved in the CNCI. These were used in determining overall modern faunal assemblies (Fig. 10A).

Almost 30% of the 3,800 leafhopper species in Canada and the United States satisfy the biogeographical test for grassland endemics; that is, they are not usually found in woodlands, or are found only on plants that are characteristic of extensive grasslands (Hamilton 2012). These include some species with ranges less rigorously aligned with grasslands but that are obligates on prairie plants. A large percentage of the latter is represented by species known from few specimens or few sites (Hamilton 1999a, 1999b, 2002b, 2012) and could potentially be endangered by human activities, including habitat loss and climate change.

The estimated 1,100 grassland-endemic species of Canada and the United States is far greater than the grass-feeding leafhopper fauna endemic to southeastern forests (109 species) or to the neotropical tip of Texas (14 species). It is also greater than the number of species that are widespread in distribution. Only 25 grassland-endemic species are found across many regions, 19 are widespread in boreal forests, 12 are widespread in the east, and five are also widespread in the south.

Most of the common grassland species can be mapped roughly across geographically contiguous areas. The number of species endemic to each of these areas form four distinct groups separated by wide gaps, and these are listed here by order of magnitude:

**Moderate endemism:** Beringia (four endemics), eastern prairies (five endemics)

**High endemism:** western prairies (41 species), central prairies (59 endemics)

**Very high endemism:** Pacific Northwest grasslands (91 endemic species and many subspecies), northern prairies (92 endemics)

**Extreme endemism:** southwestern semi-desert grasslands (489 endemics)

### Canadian Grassland-Endemic Leafhoppers

There were only 90 grass-feeding species known in our fauna when they were first analyzed (Hamilton 1985a). Specimens were collected mostly before 1960, and it was impossible to guess how many species feeding on other plants were associated with grasslands, or how any of these related to the faunas in other parts of the continent. Today, the size and composition of the CNCI leafhopper collections is fully adequate to the task of analyzing the fauna and distribution patterns on Canadian grasslands. Inevitably, a few species or localized grasslands are under-represented, but these constitute only a minor fraction of the whole. Of the 296 leafhopper species associated with grasslands in Canada, 263 definitely

appear to be endemics, either grassland-associated or grassland-dependent (Table 2). This contrasts strongly to only 19 other grass-feeding leafhoppers widespread in northern woods, as well as 10 apparently confined to Beringia for which we have little biological information.

There are 33 leafhoppers found *only* in Canada that are endemic to grasslands (Table 2), compared with 23 other leafhoppers endemic to some other environment in all of the rest of Canada. Thus, grassland leafhoppers include more than half of all the endemic leafhopper species of Canada, although grassland leafhoppers represent only a quarter of the total leafhopper fauna of Canada.

Another 263 leafhopper species in Canada are more broadly endemic to grasslands. This raises the numbers of all leafhopper endemics in Canadian grasslands to significantly larger proportions in five localized grasslands (Fig. 7): Spruce Woods Forest Reserve in Manitoba (53 species); Canadian Forces Base Suffield in Alberta (66); and in Saskatchewan, Grasslands National Park (70), Saskatoon (88), and Elbow, the latter of which in 1960 had an astonishing 92 endemic species or 52% of *all* Canadian prairie endemics (Hamilton 2005a). By contrast, most prairie sites in the eastern United States support seven or fewer endemics (Hamilton 1995) and in western areas are usually fewer than 20 (R.F. Whitcomb, unpublished field notes). Comparable faunal diversity in the Canadian Prairies is otherwise known only from the Research Ranch near Elgin, Arizona. Northern leafhoppers are more frequently endemic to grasslands in Canada than in the United States (Table 2) because they are less likely to transfer to other hosts when constrained by a limited growing season (Hamilton and Whitcomb 2010). A few others that are widespread in the United States are restricted to Canadian grasslands by a more limited grass flora. For example, some specialists on little bluestem will transfer to broomsedge (Hamilton 2012), a weedy species in woodland openings and old field situations in the eastern states, but this grass does not occur in Canada.

All large-area grasslands are now known to have at least a few endemic leafhoppers, and even some comparatively small sites. For example, at Toad River, British Columbia, along the Alaska Highway, a population of a grassland-endemic leafhopper, *Latalus intermedius*, was present in huge numbers, almost 500 individuals in 100 sweeps, in 1968. This species is otherwise found sparsely from the highest mountain in Arizona northward in intermontane grasslands of the western United States. The factors that create such disjunctions are unknown; however, this species is clearly not limited by climate.

There is only one case where I cannot decide whether a particular leafhopper–grass association represents a grassland endemic. *Latalus remotus* is associated in widely spaced intervals from Cape Breton Island to Manitoulin Island with *Oryzopsis asperifolia* Michx., which is a spiky grass like a starved yucca found in sandy woods. This grass is said to be common in woods in eastern Canada (Roland and Smith 1969; Dore and McNeill 1980), but I have rarely seen it and none of the botanists I have consulted were able to direct me to a stand of it, and so I have no way of verifying an observation made personally at only two sites. The phenomenon of a woodland leafhopper monophagous on a particular grass would be unexpected, but so, too, is the phenomenon of a grassland leafhopper that is never in an open glade or larger grassy area. It may be a relict of a time when this grass lived on the fringes of glacial moraines, but now has somehow adapted itself to open woodlands: the “exception that proves the rule.”

### Distribution of Endemics

Recent studies in the United States (Fig. 6) enable an overall picture to be developed that shows widely distributed leafhoppers in North American grasslands to include 65 endemic

to the prairies as a whole, 31 endemics widespread in Cordilleran valleys, 14 generally distributed throughout these regions, and 33 western endemics found widely across most or all of the grasslands west of the Mississippi River. Overall, Cordilleran grasslands have 610 endemics, both widespread and localized, and North American prairies have 757 such endemics. Endemic leafhoppers generally have patterns of distribution that are determined primarily by the areas where their hosts are most abundant and may be subdivided by phenology (timing of plant growth) rather than by climatic factors such as temperature and precipitation (Whitcomb *et al.* 1994). The largest and best substantiated subsets of both Cordilleran and prairie leafhopper faunas (Fig. 10A) show that there is a divide between northern and southern grasslands separated by a reduced fauna (“hiatus”) in the arid southern part of Oregon, the moon-like lava beds of the Snake River Valley of Idaho, the arid central part of Wyoming, and the Great Sand Hills of northern Nebraska. The northern plains and Pacific Northwest are usually dominated by “cool season” grasses, whereas the southern plains and southwestern semi-deserts are mostly covered with “warm season” grasses, so that both grass species and their optimal growth periods differ in these grasslands. This correlation between geography and floral dominance explains the considerable difference between the leafhopper faunas of these regions and makes credible such a geographical split. The boundary between the two cannot be defined precisely, as cool season grasses predominate unusually far south during extended droughts (Weaver 1954).

There are no obvious major faunal divides across the southern Great Plains and southwestern grasslands of the United States. Many species range broadly across various ecoregions (Whitcomb *et al.* 1994). Cordilleran and southern prairie leafhoppers meet in the Rio Grande lowlands as an ecotone (Fig. 10A). Leafhoppers endemic to the western or “shortgrass” plains extend to varying degrees eastward and northward across the whole southern plains that are dominated by warm season grasses (e.g., Whitcomb and Hicks 1988). A small but distinct eastern fauna is also evident, but this is characteristic of plains east of the Mississippi River rather than being specific to the tallgrass prairies that occupy this zone. Accordingly, the contiguous grasslands of the United States and Canada have five main leafhopper-defined ecozones (Fig. 10A), on the basis of the endemic species.

We can make finer distinctions in Canada by comparing six geographically adjacent and ecologically similar areas, each with three subsets (districts). Five remote districts that are too small to be represented on the grassland map in Shorthouse (2010: Fig. 1) are marked below with an asterisk (\*). East coast tidal grasslands were not considered, and two species known only from the biological “hotspot” of the Canadian Prairies, at Elbow (Hamilton 2005a), are not included in any of the districts of the Prairies (area 4), as this one site encompasses faunal elements of all three districts. From north to south and west to east (Figs. 8 and 9A), the major grassland areas and their districts are as follows:

1. Northern grasslands (1A: arctic grasslands; 1B: Yukon River valleys; \*1C: Haida Gwaii (Queen Charlotte) Islands)
2. Cariboo grasslands (2A: Fraser River valleys; 2B, Thompson valley; 2C, Peace River district)
3. South valley grasslands of British Columbia (3A: Georgia Strait; 3B: Okanagan-Similkameen; 3C: Kootenays)
4. Prairies (4A: aspen parkland; 4B: steppe; 4C: “true” prairies)
5. Prairie Peninsula (5A, Rainy River District; 5B, oak openings; \*5C, alkaline fens/marshes)
6. Great Lakes grasslands (\*6A, alvars; \*6B, beaches; \*6C, sand plains)

The 18 grassland districts (areas 1–6, each divided into three subdivisions A–C)

used here for discussion purposes may be somewhat more finely split than necessary. The exception is “true” prairie (4C) that shows a clear differentiation into tallgrass prairie and oak savanna (Hamilton 2005b). Oak savanna has a unique set of endemics (Hamilton 1985a, 2004).

The greatest proportion of grassland-endemic leafhoppers in Canada (174 species) and the majority of the 68 most common inland species (indicated with an asterisk in Table 2) are found on the extensive coterminous prairies or Prairies Ecozone. This portion of Canadian grasslands differs from the eastern grasslands or “Prairie Peninsula” in having arid-adapted plants such as saltgrass and salt meadow grass as subdominants or localized patches (Hamilton 2012). The three main subtypes of prairie already reported (Hamilton 2005a) are (1) aspen parkland (4A) with 96 endemics, where the dominant grasses are fescues in dry sites or mat muhly in wet sites; (2) the aridity-maintained steppe (4B in Table 2 and Fig. 8) with 127 endemics, where the dominant grasses are blue grama and needlegrass and the subdominants prairie muhly, western wheat grass, and June grass; and (3) fire-maintained true prairies (4C) with 89 endemics, where the dominant grasses include bluestems in dry sites and cordgrass in wet sites. These figures do not add up to 174, as there is considerable geographical overlap among the included species.

The next largest endemic grassland fauna occupies one of the smallest geographical areas. The south valley grasslands of British Columbia have 126 endemics, of which 96 live in the Okanagan-Similkameen valley system (3B in Table 2 and Fig. 8), where the dominant grasses include *Agropyron spicatum* (Pursh) and *Poa secunda* Presl., with arid-adapted shrubs such as *Purshia* at low elevations. Another 43 are found in the East Kootenays (3C) where *Poa* is dominant, with wheat grasses and June grass subdominant, and 43 in the lowlands on both sides of Georgia Strait (3A). Again, there are large overlaps among these faunas, with connections through the Pacific Northwest grasslands of the United States.

The grasslands around the Cariboo Mountains have little in common with other grasslands in British Columbia, confirming the opinion expressed earlier that they represent postglacial prairie incursions (Hamilton 2002b). Dominant grasses include *Agropyron* and *Festuca*, with additional grasses including *Koeleria* and *Stipa* (Munroe 1956), as in aspen parkland. There are 80 grassland endemic leafhoppers more akin to the prairie fauna, of which 43 live along the Fraser River and its associated valleys (2A) and 25 are found in the adjoining Thompson valley (2B). This fauna has much in common with the 39 endemics of the Peace River district (2C).

The Prairie Peninsula faunas are only slightly less diverse than the Cariboo grasslands, although there are only two prairie endemics in the Rainy River District (5A in Table 2 and Fig. 8) of western Ontario, where some prairie plants are occasionally found. The fauna is much larger on various grasslands around the glaciation-scoured basin of the Great Lakes (Fig. 9A). On this area, 21 prairie endemics are characteristic of oak openings (5B) at the southern tip of Ontario; 23 are found in alkaline fens (5C) and marshes where some prairie plants may be found, and these, too, are really part of the Prairie Peninsula biota. Quite different are 16 endemics found in alvars (6A; Hamilton 1999a; Bouchard *et al.* 2002), where prairie plants may be locally dominant and subdominant; 21 are found on beaches (6B) and four are found on sand plains (6C), where still other prairie grasses may be locally dominant. There are relatively few species of the Prairie Peninsula that occur in more than one such habitat. By far the most common grassland species in this area is *Flexamia delongi*, which is ubiquitous on little bluestem around Lake Huron (Hamilton 1994a). Two other locally common endemics, *Chlorotettix spatulatus* and *Dorydiella kansana*, are not found in Canadian grasslands farther

west than Lake Huron, although they both range into Kansas. In total, 17 grassland-endemic leafhopper species are found in southern Ontario, but not farther west in Canada, although common on eastern prairies of the United States, with the total fauna of eastern Canadian grasslands showing its closest affinities to oak savanna in Michigan.

Such small sites are expected to be depauperate because dispersal to unsuitable surrounding habitats decimates the parent population, a process considered to be characteristic of "island" populations (MacArthur and Wilson 1967). Surprisingly, site size is not as much a determinant of leafhopper diversity as site heterogeneity. For example, a tiny site at Grosse Isle, Manitoba, situated between the parallel highway and railway embankments, grades from dry upland to swales and has 28 endemics (Hamilton 2004), comparable to good individual sites around Winnipeg (all of which sum to 48 endemics, similar to 41 for the fauna of all sites in the Okanagan-Similkameen valley system of British Columbia).

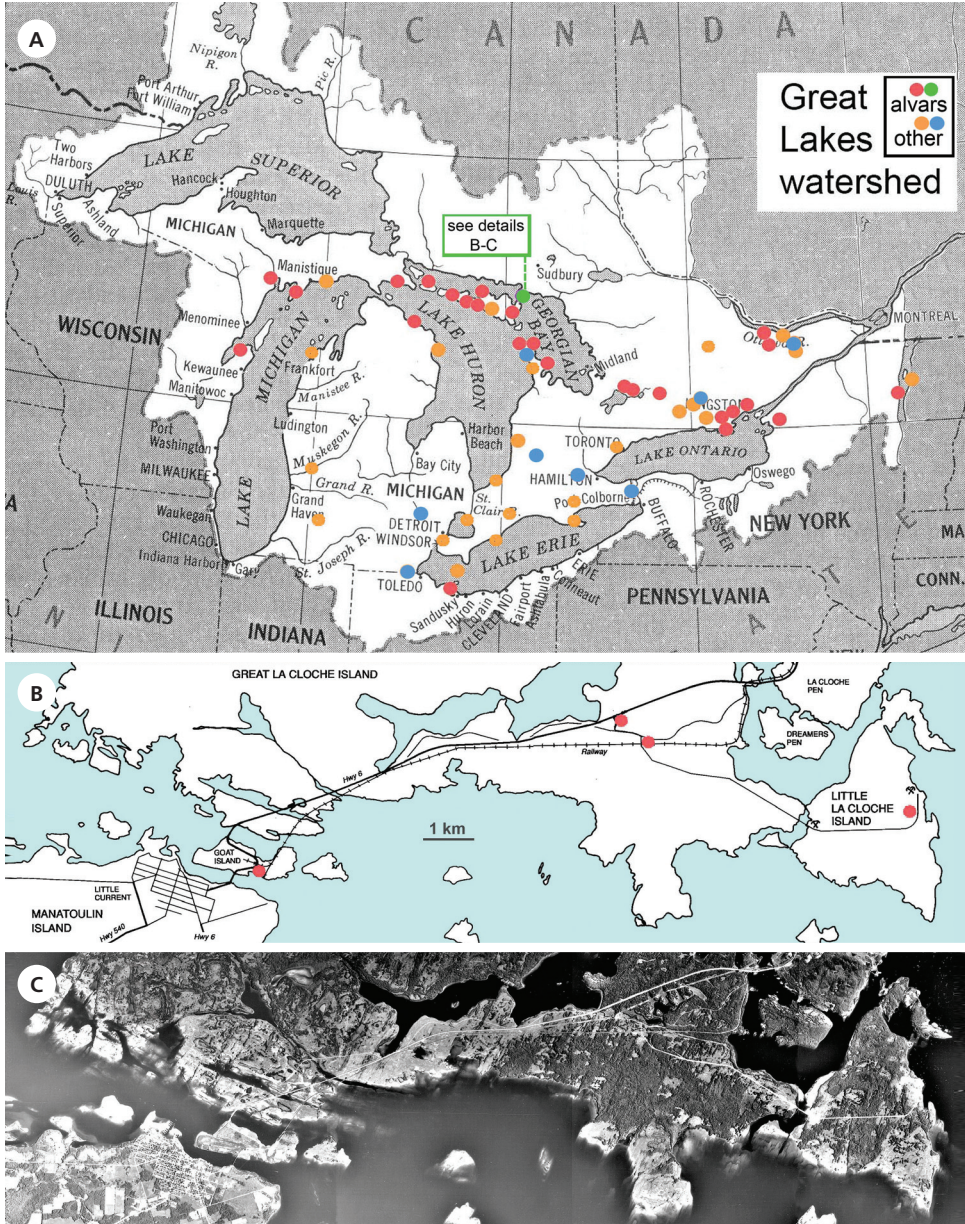
Local faunal richness highlights many small grasslands elsewhere in Canada (such as alvars and grass flats of the tidal zone) of real ecological significance. For example, the tallgrass Ojibway Prairie in Windsor, Ontario, has nine prairie-endemic leafhoppers (a tenth, on switchgrass, occurs nearby), and this is assuredly part of the grassland ecosystem; but the beach dunes from Ipperwash to Grand Bend on the southern tip of Lake Huron are also well represented with six different grassland leafhopper species. An even richer grassland ecosystem is that of alvars in Lake Huron, few of which are found on tallgrass plains or beach dunes. There are, in total, 58 grassland-endemic leafhoppers found in Ontario!

Northern grasslands have a much smaller number of endemics than other grasslands in Canada. This fauna is composed largely of wide-ranging species. Of the endemics that do occur, 21 are found in Yukon valleys (1B in Table 2 and Fig. 8) where bluegrass, June grass, and prairie sage are dominant, and only a single endemic is found in each of two remote sites on the arctic slope (1A) of northern Yukon, where the host is probably sand-adapted grasses.

### Dispersal Patterns

Much of the large leafhopper fauna of the Canadian Prairies consist of widely distributed species that are common to two or more geographical areas (Hamilton 2004, 2005a). Even among endemics, 48 of the species occur in two of the major divisions of the Prairies, and 43 range over all three, for a total of 91 shared endemics (51%). Similarly, aspen parkland (district 4A in Fig. 8) shares 23 species with the Peace River District, together with the Fraser River drainage system (2A and B). The greatest differences in faunal groups of leafhoppers are found in the Pacific Northwest, including southern British Columbia, probably because of poor dispersal across high-elevation passes such as those that separate the grasslands of Idaho and Montana (Hamilton 2002b). This is also shown by the very few leafhoppers that have surmounted the much lower Crowsnest Pass that separates the arid southwestern prairies (district 4B in Fig. 8) from the East Kootenays of British Columbia (3C). On the other hand, arid parts of the Fraser River drainage system (2A and B) are mainly populated with species that are widespread across the Prairies, despite their large geographical separation. The sole endemic leafhopper species of the Fraser River drainage system, *Hebecephalus planaria*, is found only in the southern end at Douglas Lake. The fauna of the British Columbia interior are apparently postglacial migrants that arrived before forests covered the intervening areas (Chiykowski and Hamilton 1985: Fig. 8), just as grassland leafhoppers and spittlebugs in the New England states followed grasses

growing on sand deposited by glaciers (Hamilton 2012). The Thompson valley (2B) alone lacks endemics and appears to be an ecotone between the Prairies and Pacific Northwest ecozones (Fig. 10A). Similarly, the seven species from the Prairies that are also found in southern valleys of the Yukon are probably postglacial migrants, since at least two of



**Fig. 9.** Great Lakes watershed area and associated grassland sites: A, alvars (main site in green, others in red) and other habitats (sandy sites in orange, alkaline fens in blue); B, detail showing main alvar sampling sites (red) from area marked in green on map A; C, aerial photograph of same area, showing extent of alvars as pale areas.

their hosts are sand-adapted grasses suitable for colonizing glacial debris. Perhaps *Latalus intermedius* found halfway between these areas is also a relict population dating from the same early postglacial grasslands.

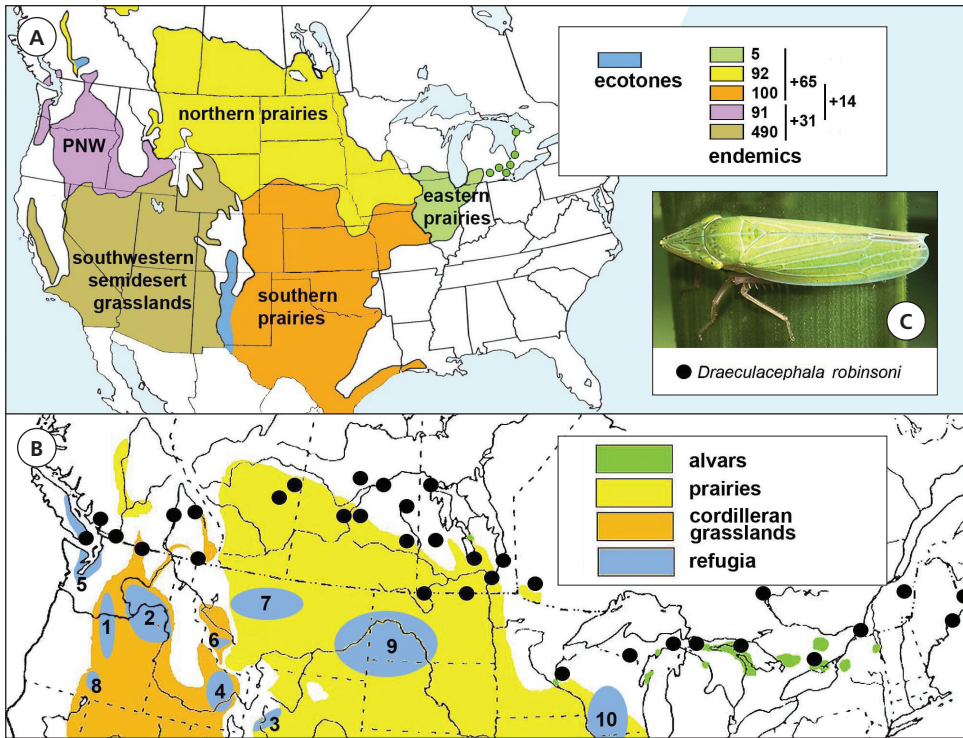
Numerous localized endemics show that Canadian grasslands are not simply northern extensions of the ecosystems found in the central Great Plains of the United States, nor do the numbers of their endemic leafhoppers diminish northward. Present-day grassland leafhopper patterns are complex and depend heavily on historical colonization patterns, especially those related to the most recent glaciation events. Postglacial ecology and climate are critical factors governing their highly regionalized biota, and characterizing the biota accurately for conservation purposes relies upon a clear understanding of the prehistory that shaped the ecosystem.

The presence of a distinctive fauna in grasslands of Canada and the northern United States (Fig. 10A), together with the surprisingly rich fauna of grassland endemics as far east as Ontario, suggests that grasslands and their associated leafhoppers were present in areas close to the ice front, and colonization pathways followed new grasslands that formed with the retreat of the glaciers (Hamilton 2012). The evidence is most clear for the Pacific Northwest, where patterns of loess deposition indicate a dry glacial-age summer from a permanent summer high pressure system over the ice front and a permanent low pressure system over the arid southwest, together driving a monsoon (Bartlein *et al.* 1998; Hamilton 2002*b*, 2012) that reversed prevailing wind patterns. This contrasted to wetter-than-normal summer conditions that created glacial-era lakes across Nevada, Utah, and the Great Divide Basin of Wyoming while also supporting drought-intolerant spruce across North American prairies. The high pressure system should have also favoured clear skies and local heat near the ice front comparable to that existing in modern grasslands. Such a stable system could have extended across eastern Montana and probably became patchy eastward. From 12,000–10,000 years ago, *Artemisia* coexisted with scattered spruce and juniper on the southern Great Plains of Canada (thus resembling an alvar flora), and this was afterwards replaced by prairie that extended farther north than present-day grasslands from deglaciation until 6,000 years ago (Ritchie 1976), probably following glacial-deposited sand. The summer monsoon also may have affected some areas around the present Great Lakes, since palynological data show prairie forb pollen in the unglaciated portion of Wisconsin (the “driftless” area) from 18,000–15,000 years ago that migrated eastward to Indiana ca. 3,000 years later before fusing with a reinstated prairie environment (Webb *et al.* 1987).

The grassland-endemic species can be divided provisionally by their adjacency to the most probable Nearctic refugia, in sequence from the best-supported to most controversial:

1. Gulf Coast grasslands from Florida to Texas were augmented by lower than normal sea levels during glacial maxima. Although this coastal plain must have been extensive, its fauna evidently became adapted to southern conditions; only seven grassland species have ranged from there as far north as Canada. One of these, *Limotettix elegans*, provides an unequivocal linear distribution pattern from coastal Texas through eastern Oklahoma to northwestern Ohio, adjacent southern Ontario, and its most northern site on the western shore of Lake Huron (Hamilton 1994*b*).

2. Beringia, including Alaskan and Yukon sites, shows clear evidence for regional endemism, with three arctic grassland endemics, as well as *Chlorita nearctica*, which is found in temperate-zone sites on south-facing slopes. Possibly as many as six of the other grassland leafhopper species may have found a refugium there, but postglacial dispersals from the south are indicated for seven species.



**Fig. 10.** Differentiating endemic species of leafhoppers to create maps of the faunal ecozones of leafhoppers across the continent (A) and mapping their probable periglacial refugia (B). The most significant refugia (1–8) are described and characterized by their endemic Homoptera- Auchenorrhyncha of the Pacific Northwest (Hamilton 2002b), and more easterly sites (9–10) are deduced in the Discussion. Not shown: Haida Gwaii Islands (refuge of a single grassland leafhopper; see Fig. 8) and Atlantic Canada with its offshore refugia (see Hamilton and Langor 1987: Figs. 37–40 and Hamilton 2010: Figs. 10–13). *Draeculacephala robinsoni* (C) is the only transcontinental grassland leafhopper whose present distribution (black spots) shows affinities to all periglacial refugia. Photograph by Rob Curtis.

3. Southwestern semi-desert grasslands appear to have persisted through the Pleistocene, according to the contents of packrat middens (Betancourt 2004). There are 62 grassland leafhoppers endemic to southwestern grasslands that have extended their ranges northward to enter Canada in the southern valleys of British Columbia, or have become widely dispersed across most western grasslands.

4. Texas high plains or *Llano Estacado* existed as an escarpment throughout the Pleistocene but lacked sufficient rainfall to create incised rivers, and any wetlands on the plateau and surrounding grasslands were confined to isolated playa lakes (Wendorf 1961; Bolen *et al.* 1989). Most of the endemic leafhoppers of the Great Plains are associated with the Texas high plains and have dispersed from there in various directions across adjacent prairies. Of these, possibly as many as 88 are represented in Canada, but mostly only along the southern border of the Canadian Prairies, augmenting the fauna of the steppe district (4B).

5. Pacific Coast glaciation must have been less extensive than often suggested (Scudder 1989). At least parts of Vancouver Island and the Haida Gwaii Islands always must have been ice-free, because these islands have our only native earthworms that survived the ice



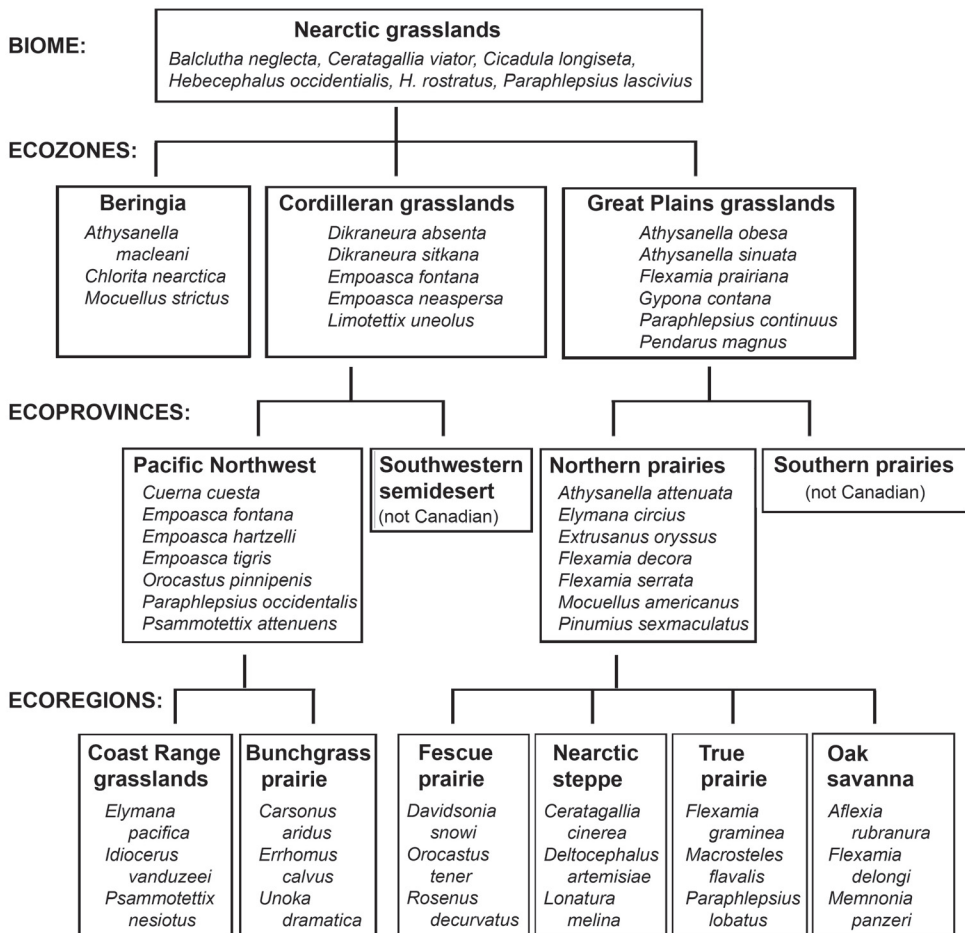
age (Fender and McKey-Fender 1990; Hendrix and Bohlen 2002), and these animals can neither cross the narrowest bodies of water nor survive glaciation. Endemic leafhoppers are associated with both these islands: one endemic species (*Psammotettix diademata*) on the Haida Gwaii Islands and four species of *Colladonus*, *Elymana*, *Idiocerus*, and *Psammotettix* in the strongly regionalized grassland around the southern tip of Vancouver Island and on the adjacent mainland. Four species of *Empoasca* and one each of *Helochara*, *Idiocerus*, and *Psammotettix* range from coastal British Columbia southward and inland, suggesting that as many as 12 grassland species could have found refugia on the coast of British Columbia.

6. Periglacial grasslands along the southern ice margin are clearly indicated in the Pacific Northwest (Hamilton 2002b), but the evidence is less clear for more easterly sites. Many grassland leafhoppers endemic to inland areas near the southern border of Canada are probably periglacial in origin (Table 1), migrating to higher elevations or northwards from different refugia as the ice melted. These include 42 found only in Pacific Northwest grasslands with six identifiable refugia (Fig. 10B, sites 1–6 and 8), as well as at least 87 on adjacent prairies that must have found refugia east of the Rocky Mountains. The distributions of endemics in southern Alberta, such as *Memnonia maia*, suggest a refugium on the badlands of Montana (Fig. 10B, site 7). There is less conclusive evidence for periglacial refugia still farther east, but the disjunct distribution of *Flexamia delongi*, now found in the Black Hills of South Dakota, in tallgrass prairie in Manitoba and Minnesota, and around Lake Huron suggests at least two additional refugia (Fig. 10B, sites 9 and 10). The undescribed species of *Laevincephalus* from the western shore of the Bruce Peninsula is our most easterly grassland endemic. It likely came from the same eastern refugium, probably located in the driftless plain of southern Wisconsin and northern Illinois. This area also has two localized grassland endemic leafhoppers, *Polyamia dilata* DeLong and *P. rossi* DeLong, both specialists on low species of panic grasses. Possibly this general periglacial refugium included the vicinity of the alkaline fen where *Flexamia huroni* is found today (Bess and Hamilton 1999). Clear evidence of a localized temperate refugia still farther east (near Montreal) was found in postglacial deposits dated 11,000 years ago. Oaks and an oak-feeding temperate-zone treehopper (Hemiptera: Membracidae) were living there when the ice front was less than 100 km northward (Mott *et al.* 1981). Such a periglacial fauna may have extended all the way to the east coast. The grass-feeding *Draeculacephala robinsoni* Hamilton (Fig. 10C) has a transcontinental range across southern Canada (Fig. 10B), including Cape Breton Island, widely separated from populations representing another glacial-age refugium in the southeastern United States (Hamilton 1985b: Fig. 68). This suggests at least one Atlantic refugium, presumably that of the emergent offshore Grand Banks (Hamilton and Langor 1987).

7. The faunas of the Cariboo grasslands and aspen parkland are essentially similar, with mostly widespread species, some of which (such as *Laevincephalus poudris*) have isolated populations in the eastern mountains of Colorado. Their endemics are few and scattered; they do not group logically with any of the above postulated refugia. These faunas also share a significant number of species with the Beringian fauna. This evidence suggests that they represent the remains of the glacial maximum Great Plains fauna that was adapted to cooler, wetter conditions favouring plants such as fescue, mat muhly, willows, and spikerushes and have been forced into numerous peripheral areas of higher elevation or latitude during postglacial warming. Some of these fescue grasslands (such as those of the Cariboo district) became isolated as forests re-established themselves.

### Conservation Issues

The richly endemic fauna of grassland leafhoppers recorded in this analysis contrasts strongly with current opinion, derived largely from the depauperate faunas of European heaths and prairie sites on the Prairie Peninsula, that there is little diversity in grassland leafhoppers (e.g., Joern and Laws 2013). These endemics in Canada show distribution patterns that differ from ranges of many other insect species, probably due to strong host-plant associations, all of which could impact grassland conservation priorities. Leafhoppers are associated only vaguely with broadly defined ecoregions, such as tallgrass or shortgrass prairies and ecoregions of Canadian Prairies that are based on soil



**Fig. 11.** Proposed hierarchical classification of Nearctic grasslands, showing most common and widespread examples of the complex fauna of their endemic leafhoppers. Not all examples fit the precise boundaries of any one ecosystem, but at least 85% of most species are found within each ecosystem and generally occur across the most extensive areas. Compared with the grassland districts in Fig. 8, Beringia is 1A and B, the Coast Range grasslands are 1C and 3A, bunchgrass prairie is 3B and C, fescue prairie is 2A–C (see Volume 3 Frontispiece 1-2 and 6) and 4A, Nearctic steppe is 4B (Frontispiece 3-5), true prairie and oak savanna (Frontispiece 7) are 4C, and eastern extensions of oak savanna are 5 and 6 (Frontispiece 8).

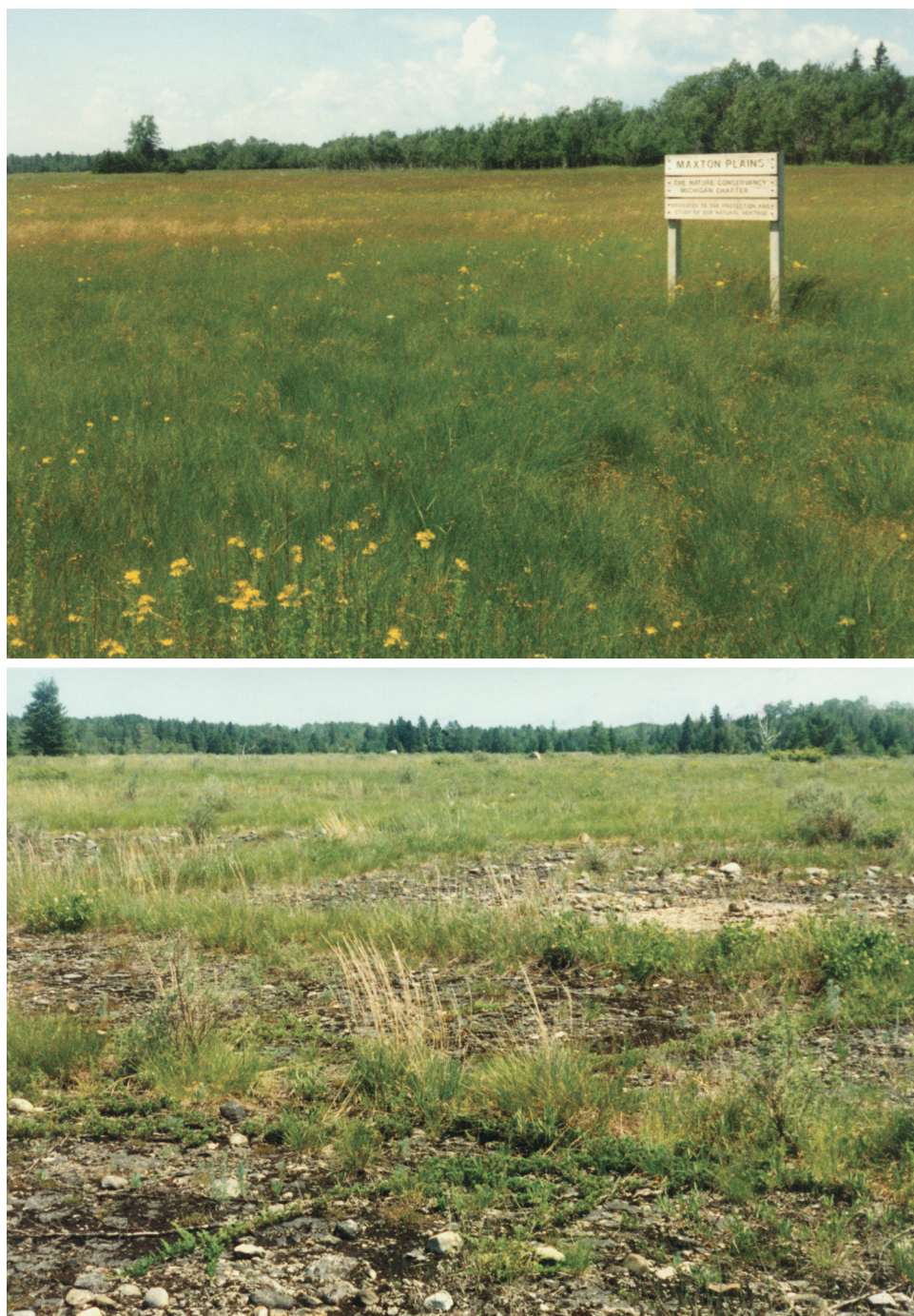
profiles. This may require overlapping versions of ecoregions tailored to different target organisms to embrace the whole of grassland biodiversity, or a sophisticated version of a hierarchical classification of grasslands (Fig. 11) to differentiate between localized and broader patterns of endemism. The only part of any such a scheme that is not objective is the placement of Beringia as a separate ecozone rather than as an ecoregion of northern prairies. The data to support one position over another are lacking in leafhoppers, but more northerly insects (such as Lepidoptera) show the essential Palaearctic character of Beringia more clearly.

The data also show that we should avoid the tendency to make jigsaw puzzles of the biotic world. The ranges of species never exactly coincide; there are always gaps or exceptional outlier populations. Biomes (e.g., grasslands and forests) and biotic regions (e.g., Nearctic and Neotropical) can overlap in complex ways without blending (the Prairie Peninsula and much of Mexico are two notable examples), and ecoregions can overlap as ecotones or have diffuse borders as a broad-scale hiatus.

Grassland-endemic leafhoppers are usually associated with patterns of dominant and subdominant plants upon which they have specialized over the millennia (Hamilton 2006). They do not follow expected island biogeography selection pressures, being far more diverse than expected in tiny grassland areas (such as hillsides of the Pacific Northwest and in fragmented grasslands along coulees) rather than on the open plains. Nor is leafhopper diversity associated with areas of high vegetational productivity, having far more endemics in low-productivity grasslands (such as those of the Alberta plains) than in the tallgrass areas of Illinois, and being much more common and diverse on small grasses such as little bluestem than on giants such as big bluestem living in the same habitats. There are more grassland-endemic species on Canadian Prairies than even in the heart of North American grasslands: the central plain states of the United States. Even the smallest reserves can support grassland leafhoppers, just as tiny grasslands have survived throughout postglacial times in otherwise forested sites from coast to coast. Such tiny grasslands must be part of any conservation strategy that seeks to preserve the full spectrum of Canada's grassland biota.

The smallest and most endangered of Canada's grasslands are also some of the most biodiverse. We have already lost the prairie leafhopper hotspot at Elbow to dam construction. Now, rampant conversion of arid grasslands in the Okanagan to vineyards threatens the hotspot of British Columbia, and population pressures mount in the still more restricted grasslands in the vicinity of Victoria and Vancouver that have a different mixture of endemic species. Grassland preserves in Manitoba and eastern Saskatchewan are generally small and the few tallgrass sites that still exist outside the oak savanna region (Fig. 2; Hamilton 2005a, plate 5) are not protected. Only the many alvars and oak openings of Ontario are listed (Ontario Ministry of Natural Resources 1993) and many of these are already under some form of conservation.

Nor must we forget the larger picture. Wisconsin glaciation is merely the most recent and best-studied part of the Pleistocene. The whole of the ice age experienced repeated episodes of increasingly severe temperature cycles separated by comparatively brief interglacials and interstadials. Leafhoppers that live in Canada today have acclimatized themselves to such cycles over more than a million years; they are not just the products of the last few thousand years. Ecology can tell us only a limited amount about such biological resilience. To understand the complete story, a nuanced and detailed understanding of the ice age is essential, and this understanding must include the unobtrusive but hitherto inexplicable, such as *Psammotettix diademata* as a grassland endemic on such a remote



**Fig. 12.** Managed (top) and unmanaged (bottom) alvar sites on Drummond Island, Michigan, photographed on the same day. The pristine-looking managed site has few if any leafhoppers of interest, while the scruffy-looking and unprotected site nearby has a rich fauna of endemic leafhoppers, as well as some rare species with unknown biology that are thus not listed under any particular fauna (e.g., this is the type locality for *Notus isolatus* Hamilton, otherwise known only from one unspecified site near Montréal, Quebec). Photographs by the author.

and seemingly inhospitable site as North Beach adjacent to boreal forest on Haida Gwaii, or an undescribed *Laevicephalus* with a novel host association at Sauble Beach on Lake Huron, or *Latalus remotus* as a grass-feeding endemic in open woodlands.

Knowledge of climatic history and its part in developing the rich endemic biota of the most distinctive grasslands types in Canada is essential to characterize their ecology and to set appropriate conservation priorities. For example, keeping old-growth oaks intact is an important part of preserving remnant oak savanna (e.g., at the so-called tallgrass prairie near Tolstoi, Manitoba), just as it is important to maintain creeping juniper and other relict plants as components of alvars (Fig. 12). Likewise, it is important to characterize correctly the habitats we attempt to preserve—because tallgrass prairie may have quite a different appearance in western sites (Fig. 2) than in eastern areas (Fig. 4)—and to recognize that not all endemics are specialized on dominant vegetation, such as *Limotettix elegans* on low spikerushes in so-called tallgrass sites.

Even the largest and best conserved grasslands may be threatened by unexpected factors. Steppe vegetation in southern Alberta and Saskatchewan is often invaded by exotic grasses such as crested wheatgrass that are unsuitable habitats for native insects and damaging in the long term to floral integrity.

As R.F. Whitcomb wrote in 2005 (unpublished):

*... we may understand that any particular place, far from being located in a simple ecosystem, is a center point of a cobweb of regressions, only some of which are in the single plane of contemporary time. Failure to appreciate the historical regressions would lead to serious misinterpretations of the grassland ecosystem and almost certain failure to construct the most useful hypotheses concerning it (Whitcomb et al. 1987). Examples of mismanagement due to a lack of historical perspective includes the use of non-native grasses such as crested wheatgrass that have been planted to secure the blowing dust of the "Great Drought" (1930-1934), a natural disaster that is now seen as a foreseeable part of a climatic cycle. We have replaced a temporary disaster with a long-term one, destruction of the very grasslands that have evolved over the millennia to withstand such episodic droughts.*

### Acknowledgements

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**Table 2.** Grassland-associated and grassland-endemic leafhopper species in Canada. Note that records from Elbow, Saskatchewan, cannot be cited as regional faunas because these faunas overlap at this one place. Records from the southernmost grassland site in the Fraser River drainage basin (2A?) come from an isolated grassland around Douglas Lake, British Columbia, and may represent immigrants from more southerly localities (3B). The number of specimens of each species represented in CNCI was estimated and divided between those collected in the first 60 years (1902–1961) and those from targeted collecting in later years (after 1961). Distributions are indicated by the two-letter postal code for state or province.

**Key:** Names CAPITALIZED: endemic to Canada; Names in **boldface**: known to be monophagous

? Denotes 43 putative grassland-associated species.

\* Denotes the 66 most common species (>100 specimens taken in more than three localities).

State records are in boldface if known to be grassland endemics there.

Alphanumeric codes: grassland districts specified in the Methods and shown in Figs. 8 and 9A.

Specimen numbers in boldface: where numbers of specimens in later collections differ from earlier samples by 10-fold or greater (minimum 10 specimens).

Name	Distribution	No. of Specimens	
		≤ 1961	> 1961
<i>Acinopterus viridis</i> Van Duzee	CA-TX / BC-SK (3B, 4B)	45	30
* <i>Aftexia rubranura</i> (DeLong)	SD-IL / MB-ON (4C, 6A)	0	<b>400</b>
? <i>Aligia californica</i> Van Duzee	CA-OR / BC (3A)	0	1
? <i>Aligia utahna</i> Hepner	UT / BC (3B)	0	1
<i>Amblysellus acuerus</i> Ross & Hamilton	KS-ND / MB-SK (4B-C)	0	<b>20</b>
<i>Amblysellus dorsti</i> (Oman)	AZ-CO / BC-SK (4A)	40	30
<i>Amblysellus punctatus</i> (Osborn & Ball)	AZ-SD / AB-MB (4B)	0	<b>10</b>
<i>Amblysellus valens</i> (Beamer & Tuthill)	CO-WY / BC-SK (2C, 4B)	5	4
<i>Amblysellus wyomus</i> Kramer	WY-MT / BC-SK (3C, 4B)	0	<b>15</b>
<i>Aplanus albidus</i> (Ball)	CA-NM / AB (4B)	1	0
* <i>Athysanella attenuata</i> Baker	UT-OK / BC-MB (2C, 4A-C)	130	130
* <i>Athysanella bifida</i> Ball & Beamer	NM-ND / AB-MB (4A-B)	130	100
<i>Athysanella incongrua</i> Baker	WY-IA, NH / MB (4B-C)	0	5
* <i>Athysanella kadokana</i> Knull	CO-NE / AB-MB (4A-C)	20	90
<i>Athysanella macleani</i> Blocker & Wesley	AK / YK (1A)	0	<b>50</b>
<i>Athysanella obesa</i> Ball & Beamer	TX-SD / AB-SK (4B)	20	30
<i>Athysanella occidentalis</i> Baker	CA-KS / BC-SK (2B, 3C, 4A-B)	20	70
ATHYSANELLA RESUSCA Blocker & Wesley	YK-NT (1B)	10	0
* <i>Athysanella robusta</i> Baker:	CO-ND / YK-MB (1B, 2C, 4A-B)	130	100
<i>A. SECUNDA</i> Blocker & Wesley	SK-MB (4A, 4C)	0	<b>40</b>
<i>Athysanella sinuata</i> Osborn	TX-NE / AB-MB (4B)	40	4
* <i>Athysanella terebrans</i> Gillette & Baker	CO-MT / AB-ON (4A-C, 6B)	40	90
<i>Athysanella utahna</i> (Osborn)	CA-CO / BC (2B, 3B)	0	5
<i>Attenuipyga balli</i> Oman	KS / SK (4B)	0	1
ATTENUIPYGA JOYCEAE Hamilton	MB (4C)	0	<b>15</b>
* <i>Attenuipyga minor</i> (Osborn)	CO-NE / BC-MB (4A-C); also a subspecies in AZ	70	75
<i>Attenuipyga omanae</i> (Beamer)	OR-ID / BC (3B)	0	2
<i>Attenuipyga platyrhynchus</i> (Osborn)	KS-IL / ON-QC (5C, 6A)	10	50
* <i>Auridius auratus</i> (Gillette & Baker)	UT-SD / BC-SK (1B, 2A-C, 3B-C, 4A-B)	190	200
<i>Auridius crocatus</i> Hamilton, <i>stat.nov.</i>	CA-ID / BC (2B, 3B-C)	4	1

<i>Auridius helvus</i> (DeLong):	AZ-MI / BC-MB (2C, 3C, 4B)	10	10
* <i>Auridius ordinatus</i> (Ball)	CO-ND / YK-SK (1B, 2C, 4A-C)	150	20
<i>Auridius sandaraca</i> Hamilton	MI / AB-ON (2C, 4A, 4C, 6A)	0	15
* <i>Balclutha neglecta</i> (DeLong & Davidson)	CA-FL / BC-ON (2C, 3B, 4A-C, 5B-C, 6A)	210	140
<b><i>Ballana atridorsum</i></b> (Van Duzee)	CA-WI / BC-AB (3B)	10	0
<b><i>Ballana ortha</i></b> DeLong	CA-ND / BC-SK (3B, 4B)	10	0
<b><i>Ballana velosa</i></b> DeLong	CA-MT / BC (2B, 3A-B)	10	0
<i>Ballana venditaria</i> (Ball)	CA-UT / BC (3B)	0	1
? <i>Caladonus coquilletti</i> (Van Duzee)	CA-AZ / BC (3B)	1	30
? <i>Calanana rubralineata</i> (Beamer)	CA / BC (3A)	10	0
<b><i>Carsonus aridus</i></b> (Ball)	NV-CO / BC (3B)	25	0
<i>Ceratagallia arida</i> (Oman)	NM-TX / BC (3C)	1	0
? <i>Ceratagallia califa</i> Oman	CA / AB (4B)	1	1
<i>Ceratagallia cerea</i> Hamilton	NM-TX / AB (4B)	0	2
* <b><i>Ceratagallia cinerea</i></b> (Osborn & Ball)	UT-CO / AB-SK (4B)	95	35
<i>Ceratagallia nanella</i> (Oman)	CA-MN / BC, MB (3B, 4B)	1	1
CERATAGALLIA OKANAGANA Hamilton:	BC (3B)	0	1
<i>Ceratagallia omani</i> Hamilton	OR / BC (3A)	0	1
<i>Ceratagallia robusta poudris</i> (Oman)	AZ-NE / BC (4B)	0	1
<i>Ceratagallia semiarida</i> Hamilton	MT / AB-MB (4A-B)	70	4
<i>Ceratagallia uhleri</i> (Van Duzee)	CA-TX / AB-MB (4B-C)	60	2
* <i>Ceratagallia viator</i> Hamilton	CA-OH / YK-ON (1B, 2A-C, 3C, 4A-C, 5A-B, 6A-B)	280	300
? <i>Ceratagallia vulgaris</i> (Oman)	OK-VA / AB, ON (4B, 5C)	1	5
<b>CHLORITA NEARCTICA</b> Hamilton	YK (1B)	0	30
<b><i>Chlorotettix fallax</i></b> Sanders & DeLong	ND-VA / ON (5B)	0	5
<i>Chlorotettix similis</i> DeLong	CA-ID / BC (3A-B)	2	5
* <b><i>Chlorotettix spatulatus</i></b> Osborn & Ball	NM-FL / ON (5B, 6B)	0	115
* <i>Cicadula junea</i> Hamilton	AK / SK-MB (2C, 4A, 4C)	145	15
* <i>Cicadula longiseta</i> (Van Duzee)	CA-MT / YK-MB (1B, 2A, 2C, 4A-B)	80	140
? <i>Colladonus arculus</i> Ball	CA-WA / BC (3B)	5	5
<i>Colladonus atriflavus</i> Downes	WA / BC (3A)	20	2
? <i>Colladonus aureolus</i> (Van Duzee)	CA-ID / BC (2A east of pass, 3A-B)	10	0
? <i>Colladonus holmesi</i> Bliven	CA-WA / BC (2B, 3B)	35	10
COLLADONUS KELTONI Hamilton	BC (2B, 3B)	5	9
? <i>Colladonus mendicus</i> (Ball)	CA-UT / BC (3B)	0	1
? <i>Colladonus olus</i> Nielson	MI / SK, ON (4A, 6B)	1	1
? <i>Colladonus ponderosus</i> Ball	CA-AZ / BC (3B)	1	0
<b><i>Commellus colon</i></b> (Osborn & Ball)	CO-WI / SK-MB (4C)	5	10
<b><i>Commellus comma</i></b> (Van Duzee)	AZ-NY / AB-SK (4B)	0	1
? <i>Commellus hyphen</i> Hamilton	ND / SK (4A)	3	0
* <b><i>Commellus sexvittatus</i></b> (Van Duzee)	AZ-MI / YK-MB (1B, 2A, 2C, 4A-C)	70	110
<i>Cuerna alpina</i> Oman & Beamer	CO-ND / AB-SK (4B)	20	0
<i>Cuerna cuesta</i> Hamilton	WA-MT / BC (2A, 3B-C)	60	5
<i>Cuerna fenestella</i> Hamilton	MN / MB-ON (4C, 5B)	4	8
CUERNA NIELSONI Hamilton	SK-MB (4B)	5	0

<i>Cuernia sayi</i> Nielson	MO-MI / AB (4C)	20	0
<b>Davidsonia major</b> Dorst	CO-VT / AB-ON (4B, 5C)	80	1
<i>Davidsonia snowi</i> Dorst	CO-WI / AB-MB (2A, 2C, 4A)	70	0
<i>Deltocephalus artemisiae</i> (Gillette & Baker)	OR-CO / AB-SK (4B)	60	10
? <i>Deltocephalus castoreus</i> Ball	CA-MT / BC-QC (1B, 2A, 3A-B, 4A)	30	40
? <i>Deltocephalus gnarus</i> Ball	KS-IL / AB-MB (4B-C)	2	0
<i>Deltocephalus lineatifrons</i> Oman	CO-ND / BC-MB (2A, 4B)	10	10
* <b>D. SERPENTINUS</b> Hamilton	AB-ON (4A-C)	60	50
<i>Destria crocea</i> (Beirne)	WI / SK-MB, NB-PEI (4A, 4C, 6B, coast)	60	20
<b>Dicyphonia ornata</b> (Baker)	AZ-NE / AB-SK (4B)	1	5
* <i>Dikraneura absenta</i> DeLong & Caldwell	CA-NM / BC (2B, 3A-B)	210	110
? <i>Dikraneura omani</i> Knight	CA-ID / BC (3A)	3	0
<i>Dikraneura rufula</i> Gillette	CA-WA / BC (3A)	5	0
* <i>Dikraneura sitkana</i> DeLong	CA-WY / BC (3B)	0	120
<b>Dikrella nevadensis</b> (Lawson)	NV / BC (3B)	0	10
? <i>Diplocolenus aquilonius</i> Ross & Hamilton	AK / YK (1A)	0	4
* <i>Diplocolenus brevior</i> Ross & Hamilton	OR-ID / YK-AB (1B, 2A-C, 3B, 4A-B)	90	180
* <i>Dorydiella kansana</i> Beamer	KS-PA / ON (5B-C, 6A)	0	180
<i>Driotura robusta</i> Osborn & Ball	CO-SC / AB-MB (4A-B)	20	10
* <b>ELYMANA CIRCIUS</b> Hamilton	BC-ON (2A, 2C, 4A-B, 5C)	80	50
<b>ELYMANA PACIFICA</b> Hamilton	BC (3A, tidal grasslands only)	30	35
? <i>Empoasca albolinea</i> Gillette	CA-MA / ON (5C)	0	20
<i>Empoasca angustifoliae</i> Ross	WA-CO / AB (4B)	0	20
<i>Empoasca aureoviridis</i> (Uhler)	CO / BC (2A)	5	0
<b>EMPOASCA CAESARSI</b> Hamilton	BC (3B)	0	5
<i>Empoasca carsona</i> DeLong & Davidson	AZ-UT / BC (2A, 3A-C)	10	80
<b>EMPOASCA DISSIMILARIS</b> Hamilton	BC-AB (2A-C, 3A-B)	40	10
* <b>Empoasca exiguae</b> Ross	NV-MT / BC-ON (2A-B, 3B-C, 4A-B, 5C)	35	200
* <i>Empoasca fontana</i> Ross	WA-CO / BC (3A-C)	90	170
? <i>Empoasca hartzelli</i> Baker	CA-NM / BC (3A, 3C)	10	25
*? <i>Empoasca lucidae</i> Ross	CA-CO / YK-AB (1B, 2A-B, 3A)	15	110
* <b>Empoasca medora</b> DeLong	CO-SD / AB-MB (4A-B)	145	0
? <i>Empoasca mexicana</i> Gillette	CA-NM / SK (4A)	20	0
* <b>Empoasca neaspersa</b> Oman & Wheeler	CA-CO / BC (3B)	45	30
<b>Empoasca nigra</b> Gillette & Baker	UT-CO / BC (3B), lengthy series from Osoyoos	0	35
* <b>Empoasca nigroscuta</b> Gillette & Baker	NV-CO / YK-SK (1B, 2C, 3B, 4A-B)	40	45
<i>Empoasca obtusa</i> Walsh	MT-IL / SK-MB (4C)	0	20
<b>EMPOASCA ROSSI</b> Hamilton	BC (2A, 3A-B)	30	25
<b>EMPOASCA TIGRIS</b> Hamilton	BC (3A-B)	45	2
* <b>Empoasca typhlocyboides</b> Gillette & Baker	NV-CO / BC-SK (2C, 4A)	50	80
? <i>Endria lassa</i> (Ball)	CA-MT / BC (3C)	0	1
<b>Errhomus calvus</b> Oman	WA / BC (3B)	15	6
<i>Erythroneura calva</i> Beamer	WI / AB-MB (4B-C)	10	0
*? <i>Erythroneura carbonata</i> McAtee	KS-MD / AB-MB (4A-C)	65	80
<i>Erythroneura dolosa</i> Beamer & Griffith	WA / BC (3B)	1	0
? <i>Euscelis maculipennis</i> DeLong & Davidson	CA-WA / BC-MB (3A-C, 4A-C)	15	15



<i>Eutettix glennanus</i> Ball	AZ-TX / BC (3B)	15	10
* <i>Extrusanus oryssus</i> Hamilton	MN / AB-MB (2C, 4A-C)	150	135
* <i>Flexamia abbreviata</i> (Osborn & Ball)	NV-IL / AB-MB (4A-B)	70	75
<i>Flexamia atlantica</i> (DeLong)	WY-MA / MB (4C)	0	1
<i>Flexamia dakota</i> Young & Beirne	TX-IA / SK (4B? Elbow)	0	1
* <i>Flexamia decora</i> Beamer & Tuthill	UT-ND / AB-MB (2C, 4A-C)	60	230
* <i>Flexamia delongi</i> Ross & Cooley	SD-MI / SK-ON (4C, 6A-B)	10	<b>400</b>
* <i>Flexamia flexulosa</i> (Ball)	AZ-OK / AB-MB (4A-B)	55	80
* <i>Flexamia graminea</i> (DeLong)	TX-ME / SK-MB (4C)	0	<b>130</b>
<i>Flexamia grammica</i> (Ball)	CO-IL / AB-SK (4A-B)	40	20
* <i>Flexamia inflata</i> (Osborn & Ball)	WA-NY / BC, SK-ON (3B, 4C, 5B-C)	5	<b>120</b>
* <i>Flexamia prairiana</i> DeLong	AZ-IL / MB-ON (4C, 6B)	10	<b>310</b>
<i>Flexamia reflexa</i> (Osborn & Ball)	TX-MD / ON (6B)	0	<b>40</b>
* <i>Flexamia serrata</i> Beamer & Tuthill	UT-IL / BC-MB (2A, 4A-C)	30	260
<i>Flexamia stylata</i> (Ball)	AZ-KS / AB-MB (4B-C)	20	20
<i>FLEXAMIA</i> sp.nov.	MB (4C Gladstone)	1	0
<i>Forcipata sicula</i> DeLong & Caldwell	OR-ID / BC (3A)	3	0
<i>Graminella ampla</i> Beamer	ND-MN / SK-MB (4B-C)	0	4
<i>Graminella mohri</i> (Van Duzee)	TX-IN / ON (6A-B)	0	<b>50</b>
<i>Graminella oquaka</i> DeLong	IA-VA / ON (5B)	0	<b>30</b>
<i>Graminella pallidula</i> (Osborn)	KS-MD / ON (5B, 6B)	5	30
* <i>Gypona contana</i> DeLong	AZ-IL / AB-MB (4A-C)	150	65
? <i>Gypona melanota</i> Spångberg	MN-GA / ON (5B)	0	<b>20</b>
<i>Gyponana hasta</i> DeLong	CA-TX / BC (3A-C)	30	30
? <i>Gyponana vincula</i> DeLong	UT-CT? / AB-MB (4A-C)	10	25
<i>Hardya dentata</i> (Osborn & Ball)	OR-KS / BC-SK (2A southernmost, 3B-C, 4A-B)	55	25
<i>Hebecephalus callidus</i> (Ball)	WA-MT / BC (3C)	0	7
<i>Hebecephalus crassus</i> (DeLong)	WY-ID / BC (1B, 3B)	0	<b>10</b>
* <i>H. occidentalis</i> Beamer & Tuthill	AZ-AK / YK-MB (1B, 2A, 2C, 3B-C, 4A-C)	240	330
<i>HEBECEPHALUS PLANARIA</i> Hamilton	BC (2A?)	0	<b>20</b>
* <i>Hebecephalus rostratus</i> Beamer & Tuthill	AZ-OK / YK-MB (1B, 4A-C)	80	140
<i>Hebecephalus sagittatus</i> Beamer & Tuthill	OR-ID / AB (1B, 3B)	3	2
<i>Hebecephalus truncatus</i> Beamer & Tuthill	MT-AK / YK-MB (1B, 3B, 4A-C)	30	45
? <i>Hecalus atascaderus</i> (Ball)	CA-MT / BC (3A, 3C)	9	0
<i>HECALUS FINNAMOREI</i> Hamilton	SK (4B)	0	<b>20</b>
* <i>Hecalus viridis</i> (Uhler)	CA-MD / BC-ON (2B, 3B, 4A-C, 5B-C, 6B)	50	135
<i>Helochara delta</i> Oman	WA-OR / BC (3A)	60	4
? <i>Idiocerus amoenus</i> Van Duzee	CA-CO / BC (2A, 3B)	1	6
<i>IDIOCERUS CANAE</i> Hamilton	AB (4B)	0	1
? <i>Idiocerus cinctus</i> DeLong & Caldwell	OR-MT / BC (2A, 3A-C)	1	<b>10</b>
<i>Idiocerus cingulatus</i> Ball	AZ-NM / BC (3A-C)	0	<b>20</b>
<i>Idiocerus concinnus</i> Ball	CA-UT / BC (3A)	7	25
? <i>Idiocerus distinctus</i> Gillette & Baker	CA-CO / BC (3A-C)	2	1
* <i>Idiocerus freytagi</i> Hamilton	CA-MI / BC-ON (2A, 2C, 3A-C, 4A-C, 5B-C, 6B)	80	125
? <i>Idiocerus indistinctus</i> Hamilton	MT / BC (2A)	0	4
<i>Idiocerus interruptus</i> Gillette & Baker	WA-CO / AB (4B)	8	0

<i>?Idiocerus moniliferae</i> Osborn & Ball	KS-NY / SK-MB (4B)	0	9
<i>?Idiocerus morosus</i> Ball	OR-ID / BC (2A, 3B)	3	50
<i>Idiocerus pericallis</i> Hamilton	CA / BC (2A-B)	0	8
<i>Idiocerus perplexus</i> Gillette & Baker	WA-MT / BC (3A)	0	1
* <i>Idiocerus ramentosus</i> Uhler	AZ-OH / BC-ON (2A, 2C, 3C, 4A-C, 5B-C)	140	25
* <i>Idiocerus raphus</i> Freytag	IA-NY / BC-QC (2A, 3C, 4A-C, 5B-C)	240	30
<i>Idiocerus rotundens</i> DeLong & Caldwell	MN-OH / ON (5C)	0	5
<i>Idiocerus snowi</i> Gillette & Baker	CA-CO / BC (3B)	0	10
<i>Idiocerus tahotus</i> Ball & Parker	CA-ID / BC (3B)	5	60
<i>IDIOCERUS VANDUZEEI</i> Hamilton	BC (3A)	15	30
<i>Idiocerus varians</i> Hamilton	IL-TN / ON (5C)	3	40
<i>?Koebelia californica</i> Baker	CA-ID / BC (3A-C)	7	5
<i>Laevicephalus exiguus</i> Knull	AZ-TX / AB-MB (4B)	40	0
<i>LAEVICEPHALUS</i> nr. <i>exiguus</i>	ON (6B Sauble Beach)	0	50
<i>Laevicephalus minimus</i> (Osborn & Ball)	AZ-OH / ON (6C)	0	50
* <i>Laevicephalus poudris</i> Tuthill	CO-WY / AB-MB (4A-C)	75	115
<i>Laevicephalus salarius</i> (Knull)	NM-SD / BC (2B)	0	10
<i>L. SASKATCHEWANENSIS</i> Hamilton & Ross	SK-MB (4A-C)	1	55
* <i>L. unicoloratus</i> (Gillette & Baker)	CO-NH / SK-QC (4C, 5C)	0	450
<i>Laevicephalus vannus</i> Knull	NM-WI / MB (4C)	0	5
<i>Latalus curtus</i> Beamer & Tuthill	ID-MT / BC (2A, 3B)	25	45
<i>Latalus intermedius</i> Ross & Hamilton	AZ-WY / NT-AB (2A, 2C, 4A)	5	490
<i>Latalus latidens</i> (Sanders & DeLong)	WI-MI / MB (4A, 4C)	3	0
<i>Latalus mundus</i> Beamer & Tuthill	WA-MT / BC (3B-C)	2	65
<i>?Lebradea helvina</i> (Van Duzee)	CA / BC (3A)	0	1
<i>?Limotettix balli</i> (Medler)	CA-MI / MB-ON (4C, 6A)	0	10
<i>Limotettix bisoni</i> Knull	UT-MI / AB-ON (4A-B, 6A)	3	40
<i>LIMOTETTIX BROOKSI</i> Hamilton	AB (2C, 4A)	6	0
<i>Limotettix cacheolus</i> (Ball)	AZ-SD / AB (4B)	0	1
<i>Limotettix conservatus</i> Hamilton	CO-IA / AB-SK, ON (4A, 6B)	30	1
<i>Limotettix elegans</i> Hamilton	TX-MI / ON (5B)	0	15
<i>?Limotettix finitimus</i> (Van Duzee)	CA-MT / BC (3B-C)	1	6
<i>Limotettix frigidus</i> (Ball)	CA-NE / BC-SK (3B, 4A-B)	40	10
<i>Limotettix myralis</i> (Medler)	UT-AK / AB-SK (4A-B, 6A)	1	6
<i>Limotettix shastus</i> (Ball)	CA-OR / BC-SK (3A-C, 4A)	4	13
<i>Limotettix symphorocarphae</i> (Ball)	UT-ND / AB, MB literature record (Medler 1958: 4B)	1	0
<i>?Limotettix taramus</i> (Medler)	NM-CO / SK (4A), literature record (Medler 1958)		
* <i>Limotettix uneolus</i> (Ball)	UT-ND / BC-MB (2B-C, 3C, 4A-C)	190	100
* <i>Limotettix urnura</i> Hamilton	NE-OH / SK-ON (4B-C, 5B-C, 6A)	2	175
<i>Limotettix utahnus</i> (Lawson)	UT-IL / BC-MB (2B, 3A-B, 4A, 4C)	25	6
<i>Limotettix varus</i> (Ball)	CO-IN / MB-ON (4C, 5C)	2	1
<i>Lonatura megalopa</i> Osborn & Ball	IA-MN / SK-MB (4B)	3	5
<i>Lonatura melina</i> DeLong	AZ-KS / AB-SK (4B)	35	20
* <i>Lonatura salsura</i> Ball	CA-NE / BC-MB (2A, 4A-C)	100	190

<i>Lonatura teretis</i> Beamer	CO / AB-MB (4A, 4C)	40	10
<i>Macropsis feminis</i> Hamilton	UT-MI / AB-MB (4A, 4C)	30	30
* <i>Macropsis ferrugineoides</i> (Van Duzee)	CA-OH / AB-ON (4A-C, 5C, 6B)	45	90
* <i>Macropsis hesperia</i> Breakey	CA-CT / BC-QC (2A, 3B-C, 4A-C, 6B)	115	65
<i>Macropsis rufescens</i> Hamilton	AZ-OH / AB-MB (4A-C)	15	20
<i>Macropsis rufocephala</i> Osborn	UT-OH / AB-ON (2C, 4A-C, 5C, 6B)	45	45
<i>MACROSTELAS FLAVALIS</i> Hamilton	MB (4C)	65	0
<i>MACROSTELAS</i> sp.nov.	SK-MB (4C)	25	25
<i>Memnonia anthalopus</i> Hamilton	ND-MN / AB-MB (4A-C)	13	80
<i>Memnonia brunnea</i> (Ball)	NM-SD / AB-MB (4B-C)	3	11
<i>Memnonia consobrina</i> Ball	AZ-CO / AB-SK (4B)	0	3
<i>Memnonia flavida</i> (Signoret)	TX-VA / ON (5B)	0	20
? <i>Memnonia grandis</i> (Shaw)	TX-GA / AB (4B)	0	1
<b>MEMNONIA MAIA</b> Hamilton	AB-SK (4B)	4	60
* <i>Memnonia panzeri</i> Hamilton	KS-WI / MB-ON (4C, 6A)	0	225
<i>Mesamia diana</i> Van Duzee	CA-ID / BC (3B)	2	15
<i>Mesamia ludoviciana</i> Ball	KS-WI / AB-MB (2C, 4A-C)	50	50
<i>Mesamia nigridorsum</i> (Ball)	UT-GA / AB-ON (4A-C, 5B-C)	20	20
<i>Mesamia straminea</i> (Osborn)	CA-GA / AB (4B)	3	0
* <i>Mocuellus americanus</i> Emeljanov	MT-MN / AB-ON (2C, 4A-C)	80	355
* <i>Mocuellus caprillus</i> Ross & Hamilton	NM-ND / AB-SK (4A-B)	160	280
<i>Mocuellus larrimeri</i> (DeLong)	WA-MT / BC (2A, 3B-C)	3	45
<b>MOCUELLUS STRICTUS</b> Ross & Hamilton	YK-AB (1B, 2C)	1	50
<i>Neocoelidia tumidifrons</i> Gillette & Baker	CO-MD / AB-PEI (4A-C, 5C, 6C)	30	25
* <i>Neohecalus lineatus</i> (Uhler)	GA-ME / QC-PEI ( <b>tidal grasslands only</b> )	0	150
<i>Neohecalus magnificus</i> Hamilton	OK-MI / MB-ON (4C, 5B)	2	8
* <i>Neokolla confluens</i> (Uhler)	CA-AZ / BC-SK (2B, 3A-B, 4B)	80	70
<i>Norvellina clarivida</i> (Van Duzee)	NM-UT / AB (2C, 4A-B)	15	5
<i>Norvellina columbiana</i> (Ball)	NM-WA / BC-AB (2B, 3B, 4B)	3	7
? <i>Norvellina rostrata</i> Lindsay	CA / BC (3A)	1	0
<i>Norvellina rubida</i> (Ball)	OR-WY / BC (3B-C in pass)	0	6
<i>Oncopsis coloradensis</i> (Baker)	CO / AB (3C in pass, 4B)	20	75
? <i>Oncopsis incidens</i> Hamilton	WA / BC, SK-MB (3B, 4A-C)	6	1
<i>Oncopsis junio</i> Hamilton	UT-CO / BC, SK (2A-B, 3B, 4 at Elbow)	15	25
* <b>ONCOPSIS MARILYNAE</b> Hamilton	BC-MB (2A, 3A-C, 4A-B)	20	105
* <i>Orocastus labeculus</i> (DeLong)	WY-ND / BC-SK (3C, 4A-B)	60	75
* <i>Orocastus perpussillus</i> (Ball & DeLong)	UT-ND / BC-MB (1B, 2A, 2C, 4A-B)	200	180
<i>Orocastus pinnipenis</i> Ross & Hamilton	OR-MT / BC (3B-C)	6	20
<b>OROCASTUS</b> sp.nov.	BC (3B Hedley)	0	5
<i>Orocastus tener</i> (Beamer & Tuthill)	UT-CO / YK-SK (1B, 2C, 4A)	25	25
<i>Paraphlepsius continuus</i> (DeLong)	CO-FL / SK-MB (4A-B)	40	25
<i>Paraphlepsius hemicolor</i> (Sanders & DeLong)	KS-MI / MB (4C);	0	1
* <i>Paraphlepsius lascivius</i> (Ball)	CA-KS / YK-MB (1B, 2A, 3B, 4A-C)	90	15
<i>Paraphlepsius lobatus</i> (Osborn)	KS-IN / SK-ON (4C, 5B, 6A-B)	0	70

<i>Paraphlepsius occidentalis</i> (Baker)	CA-MT / BC (3A-C in pass)	8	20
<i>Paraphlepsius solidaginis</i> (Walker)	ID-ME / AB-ON, NS (3B, 4A-C, 5C)	65	25
<i>Paraphlepsius umbrosus</i> (Sanders & DeLong)	<b>MN-WI</b> / SK-ON (4C, 6B)	3	20
<b><i>Pendarus magnus</i></b> (Osborn & Ball)	<b>TX-WI</b> / AB-MB (4A-C)	25	15
* <i>Pinumius sexmaculatus</i> (Gillette & Baker)	<b>UT-CO</b> / BC-SK (2A?, 2C, 4A-B)	80	205
<b><i>Polyamia caperata</i></b> (Ball)	KS-NH / MB-ON (4C, 5B-C, 6A)	0	<b>55</b>
? <i>Polyamia herbida</i> DeLong	MO-NY / ON (6A)	0	5
<i>Prairiana angustens</i> DeLong	ND-IN / ON (6B)	0	3
* <i>Prairiana cinerea</i> (Uhler)	<b>CO-WI</b> / BC-ON (2A-B, 4A-C, 5A)	80	30
<i>Prairiana kansana</i> (Ball)	KS-KY / AB-ON (4A-C, 6B)	1	15
<i>Psammotettix amplus</i> (DeLong & Davidson)	<b>CA-WA</b> / BC (3B)	0	1
<i>P. attenuens</i> (DeLong & Davidson)	<b>OR-CO</b> / BC (3A-C)	30	40
? <i>Psammotettix dentatus</i> Knull	<b>CA-UT</b> / BC (3A)	8	35
<b>PSAMMOTETTIX DIADEMATUS</b> Hamilton	<b>BC</b> (1C)	0	3
* <b><i>Psammotettix knullae</i></b> Greene	AK-IL / YK-ON (1B, 2C, 3B, 4A-C, 6C)	70	425
<b>PSAMMOTETTIX NESIOTUS</b> Hamilton	<b>BC</b> (3A)	50	25
* <b><i>Rosenus cruciatus</i></b> (Osborn & Ball)	<b>IA-MI</b> / BC-MB (2C, 4A-B)	140	140
<b>ROSENUS DECURVATUS</b> Hamilton & Ross	<b>BC</b> (2C), all from 1 site (type-locality)	0	<b>220</b>
<i>Scaphytopius diabolus</i> (Van Duzee)	CA-CO / BC (3B)	6	30
<i>Scaphytopius oregonensis</i> (Baker)	CA-MT / BC (3B-C)	50	20
* <i>Sorhoanus debilis</i> (Uhler)	<b>OR-CO</b> / BC-AB (2B, 3B-C)	80	125
<i>Sorhoanus xiphosura</i> Hamilton	<b>OR-MT</b> / BC (3B-C)	2	15
<b><i>Stenometopiellus cookei</i></b> (Gillette)	<b>CO-SD</b> / AB-SK (4A-B)	15	15
<b><i>Stirellus bicolor</i></b> (Van Duzee)	AZ-NH / SK-MB (4C)	0	<b>90</b>
<b><i>Stragania atra</i></b> (Baker)	CA-WY / AB-SK (4B)	10	1
<b><i>Stragania rufoscutellata</i></b> (Baker)	<b>CA-NM</b> / AB-SK (2C, 3B, 4A-B)	80	5
<b>TELUSUS</b> sp.nov.	<b>AB-SK</b> (4B)	3	<b>20</b>
<i>Texananus cumulatus</i> (Ball)	<b>UT-MI</b> / AB-MB (4B)	4	1
<i>Texananus dolus</i> DeLong	<b>MT-WI</b> / BC, SK-MB (3B-C, 4A, 4C)	1	15
<i>Texananus extremus</i> (Ball)	<b>CA-CO</b> / BC-AB (3B, 4B)	0	2
<i>Texananus latipex</i> (DeLong)	<b>CA-UT</b> / BC (3B)	0	1
* <b><i>Texananus marmor</i></b> (Sanders & DeLong)	<b>MT</b> / AB-ON (4B-C, 6A)	90	95
<i>Texananus oregonus</i> (Ball)	<b>CA-AZ</b> / BC (3B)	3	8
<i>Texananus proximus</i> Crowder	<b>WA-UT</b> / BC (3B)	4	0
<i>Twiningia fasciata</i> (Beamer)	CA-WA / BC (2A in pass, 3B)	6	1
<i>Twiningia pellucida</i> (Ball)	CA-MT / BC ( <b>3A-C</b> )	1	<b>30</b>
<b>UNOKA DRAMATICA</b> Hamilton	<b>BC</b> (2A, 3B)	0	<b>90</b>
<b><i>Unoka gillettei</i></b> Metcalf	<b>NM-UT</b> / AB (4B-C)	5	10
<i>Xerophloea peltata</i> (Uhler)	<b>TX-IL</b> / AB-MB (4B-C)	15	6
<i>Xerophloea zionis</i> Lawson	CA-MT / BC, MB (2A-B, 3A-C, 4B)	0	<b>20</b>
<i>Xyphon triguttatum</i> (Nottingham)	<b>CA-UT</b> / BC (3B)	1	0

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## Chapter 12

# Aphids (Hemiptera: Aphidoidea) of the Prairies Ecozone of Canada

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**Abstract.** Three hundred fifty-seven species of aphids are found in the Prairies Ecozone, of which 81 are adventive. The distribution of aphids in the region is determined by the availability of host plants and has been strongly affected by agricultural practices. The faunal elements unique to this ecozone relative to the rest of Canada represent the northern limits of species feeding on dryland shrubs centred in the Great Basin of the United States.

**Résumé.** On dénombre dans l'écozone des prairies 357 espèces de pucerons, dont 81 sont adventives. La répartition de ces insectes dans la région dépend de la disponibilité des espèces végétales hôtes, qui est fortement influencée par les pratiques agricoles. Les éléments fauniques uniques à cette écozone par rapport au reste du Canada représentent la limite nord des espèces qui se nourrissent d'arbustes dans les zones arides du Grand Bassin des États-Unis.

### Introduction

In general, a particular aphid species feeds on a restricted range of hosts, usually constituting a single genus or tribe, but sometimes a single species of plant (Dixon 2005). Furthermore, a number of species alternate between plant species; a perennial (tree or shrub) serves as the overwintering primary host on which sexual reproduction occurs, and a secondary host (frequently an herbaceous plant) is used in summer. Therefore, these aphid species require both hosts to be available in the same area (although some species can persist without a sexual phase on the secondary host in the absence of their normal primary host). Aphid distributions are thus limited by the host distributions. On the other hand, if local conditions are appropriate for the persistence of the host plant, the aphids will usually find and use them. Differences in life history strategies among host plants are reflected in differences in strategies among aphids. Two groups of aphids may be distinguished: those that are associated with reliable perennial hosts, and those that depend on environmental disturbances that encourage the propagation of weedy host plants and that are usually more adept at long-distance dispersal. The major disruption of the Prairies Ecozone by agriculture has favoured the latter so that the most commonly encountered aphids in the region today belong to widespread species associated with crop plants and their weeds.

The scope of the current work includes all aphids found within the Prairies Ecozone as outlined in Shorthouse (2010), including the contained highlands and the Parkland

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Ecoregion. Harper and Bradley (1987) provided a list of 147 aphid species with their host associations for Alberta, and Robinson and Lamb (1991) listed 324 species found in Manitoba. The only treatment of aphids for Saskatchewan is included in Maw *et al.* (2000). A significant number of the species in the Alberta list are from montane habitats. For example, 22% of the species listed are in the conifer-feeding genus *Cinara*. About 15% of the species from Manitoba were collected only in the far southeastern part of the province (Boreal Plains and Boreal Shield, especially Sandilands Provincial Forest and Whiteshell Provincial Park), or from the Hudson Bay Lowlands (Churchill), and thus are outside the region being considered here. Material in the Canadian National Collection of Insects, Arachnids, and Nematodes was examined and previously undetermined material identified. This material includes the collection of the late A.M. Harper and representative slides of almost all specimen series from the collection of the late A.G. Robinson.

Aphid classification (Table 1) follows Remaudière and Remaudière (1997) as updated by Nieto Nafria *et al.* (1998). Angiosperm family names follow APG III (Angiosperm Phylogeny Group 2009). Among the plant genera included in Table 2, this classification differs from the familiar available floral references mainly in the transfer of some Scrophulariaceae to Orobanchaceae and of *Sambucus* and *Viburnum* from Caprifoliaceae to Adoxaceae; the placement of Aceraceae within Sapindaceae, Asclepiadaceae within Apocynaceae, and Chenopodiaceae within Amaranthaceae; and the arrangement of the lily-like monocots.

Because of the strong association between aphids and their host plants, the list of aphid species in the ecozone (Table 2) is organized by host taxa. A summary of number of species associated with various host groups, habitat types, and life cycle characteristics is given in Table 3. The following discussion highlights or expands on information presented within Table 2.

### Grasslands

The most characteristic aphids of North American grasslands are those associated with dryland shrubs. Several genera of aphids are restricted to *Artemisia* hosts or contain a preponderance of species on *Artemisia*. *Epameibaphis*, *Pseudoepameibaphis*, *Artemisaphis*, *Flabellomicrosiphum*, and *Microsiphoniella* (all restricted to *Artemisia*) are endemic to the dry basins of western North America. Two species of *Pseudoepameibaphis* are found in the southern parts of all three Prairie Provinces; two species of *Epameibaphis* and one each of *Artemisaphis*, *Flabellomicrosiphum*, and *Microsiphum* are known to occur in southern Alberta (the latter also in Manitoba). Species of *Obtusicauda* (five in western North America, with one of these known to occur in the Canadian prairies, and several species in Asia) are also restricted to *Artemisia*. The *Aphis* subgenus *Zyxaphis* is endemic to western North America on plants of the genera *Artemisia*, *Chrysothamnus*, and *Ericameria*. At least one species of *Zyxaphis* (*A. canae*) has been collected in Alberta and Saskatchewan. The genus *Pleotrichophorus* has radiated extensively on shrubs of the family Asteraceae in the Great Basin. Of the approximately 60 species worldwide, most are found in the Great Basin and other dry basins of western North America, with 16 species occurring on shrubby Astereae (*Chrysothamnus*, *Ericameria*, *Gutierrezia*, and *Haplopappus*), 18 species on *Artemisia*, and four on *Achillea*. In the Canadian Prairie Provinces, seven species of *Pleotrichophorus* have been collected on *Artemisia* and two on *Achillea*. In addition, *P. villosae*, found on *Heterotheca villosa* (= *Chrysopsis villosa*), is known only from southern Manitoba, and an unidentified species has been collected on *Iva axillaris* at Regina, Saskatchewan.

**Table 1.** Classification of aphid genera found in the Prairies Ecozone, according to the scheme of Remaudière and Remaudière (1997) with updated nomenclature by Nieto Nafria *et al.* (1998).

Higher Taxon	Genera
Adelgidae	<i>Adelges, Pineus</i>
Phylloxeridae	<i>Phylloxera</i>
Aphididae <sup>1</sup>	
Anoeciinae	<i>Anoecia</i>
Aphidinae	
Aphidini	<i>Aphis, Asiphonaphis, Brachyinquis, Hyalopterus, Hysteroneura, Misturaphis, Rhopalosiphum, Schizaphis</i>
Macrosiphini	<i>Abstrusomyzus, Acyrthosiphon, Amphorophora, Aphthargelia, Artemisiaphis, Aspidaphis, Atarsos, Brachycaudus, Brachycorynella, Brevicoryne, Cachryphora, Capitophorus<sup>2</sup>, Carolinaia, Catamergus, Cavariella<sup>2</sup>, Ceruraphis, Chaetosiphon, Coloradoa, Cryptaphis, Cryptomyzus, Diuraphis, Epameibaphis, Ericaphis, Hayhurstia, Hyadaphis, Hyalomyzus, Hyperomyzus, Illinoia, Liosomaphis<sup>2</sup>, Lipaphis, Macrosiphoniella, Macrosiphum, Metopolophium, Microlophium, Microsiphoniella, Muscaphis, Myzaphis, Myzodium, Myzus, Nasonovia, Nearctaphis, Obtusicauda, Ovatus, Pleotrichophorus, Pseudacaudella, Pseudocercidis, Pseudoepameibaphis, Pseudacaudella, Rhopalomyzus, Sitobion, Uroleucon, Utamphorophora</i>
Calaphidinae	
Calaphidini	<i>Betulaphis, Boernerina, Calaphis, Euceraphis, Oestlundiella, Symydobius</i>
Panaphidini	<i>Myzocallis, Hoplochaitophorus, Neosymydobius, Therioaphis, Tinocalli</i>
Chaitophorinae	
Siphini	<i>Sipha</i>
Chaitophorini	<i>Chaitophorus, Periphyllus, Pseudopterocomma</i>
Drepanosiphinae	<i>Drepanaphis</i>
Eriosomatinae	
Eriosomatini	<i>Colopha, Eriosoma, Tetraneura</i>
Pemphigini	<i>Clydesmithia, Mordwilkoja, Neoprociphilus, Pachypappa, Pemphigus, Prociphilus, Thecabius</i>
Fordini	<i>Forda, Geoica, Smynthurodes</i>
Hormaphidinae	<i>Hamamelistes</i>
Lachninae	
Eulachnini	<i>Cinara, Essigella, Eulachnus</i>
Lachnini	<i>Lachnus, Longistigma, Maculolachnus</i>
Tramini	<i>Trama</i>
Mindarinae	<i>Mindarus</i>
Phyllaphidinae	<i>Stegophylla</i>
Pterocommatinae <sup>2</sup>	<i>Fullawayia, Pterocomma</i>
Saltusaphidinae	<i>Izyphia, Subizyphia, Subsaltusaphis, Thripsaphis</i>
Tamaliinae	<i>Tamalia</i>

<sup>1</sup> Other schemes divide Aphididae into several families, with family Aphididae composed of Aphidinae and Pterocommatinae only. However, there is a dispute about the relationships among some of the subfamilies and their assignment to the more narrowly defined families. Thus, we choose here to follow the current aphid catalogue (Remaudière and Remaudière 1997).

<sup>2</sup> Recent molecular evidence (von Dohlen *et al.* 2006) suggests that Pterocommatinae are most closely related to certain genera within Macrosiphini (*Cavariella* in particular, likely also *Capitophorus* and *Liosomaphis*), but a revised classification has not been formally proposed.

**Table 2.** Aphids on host plants with a summary of ecoregion associations. Aphids with host alternation between overwintering (primary) hosts on which sexual reproduction occurs and summer (secondary) hosts are listed under both host taxa. Host family-level classification follows APG III (Angiosperm Phylogeny Group 2009). Abbreviations: Cyc = life cycle relationship of aphid to host: 0 = can complete all phases of life cycle on single host; 1 = plant is a primary (winter) host; 2 = plant is a secondary (summer) host; 2\* = plant is sole host in Prairies Ecozone (life cycle is incomplete (lacks sexual generations) in absence of primary host). Distribution: G = grassland; (G) = in depressions and other shrubby protected areas in grassland; P = parkland; V = river valley forest; E = eastern parkland; long-grass prairie and eastern forest elements (southern Manitoba and eastern Saskatchewan (Assiniboine drainage)); U = eastern uplands (southern Manitoba uplands and Moose Mountain, Saskatchewan); C = Cypress Hills; W = persistent wetlands within grassland zones; A = agricultural systems (on both crops and weeds); H = horticultural contexts, including shelterbelts, abandoned homesteads, and urban forests; a = adventive species. Square brackets indicate species or ecoregion associations expected, but not yet recorded.

Host	Cyc	Distribution	Comment
<b>Bryophyta</b>			
<i>Muscaphis escherichi</i> Börner 1939	2	[P]E	
<i>Muscaphis utahensis</i> C.F. Smith & Knowlton 1965	0	P	
<i>Myzodium modestum</i> (Hottes 1926)	1	[P]	
<i>Pseudacaudella rubida</i> (Börner 1939)	0	[P]	
<b>Pteridophyta</b>			
<i>Onoclea sensibilis</i> L., <i>Matteuccia struthiopteris</i> (L.) Todaro	0	PE	
<i>Pteridium aquilinum</i> (L.) Kuhn	0	PE	
<b>Pinophyta</b>			
Cupressaceae			
<i>Juniperus communis</i> L.	0	P	
<i>Juniperus horizontalis</i> Moench	0	E	
<i>Thuja</i> , <i>Juniperus</i> spp.	0	E	
Pinaceae			
<i>Abies</i> spp.	0	H, a	
<i>Abies balsamea</i> (L.) Mill.	0	H	
<i>Larix laricina</i> (Du Roi) K. Koch	0	H	past records as <i>M. abietinus</i>
<i>Picea</i> spp.	2	PH	
<i>Picea abies</i> (L.) Karst.	0	H	roots
<i>Picea glauca</i> (Moench) Voss	1	PH	
	1	H	
	0	C	

	<i>Cinara fornacula</i> Hottes 1930	0	CPUEH
	<i>Cinara hottesi</i> (Gillette & Palmer 1924)	0	UEH
	<i>Cinara obscura</i> Bradley 1953	0	CPUEH
	<i>Mindarus obliquus</i> (Cholodkovsky 1896)	0	CPH
	<i>Pinus similis</i> (Gillette 1907)	1	H
	<i>Pinus</i> sp.	1	CH
	<i>Cinara nigra</i> (Wilson 1919)	0	CP
	<i>Cinara pergandei</i> (Wilson 1919)	0	E
	<i>Essigella knowltoni</i> Hottes 1957	0	C
	<i>Eulachnus rileyi</i> (Williams 1911)	0	H
	<i>Cinara pinea</i> (Mordvilko 1895)	0	H, a
	<i>Eulachnus agilis</i> (Kaltenbach 1843)	0	H, a
	<i>Adelges coolleyi</i> (Gillette 1907)	2	H
	<i>Aphis middletonii</i> Thomas 1879	0	GPVEAH roots
	<i>Forda formicaria</i> von Heyden 1837	2*	GPVEAH, a roots
	<i>Forda marginata</i> Koch 1857	2*	GPVEAH, a roots
	<i>Geotica utricularia</i> (Passerini 1856)	2*	GPVEAH, a roots
	<i>Aphis fabae</i> Scopoli 1763 ( <i>sensu lato</i> )	2	PVEAH, a several subspecies
	<i>Aphis gossypii</i> Glover 1877	0	AH, a
	<i>Aphis nasturtii</i> Kallenbach 1843	2	PVEAH, a
	<i>Aphis spiraeicola</i> Patch 1914	2	PVEAH, a
	<i>Prociphilus erigeronensis</i> (Thomas 1879)	2	PE roots
	<i>Smynthuroides betae</i> Westwood 1849	2*	GP, a roots
	<i>Longistigma caryae</i> (T.W. Harris 1841)	0	EH on bark of large trees
	<i>Macrosiphum euphorbiae</i> (Thomas 1878)	2	GPVEA
	<i>Myzus persicae</i> (Sulzer 1776)	2	AH, a irruptive
	<i>Aphis mimuli</i> Oestlund 1887	2	EW
	<i>Rhopalosiphum nymphaeae</i> (Linnaeus 1761)	2	W, a
	<i>Aphis sambuci</i> Linnaeus 1758	0	H, a
	<i>Pinus banksiana</i> Lamb.,		
	<i>Pinus contorta</i> Douglas ex Loudon		
	<i>Pinus contorta</i>		
	<i>Pinus nigra</i> Arnold		
	<i>Pinus sylvestris</i> L.		
	<i>Pseudotsuga menziesii</i> (Mirb.) Franco		
<b>Magnoliophyta</b>			
	polyphagous on various monocots and dicots		
<b>Dicots</b>			
	various dicots		
	emergent aquatic dicots		
Adoxaceae			
	<i>Sambucus racemosa</i> L.		

Host	Cyc	Distribution	Comment
<i>Fiburnum</i> spp.	0	E	
	1	PV	
Amaranthaceae (incl. Chenopodiaceae)			
<i>Atriplex</i> , <i>Chenopodium</i> spp.	0	GPVE, a	roots
<i>Chenopodium</i> spp., <i>Beta vulgaris</i> L.	2	PVEA	roots
	2	PVEA	roots
<i>Sarcobatus vermiculatus</i> (Hook.) Torr.	0	[G]	
Apiaceae			
various genera	0	PE	
	0	E	
	0	E	
	2	PVE, a	
	2	PE	
	2	P	
	2	PVAH, a	
	2	P	
	2	EVW	
	2	PV	
	2	E, a	
Poeynaceae [incl. Asclepiadaceae]			
<i>Asclepias syriaca</i> L.	2	E	
	0	E, a	irruptive
	0	E	
Asteraceae			
various genera	2	H, a	
	2	PE, a	
	0	E	
	0	E	
	0	E	
	0	GPVE	includes <i>U. escalantii</i>
	0	P	
	0	G	
	0	PE	
	0	E	





Host	Cyc	Distribution	Comment
<i>Uroleuon pepperi</i> (Olive 1965)	0	E	
<i>Brachycaudus cardui</i> (Linnaeus 1758)	2	PAH, a	
<i>Hyperomyzus sandilandicus</i> (Robinson 1974)	2	E	
<i>Uroleuon eupatoriicola</i> (Patch 1919)	0	E	
<i>Atarsos grindeliae</i> Gillette 1911	0	E[G]	
<i>Illinoia grindeliae palmerae</i> (MacGillivray 1958)	0	F[G]	
<i>Uroleuon richardsi</i> (Robinson 1964)	0	E[G]	
<i>Uroleuon helianthicola</i> (Olive 1963)	0	E	
<i>Uroleuon maxmilianicola</i> (Robinson 1985)	0	E	
<i>Uroleuon obscuricaudatum</i> (Olive 1965)	0	E	
<i>Pleotrichophorus villosae</i> Robinson 1974	0	E[G]	
<i>Uroleuon carberriense</i> Robinson 1986	0	PE	
<i>Uroleuon hieracicola</i> (Hille Ris Lambers 1962)	0	E	
<i>Pleotrichophorus</i> sp.	0	G	
<i>Uroleuon ivae</i> (Robinson 1985)	0	GE	
<i>Pemphigus bursarius</i> (Linnaeus 1758)	2	H, a	
<i>Acyrtosiphon lactucae</i> (Passerini 1860)	0	(G)PAH, a	
<i>Uroleuon deltense</i> Robinson 1985	0	E	
<i>Hyperomyzus nabali</i> (Oestlund 1886)	2	E	
<i>Uroleuon rudbeckiae</i> (Fitch 1851)	0	PE	
<i>Aphis dacknountainensis</i> Rojanavongse & Robinson 1977	0	E	
<i>Aphis lugentis</i> Williams 1911	0	P	
<i>Cachryphora serotinae</i> (Oestlund 1887)	0	E	
<i>Uroleuon arnesense</i> Robinson 1985	0	E	
<i>Uroleuon brevitarsus</i> (Robinson 1974)	0	E	
<i>Uroleuon caligatum</i> (Richards 1966)	0	E	
<i>Uroleuon gigantiphagum</i> Moran 1984	0	PVE	
<i>Uroleuon nigrotibium</i> (Olive 1963)	0	E[G]	
<i>Uroleuon nigrotuberculatum</i> (Olive 1963)	0	PVE	
<i>Uroleuon pitelouti</i> (Richards 1972)	0	E	
<i>Hyperomyzus lactucae</i> (Linnaeus 1758)	2	AH, a	
<i>Hyperomyzus pallidus</i> Hille Ris Lambers 1935	2	AH, a	
<i>Macrosiphoniella tanacetaria</i> (Kaltenbach 1843)	0	H, a	
<i>Aphis knowltoni</i> Hottes & Frison 1931	0	GE	roots

<i>Xanthium strumarium</i> L.									
Berberidaceae									
<i>Berberis</i> spp.									
Betulaceae									
<i>Alnus</i> spp.									
<i>Betula</i> spp.									
	<i>Trama rara</i> Mordvilko 1908		0						roots; no sexual forms known
	<i>Uroleucon taraxaci</i> (Kaltenbach 1843)		0						
	<i>Capitophorus xanthii</i> (Oestlund 1886)		2						
	<i>Liosomaphis berberidis</i> (Kaltenbach 1843)		0						
	[ <i>Boernerina variabilis</i> Richards 1961]		0						
	<i>Euceraphis gillettei</i> Davidson 1915		0						
	<i>Illinoia alni</i> (Mason 1925)		0						
	<i>Oestlundella flava</i> (Davidson 1912)		0						
	<i>Prociphilus tessellatus</i> (Fitch 1851)		0						
	<i>Pterocallis alnifoliae</i> (Fitch 1851)		0						
	[ <i>Betulaphis quadratuberculata</i> (Kaltenbach 1843)]		0						
	[ <i>Calaphis betulaccolens</i> (Fitch 1851)]		0						
	<i>Calaphis flava</i> Mordvilko 1928		0						
	<i>Calaphis manitobensis</i> Richards 1968		0						
	<i>Euceraphis betulae</i> (Koch 1855)		0						
	<i>Euceraphis papyrifericola</i> Blackman in Blackman & de Boise 2002		0						in past misidentified as <i>E. betulae</i>
	<i>Symydobius americanus</i> A.C. Baker 1918		0						
	[ <i>Hamamelistes spinosus</i> Shimer 1867]		2*						present on adjacent boreal plain
Brassicaceae									
various genera	<i>Brevicoryne brassicae</i> (Linnaeus 1758)		0						
	<i>Lipaphis pseudobrassiccae</i> (Davis 1914)		0						
	<i>Pemphigus populitransversus</i> Riley 1879		2						
Caprifoliaceae									
<i>Lonicera</i> spp.	<i>Hyadaphis foeniculi</i> (Passermi 1860)		1						
	<i>Prociphilus xylostet</i> (DeGeer 1773)		1						
	<i>Rhopalomyzus lonicerae</i> (Siebold 1839)		1						
	<i>Rhopalomyzus poae</i> (Gillette 1908)		1						
	<i>Gyosoaphis oestlundii</i> Hottes 1930		0						
	<i>Rhopalomyzus grabhami</i> (Cockerell 1903)		1						
<i>Lonicera dioica</i> L.									
<i>Lonicera involucrata</i> (Richardson) Banks ex Spreng.									
<i>Lonicera tatarica</i> L.	<i>Hyadaphis tataricae</i> (Ajzenberg 1935)		1						
<i>Symphoricarpos occidentalis</i> Hook.	<i>Amphicercidius pulverulens</i> (Gillette 1911)		0						
	<i>Aphthargelia symphoricarpi</i> (Thomas 1878)		0						

Host	Cyc	Distribution	Comment
Comaceae			
<i>Cornus sericea</i> L.	1	PE, a	<i>Anoezia corni</i> (Fabricius 1775)
	1	E	<i>Anoezia cornicola</i> (Walsh 1863)
	0	PE	<i>Aphis cornifoliae</i> Fitch 1851
	1	PE	<i>Aphis helianthi</i> Monell in Riley & Monell 1879
	0	PE	<i>Aphis neogillettei</i> Palmer 1938
	1	P	<i>Aphis maculatae</i> Oestlund 1887
	0	PE	<i>Macrosiphum hamiltoni</i> Robinson 1968
	0	PE	<i>Macrosiphum manitobense</i> Robinson 1965
Crassulaceae			
<i>Hylotelephium telephium</i> (L.) H. Ohba	0	H, a	<i>Aphis sedi</i> Kaltenbach 1843
Dipsacaceae			
<i>Dipsacus fullonum</i> L.	2	H, a	<i>Macrosiphum rosae</i> (Linnaeus 1758)
Elaeagnaceae			
<i>Elaeagnus</i> , <i>Hippophae</i> spp.	1	H, a	<i>Capitophorus hippophaes</i> (Walker 1852)
<i>Elaeagnus angustifolia</i> L.	1	H, a	<i>Capitophorus elaeagni</i> (Del Guercio 1894)
<i>Shepherdia</i> spp.	1	P	<i>Capitophorus hudsonicus</i> Robinson 1979
	1	GPVE	<i>Capitophorus shepherdiae</i> Gillette & Bragg 1916
	1	GPVE	<i>Capitophorus xanthii</i> (Oestlund 1886)
Ericaceae			
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	0	C	<i>Tamalia coweni</i> (Cockerell 1905)
Fabaceae			
various genera	0	AHPE, a	<i>Acyrtosiphon pisum</i> (Harris 1776)
	2	PVE	<i>Neartaphis crataegifoliae</i> (Fitch 1851)
<i>Astragalus</i> spp.	0	P	<i>Aphis gallowayi</i> Robinson 1991
<i>Astragalus</i> , <i>Hedysarum</i> , <i>Oxytropis</i>	0	P	<i>Aphis astragalina</i> Hille Ris Lambers 1974
<i>Caragana arborescens</i> Lam.	0	H, a	<i>Acyrtosiphon caraganae</i> (Cholodkovsky 1908)
	0	H, a	<i>Therioaphis tenera</i> (Ajzenberg 1956)
<i>Glycine max</i> (L.) Merr.	2	A, a	<i>Aphis glycines</i> Matsumura 1917
<i>Lupinus</i> spp.	0	C	<i>Aphis lupini</i> Gillette & Palmer 1929
	0	H	<i>Macrosiphum albifrons</i> Essig 1911
<i>Medicago</i> , <i>Trifolium</i> spp.	0	A, a	<i>Therioaphis trifolii</i> (Monell 1882)
<i>Melilotus</i> spp.	0	A, a	<i>Therioaphis riehmi</i> (Börner 1949)

irruptive

native in western mountains

<i>Trifolium</i> spp.					2	PA
<i>Vicia cracca</i> L.					0	E, a
Fagaceae						
<i>Quercus macrocarpa</i> Michx.						
	<i>Nearctaphis bakeri</i> (Cowen 1895)					
	<i>Aphis craccæ</i> Linnaeus 1758					
	<i>Hoplochaitophorus quercicola</i> (Monell in Riley & Monell 1879)				0	EU
	<i>Lachnus allegheniensis</i> McCook 1877				0	EU
	<i>Myzocallis discolor</i> (Monell in Riley & Monell 1879)				0	EU
	<i>Myzocallis punctatus</i> (Monell in Riley & Monell 1879)				0	EUH
	<i>Neosymydobius mimicus</i> Hottes 1926				0	EU
	<i>Stegophylla quercicola</i> (Monell in Riley & Monell 1879)				0	EU
Geraniaceae						
<i>Geranium</i> spp.						
	<i>Amphiphora geranii</i> Gillette & Palmer 1929				0	CV
	<i>Amphiphora coloutensis</i> Smith & Knowlton 1983				0	P
	<i>Macrosiphum geranii</i> (Oestlund 1887)				0	E
Grossulariaceae						
<i>Ribes</i> spp.						
	<i>Aphis manitobensis</i> Robinson & Rojanavongse 1976				1	E
	<i>Aphis mimuli</i> Oestlund 1887				1	E
	<i>Aphis oenotheræ</i> Oestlund 1887				1	E
	<i>Aphis varians</i> Patch 1914				1	P
	<i>Cryptomyzus galeopsidis</i> (Kaltenbach 1843)				1	HP, a
	<i>Cryptomyzus ribis</i> (Linnaeus 1758)				1	HP, a
	<i>Hyperomyzus lactuæ</i> (Linnaeus 1758)				1	AH, a
	<i>Hyperomyzus nabali</i> (Oestlund 1886)				1	E
	<i>Hyperomyzus pallidus</i> Hille Ris Lambers 1935				1	AH, a
	<i>Hyperomyzus ribiellus</i> (J. J. Davis 1919)				1	EP
	<i>Nasonovia cynosbati</i> (Oestlund 1887)				1	P
	<i>Nasonovia houghtonensis similis</i> Heie 1979				1	P
Lamiaceae						
various genera						
<i>Galeopsis tetrahit</i> L.					2	HP, a
<i>Monarda fistulosa</i> L.					2	HP, a
	<i>Aphis neomonardæ</i> Rojanavongse & Robinson 1977				0	E
	<i>Hyalomyzus monardæ</i> (Davis 1912)				2	E
	<i>Ovatus crataegarius</i> (Walker 1850)				2	H
<i>Mentha arvensis</i> L.						
Lythraceae						
<i>Lythrum salicaria</i> L.						
	<i>Myzus lythri</i> (Schrank 1801)				2	W, a
Malvaceae						

Host		Cyc	Distribution	Comment
<i>Alcea rosea</i> L.	<i>Uroleucon eoessigi</i> (Knowlton 1947)	0	E	
Myricaceae				
<i>Myrica gale</i> L.	<i>Illinoia canadensis</i> (MacGillivray 1958)	0	E	
Oleaceae				
<i>Fraxinus</i> spp.	<i>Prociphilus americanus</i> (Walker 1852)	1	H[E]	
Onagraceae				
<i>Chamerton angustifolium</i> (L.) Holub	<i>Aphis oenotherae</i> Oestlund 1887	0	E	
	<i>Aphis varians</i> Patch 1914	2	P	
	<i>Macrosiphum valerianae</i> (Clarke 1903)	0	P	
<i>Epilobium</i> spp.	<i>Aphis salicariae</i> Koch 1855	0	P, a	
<i>Oenothera biennis</i> L.	<i>Aphis oenotherae</i> Oestlund 1887	0	P	
	<i>Aphis oestlundii</i> Gillette 1927	2	E	
<i>Oenothera</i> spp.	<i>Anoecia oenotherae</i> Wilson 1911	0	E	
Orobanchaceae				
<i>Castilleja</i> spp.	<i>Nasonovia castelleiae</i> (Sampson 1939)	0	P	
<i>Orthocarpus</i> , <i>Pedicularis</i> spp.	<i>Nasonovia alpina</i> (Gillette & Palmer 1928)	0	P	
Polygonaceae				
<i>Polygonum</i> spp.	<i>Aspidaphis adjuvans</i> (Walker 1848)	0	[P]E, a	
	<i>Capitophorus hippophaes</i> (Walker 1852)	2	H, a	
<i>Rumex</i> spp.	<i>Aphis rumicis</i> Linnaeus 1758	0	EW, a	
Primulaceae				
<i>Lysimachia</i> spp.	<i>Mordwilkoja vagabunda</i> (Walsh 1863)	2	PVE	
Ranunculaceae				
<i>Aquilegia</i> spp.	<i>Nasonovia aquilegiae</i> Essig 1917	0	GP	
<i>Clematis ligusticifolia</i> Nutt.	<i>Illinoia breviaris</i> (Gillette & Palmer 1933)	0	GV	
<i>Delphinium</i> spp.	<i>Brachycaudus rociadae</i> (Cockerell 1903)	0	[G]E	
	<i>Nasonovia wahinkae robinsoni</i> Richards 1958	0	G	
<i>Thalictrum</i> spp.	<i>Nasonovia purpurascens</i> (Oestlund 1887)	0	E[P]	
Rosaceae				
various genera	<i>Macrosiphum pseudorosae</i> Patch 1919	0	PVEH	
<i>Amelanchier alnifolia</i> (Nutt.) Nutt.	<i>Acyrtosiphon macrosiphum</i> (Wilson 1912)	0	PV	
ex M. Roem.	<i>Aphis whiteshellenis</i> Rojanavongse & Robinson 1977	0	E	

<i>Crataegus</i> spp.	<i>Eriosoma americanum</i> (Riley in Riley & Monell 1879)	2	E, P
	<i>Nearctaphis sensoriata</i> (Gillette & Bragg 1918)	1	P
	<i>Prociphilus caryae caryae</i> (Fitch 1856)	1	P
	<i>Ericaphis gentneri</i> (Mason 1947)	0	C
	<i>Eriosoma crataegi</i> (Oestlund 1887)	2	E
	<i>Nearctaphis crataegifoliae</i> (Fitch 1851)	1	PVE
<i>Crataegus, Malus,</i>	<i>Utamphorophora crataegi</i> (Monell in Riley & Monell 1879)	0	C
<i>Cotoneaster</i> spp.	<i>Aphis pomi</i> DeGeer 1773	0	EH, a
	<i>Eriosoma lanigerum</i> (Hausmann 1802)	2	E
	<i>Nearctaphis bakeri</i> (Cowen ex Gillette & Baker 1895)	1	P
	<i>Rhopalosiphum oxyacanthiae</i> (Schrank 1801)	1	PEA
<i>Fragaria</i> spp.	<i>Abstrusomyzus valulifera</i> (Robinson 1974)	0	PE
	<i>Aphis forbesi</i> Weed 1889	0	E
	<i>Chaetosiphon fragaefolii</i> (Cockerell 1901)	0	PVEH
<i>Potentilla fruticosa</i> L.	<i>Acyrtosiphon assiniboynense</i> Robinson 1973	0	PVE
	<i>Nasonovia williamsi</i> C.F. Smith & Parron 1978	0	E
<i>Prunus</i> spp.	<i>Rhopalosiphum nymphaeae</i> (Linnaeus 1761)	1	PVE, a
	<i>Hysteronera setariae</i> (Thomas 1878)	1	E
<i>Prunus</i> (s.g. <i>Prunophora</i> ) spp.	<i>Hyalopterus pruni</i> (Geoffroy 1762)	1	PE, a
<i>Prunus pensylvanica</i> L.f.	<i>Myzus cerasi</i> (Fabricius 1775)	1	PVE, a
	<i>Myzus lythri</i> (Schrank 1801)	1	E, a
<i>Prunus virginiana</i> L.	<i>Asiphonaphis pruni</i> Wilson 1919	0	(G)PVE
	<i>Rhopalosiphum cerasifoliae</i> (Fitch 1855)	1	PVWE
	<i>Rhopalosiphum padi</i> (Linnaeus 1758)	1	(G)PVA, a
<i>Rosa</i> spp.	<i>Chaetosiphon thomasi</i> Hille Ris Lambers 1953	0	PVH
	<i>Eomacrosiphon nigromaculosum</i> (MacDougall 1926)	0	P
	<i>Ericaphis wakibae</i> (Hottes 1934)	0	P
	<i>Macrosiphum rosae</i> (Linnaeus 1758)	0,1	H, a
	<i>Macrolachnus siphkensi</i> Hille Ris Lambers 1962	0	GP
	<i>Metopolophium dirhodum</i> (Walker 1849)	1	GPVEA, a
	<i>Pseudocercidis rosae</i> Richards 1961	0	PE
<i>Rosa, Fragaria</i> spp.	<i>Wahlgreniella nervata</i> (Gillette 1908)	0	PV
	<i>Chaetosiphon minus</i> (Forbes 1884)	0	EH
	<i>Rhodobium porosum</i> (Sanderson 1900)	0	EH
<i>Rosa, Potentilla</i> spp.	<i>Myzaphis rosarum</i> (Kaltenbach 1843)	0	PEH

can complete lifecycle on rose







Host	Cyc	Distribution	Comment
Saxifragaceae			
<i>Saxifraga</i> sp.	0	E	<i>Nasonovia vockerothi</i> (Richards 1963)
Tiliaceae			
<i>Tilia ×europaea</i> L.	0	H, a	<i>Eucallipterus tiliatae</i> (Linnaeus 1758)
Ulmaceae			
<i>Ulmus</i> spp.	1	E	<i>Eriosoma mimicum</i> Hottes & Frison 1961
	0	E	<i>Eriosoma rileyi</i> Thomas 1877
	1	H, a	<i>Tetraneura ulmi</i> (Linnaeus 1758)
<i>Ulmus</i> L.	1	EVH	<i>Eriosoma americanum</i> (Riley in Riley & Monell 1879)
	1	EH	<i>Eriosoma crataegi</i> (Oestlund 1887)
	1	EH	<i>Eriosoma lanigerum</i> (Hausmann 1802)
	1	E	<i>Colopha ulmicola</i> (Fitch 1859)
	1	E	<i>Colopha graminis</i> (Monell 1882)
	0	E	<i>Tinocallis ulmifolii</i> (Monell in Riley & Monell 1879)
Urticaceae			
<i>Urtica gracilis</i> Aiton	0	P	<i>Amphorophora urticae</i> Essig 1942
	0	P	<i>Microlophium carnosum</i> (Buckton 1876)
Monocots			
Asparagaceae			
<i>Asparagus officinalis</i> L.	0	H, a	<i>Brachycorynella asparagi</i> (Mordvilko 1929)
<i>Maianthemum stellatum</i> L.	0	PVE[U]	<i>Illinoia wahnaga</i> (Hottes 1952)
Link <i>Convallaria majalis</i> L.			
<i>Polygonatum biflorum</i> (Walter) Elliott	0	E	<i>Catamerigus kickapoo</i> (Hottes & Frison 1931)
Cyperaceae			
various genera, not <i>Carex</i>	2	PVEW	<i>Rhopalosiphum cerasifoliae</i> (Fitch 1855)
<i>Carex</i> spp.	2	E	<i>Carolinaia howardii</i> (Wilson 1911)
	2	PV	<i>Ceruraphis viburnicola</i> (Gillette 1909)
	0	E[G], a?	<i>Iziphya spenceri</i> Richards 1958
	0	GPEU	<i>Iziphya flabella</i> (Sanborn 1904)
	0	E	<i>Iziphya vittata</i> Richards 1958
	0	[G]	[ <i>Subiziphya clauseni</i> Quednau 1990]
	0	PE	<i>Thripsaphis balli</i> (Gillette 1908)
	0	E[P]	<i>Thripsaphis cyperii</i> (Walker 1848)



The European species, *P. glandulosus* (Kaltenbach), widely introduced elsewhere in North America, was recorded from Alberta by Harper and Bradley (1987), but no supporting material has been located. Species of the genus *Macrosiphoniella* also feed on *Artemisia* and related Asteraceae. This genus is most diverse in the Palearctic region, but several species are indigenous to North America and several others are adventive from Eurasia. Three native and two adventive species of *Macrosiphoniella* are found in the southern Prairie Provinces. *Misturaphis shiloensis* is known only from Shilo, Manitoba, on *Artemisia campestris* ssp. *caudata*. The chenopodiaceous shrub *Sarcobatus vermiculatus*, common on saline flats, is host to *Brachyunguis bonnevillensis*. Although not yet collected in Canada, this aphid is found from Arizona to Montana and may be expected to occur in southern Alberta and Saskatchewan. Protected depressions and slopes within the grasslands harbour

**Table 3.** Summary of number of indigenous and adventive aphid species with various host and ecological associations and with different life cycle types.

Category	Number of Species <sup>4</sup>	
	Native <sup>1</sup>	Adventive <sup>1</sup>
Host group		
Mosses	4	0
Ferns	2	0
Conifers	27	0
Dicot trees and shrubs <sup>2</sup>	144	38
Dicot forbs <sup>2</sup>	118	45
Grasses	12	18
Other monocots	10	3
Habitat/region		
Grasslands	47	20
River valley forests	61	14
Parkland	133	31
Eastern parkland/long-grass prairie	163	36
Eastern uplands	25	1
Cypress Hills	24	0
Wetlands	4	5
Agricultural fields	6	29
Horticultural plantings	29	49
Life cycle type		
Non-alternating	210	44
Host alternating	65	31
Asexual <sup>3</sup>	1	6
Total species	276 <sup>4</sup>	81

<sup>1</sup> Original distribution of some widespread aphids is unclear. Species that may be naturally Holarctic (such as some moss-feeding aphids) are counted as "native." Species native elsewhere in North America, but present in the Prairies Ecozone as a result of recent floristic changes arising from European settlement, are also counted as native.

<sup>2</sup> "Shrub" is used to indicate upright woody perennial "bushy" plants and includes such plants as *Rubus* species with biennial woody above-ground growth. On the other hand, low-growing plants with persistent woody crowns or stem bases (such as *Artemisia frigida*) are grouped with "forbs."

<sup>3</sup> Includes species that are host alternating in their native range, but persist asexually in the absence of their primary host (e.g., members of tribe Fordini with sexual forms on pistachio in the Mediterranean region).

<sup>4</sup> Includes five species expected in the Prairies Ecozone but not yet collected.

a number of other shrubby plants and their associated aphids, such as the aphid *Aphthargelia symphoricarpi* on *Symphoricarpos occidentalis*, *Maculolachnus sijkkensi* on *Rosa*, *Asiphonaphis pruni* on *Prunus virginiana*, and several *Capitophorus* species on *Shepherdia*.

Although a number of aphid genera contain grass specialists, the number of such species in the Nearctic grasslands is low, in contrast, for example, to the African savanna, where the genus *Sitobion* in particular has radiated extensively (Eastop 1961). The few native Nearctic aphids on grasses are infrequently collected and their distributions are unknown. *Cryptaphis bromi* is known from Winnipeg, Manitoba; Athabasca, Alberta; and Penticton, British Columbia. It is quite cryptic in its habits (a small brown aphid apparently feeding at the base of the grass plant among the dried remains of the leaf sheaths) (Robinson 1967) and may be much more common than its known incidence suggests. *Sipha agropyronensis* is currently confirmed only from Colorado, but may be more widespread. *Anoecia graminis* feeds on grass roots in Colorado, and a very similar aphid has been found at Winnipeg and at Kinsella, Alberta (Newton *et al.* 2011). Three aphid species (*Forda formicaria*, *F. marginata*, *Geoica utricularia*) of Mediterranean origin have been collected on the roots of native grasses at a number of sites in the grassland areas of the Prairie Provinces. The other grass-feeding aphids in the area are usually encountered on grain crops and are discussed below with other aphids of agricultural systems.

Among other herbaceous plants of the grasslands, *Grindelia squarrosa* is notable in that it supports three specific aphids: *Atarsos grindeliae* (which overcomes the stickiness of its host plant by lacking tarsi), *Illinoia richardsi*, and *Uroleucon grindeliae*. *Subizyphia clauseni* is known only from a collection in 1908 in the mixedgrass region of eastern Montana (Quednau 1990) and a recent collection by the authors in the Kootenay Plains (Alberta) on a dryland *Carex* species (likely *C. duriuscula* or *C. obtusata*). It probably occurs in the intervening area.

### Parkland and River Valley Forests

Species of *Populus* are the most obvious floral element of the parkland and of the major river valleys and constitute the primary (overwintering) host for a number of gall-forming, host-alternating aphids, as well as several non-alternating aphid species. Floate (2010) treated 14 species of native and two species of introduced aphids forming galls on cottonwoods. An additional poplar-gall aphid, *Clydesmithia canadensis*, previously unrecognized east of Waterton Lakes National Park, is now known from recent collections by the authors to occur as far east as Ninette, Manitoba. Two other species (*Pachypappa rosettei* and *P. sacculi*) form pseudogalls (gall-like distortions of host tissue that are not completely closed) on trembling aspen. Among non-galling aphids, *Aphis maculatae* uses various *Populus* species as summer hosts (the winter host is *Cornus sericea*). Fourteen non-alternating species (in genera *Chaitophorus*, *Fullawaya*, *Pterocomma*, and *Pseudopterocomma*) feed on *Populus* species in this area.

Other aphids are associated with other trees and shrubs in river valleys. *Acer negundo* is host to *Periphyllus negundinis*; *Amelanchier alnifolia* to *Acyrtosiphon macrosiphum* and, where *Amelanchier* co-occurs with elm, to *Eriosoma americanum*; *Crataegus* species to *Nearctaphis bakeri* and *N. crataegifolii*; *Cornus sericea* to *Aphis* (three species) and *Macrosiphum* (two species); *Lonicera involucrata* and *L. dioica* to *Rhopalomyzus* species and *Gypsoaphis oestlundii*, respectively; *Potentilla fruticosa* to *Acyrtosiphon assiniboinensis*, *Myzaphis rosarum*, and *Nasonovia williamsi*; *Prunus virginiana* to *Asiphonaphis pruni*, *Rhopalosiphum cerasifoliae*, and *R. padi*; *Ribes* species to several species of *Aphis*,

*Hyperomyzus* (subgenus *Neonasonovia*), and *Nasonovia* (subgenus *Kakimia*); and *Rosa* and *Chaetosiphon* species, and, in shaded locations, to *Eomacrosiphon nigromaculosum* and *Pseudocercidius rosae*.

Compared with those of the grasslands, a larger number of herbaceous plants of the parkland and river valley forests serve as aphid hosts. For example, about 20 species of *Uroleucon* occur on various composites, especially asters and goldenrods. Most of the poplar gall-forming species and many of the shrub-feeding species (particularly those on *Ribes*) mentioned above use herbaceous plants as summer hosts. The summer hosts of some of the poplar-gall species include roots of crop plants such as sugarbeet and potentially canola (known secondary hosts of *Pemphigus populitransversus* are cruciferous plants). The secondary hosts of *Rhopalomyzus* species are grasses.

### Eastern Forest Elements

Southern Manitoba and southeastern Saskatchewan, in addition to their grassland and parkland components, are characterized by the presence of plants that are more predominant in eastern North America. For example, *Quercus macrocarpa* (with *Hoplochaitophorus quercicola*, *Lachnus allegheniensis*, *Neosymydobius mimicus*, *Myzocallis* species, and *Stegophylla querci*) and *Ulmus americana* (with *Eriosoma* species and *Tinocallis ulmifolii*) occur naturally in this area. Boreal Plains species such as white spruce (host to *Mindarus obliquus* and several *Cinara* species) and birches (host to species of *Calaphis*, *Euceraaphis*, and *Symydobius*) occur in higher areas, such as Spruce Woods Provincial Park in Manitoba and Moose Mountain in Saskatchewan. *Hysteroneura setariae*, which alternates between *Prunus* and grasses in eastern North America (and is widespread in the tropics as completely asexual populations on grasses), has been collected in eastern Manitoba and occasionally recorded from grain crops (Robinson and Hsu 1963; Gavloski and Meers 2011).

### Cypress Hills

The aphids present in the transition from the surrounding grasslands to the higher elevations of the Cypress Hills are similar to those in the transition from the grasslands to parkland, although the transition is more abrupt. In addition, typical boreal species may be found, such as several *Cinara* species, *Mindarus obliquus*, and adelgid species on *Picea glauca*, as well as *Tamalia coweni* on *Arctostaphylos uva-ursi*. Several aphid species normally found in montane regions are also present. These include *Cinara nigra* and *Essigella knowltoni* (on *Pinus contorta*), *Ericaphis gentneri* (on *Crataegus* sp.), and *Aphis lupini* (on *Lupinus* sp.). Also found on *Crataegus* sp. is the eastern North American species *Utamphorophora crataegi*.

### Wetlands

The willows (*Salix*), sedges (*Carex*), rushes (*Juncus*), bulrushes (*Scirpus*), and cattails (*Typha*) of stream banks and persistent wetlands, including those occurring within the grassland area, are hosts to a number of aphid species. *Aphis farinosa*, *Macrosiphum californicum*, and several species of *Chaitophorus* and *Pterocomma* occur on willows. *Cavariella* species use willows as overwintering hosts and various umbelliferous plants as summer hosts. *Rhopalosiphum enigmae* lives within the leaf sheath at the base of cattail plants and *Thripsaphis* species feed on *Carex*.

## Adventive Aphids of Agricultural and Horticultural Systems

The substantial adventive aphid fauna of North America has been documented by Footitt *et al.* (2006). The cosmopolitan polyphagous aphids, *Myzus persicae* and *Aphis fabae*, occur commonly on a number of agricultural and horticultural crops, as well as on various weeds and native plants. *Macrosiphum euphorbiae*, apparently native to eastern North America, is now found worldwide. It uses *Rosa* as a winter host, but accepts a wide range of plants as summer hosts, including many ornamental and dicot crop plants.

Gavloski and Meers (2011) summarized the aphid fauna associated with grain crops. The cosmopolitan species *Rhopalosiphum padi*, the bird cherry-oat aphid (using chokecherry as overwintering host), and *Metopolophium dirhodum* (with rose as overwintering host) are among the most abundant species in most trap samples. *Sitobion avenae*, the English grain aphid, is found in both north and south temperate areas of the world. It is common in moist areas, where it occurs on species of various plants, mainly graminoid monocots, but as its name implies, it is also common on grain crops. *Diuraphis tritici* was described from North America, but may be of East Asian origin (Blackman and Eastop 2006). *Diuraphis frequens* and *D. noxia* (Russian wheat aphid) originate in Europe and central Asia, respectively. *Rhopalosiphum maidis* and *Schizaphis graminum* do not overwinter in the Canadian Prairies, but in some years, migration from more southern regions results in economically significant outbreaks. *Sipha elegans* (= *S. agropyrella*) and *S. glyceriae* are common throughout the northern hemisphere and *S. flava* is broadly distributed in the United States and South America. There are several records of *S. elegans* from various localities in the Prairies Ecozone, and the other two *Sipha* species have been found in southern Manitoba.

Aphids also feed on various dicot crops. *Lipaphis pseudobrassicae* and *Brevicoryne brassicae* occur on both cultivated (Gavloski *et al.* 2011) and weedy crucifers (Brassicaceae), including native species. Soroka and Otani (2011) include the aphids *Acyrtosiphon pisum*, *Therioaphis trifolii* (including form *maculata*), *T. riehmii*, and *Nearctaphis bakeri* in their discussion of insects on legume forage crops. The soybean aphid, *Aphis glycines*, was first recorded in North America in 2000 (Hunt *et al.* 2003) and is now distributed through most of the soybean-growing areas of the continent, including southern Manitoba.

Two drought-tolerant central Asian shrub species, extensively planted across the prairies as ornamentals and in windbreaks, and persisting at sites of abandoned farmsteads, have associated aphid species: *Acyrtosiphon caraganae*, *Therioaphis tenera* (on *Caragana arborescens*), and *Hyadaphis tataricae* (on *Lonicera tartarica*). Although *T. tenera* was only recently recognized in North America (in Quebec; Quednau 2003), it was found by the authors to be widely distributed in Alberta and Saskatchewan in 2009 and 2010. *Artemisia* species introduced by early settlers for medicinal and culinary purposes, and now naturalized in many areas, brought with them several species of *Coloradoa*, a Palearctic genus of inconspicuous aphids specializing on wormwoods and other anthemids.

## Urban Forests

Planting of trees in urban areas and as windbreaks has resulted in the extension of the range of several species of aphid found in the boreal or eastern forests. In particular, several *Cinara* species feeding on spruce are now widely distributed across the region, *Eriosoma* species occur on elm wherever it is planted, and several aphids species are found (or are expected) on ornamental birches.

## Biogeographical Aspects

The aphids associated strictly with grassland habitat are primarily a northern extension of the ranges of species occurring in the Great Plains and Great Basin of the United States. The largest proportion of the species in the Prairies Ecozone occurs in areas of transition on plants that are also found in the Boreal Plains and eastern deciduous forest. A few western montane species occur in the Cypress Hills. Because of the transformation of the region by agriculture, the most prominent species in terms of numbers are those that came from Eurasia with their crop and weed hosts.

## Research Priorities

Most aphid-collecting efforts in the Prairies Ecozone have been focused on agricultural (A.M. Harper) and forestry (G.A. Bradley) needs. The aphid fauna of southern Manitoba is well-known because of the work of A.G. Robinson. However, the distribution and abundance of most of the species found in the drier grasslands has been little studied. For example, Canadian records of many of the *Artemisia*-feeding species are based on only a few collections made by the authors in 2009 and 2010. Root aphids are a substantially unstudied component of the fauna. The few collections available contain specimens that do not fit within the known variation of described species (Newton *et al.* 2011). The secondary (summer) hosts for poplar-gall forming species are roots of various plants, but the specific associations for most species are unclear or unknown.

The lack of collections available for many species (both within Canada and in the broader range of these species) has resulted in a poor understanding of the range of variation in characters among and within taxa. Analysis of this variation would aid in the resolution of boundaries and more robust definitions of species, especially in speciose genera such as *Uroleucon* and *Pleotrichophorus*.

Even among more extensively collected taxa, there is need for more detailed analysis to delimit morphologically cryptic species. The application of DNA sequence data is a useful tool in identifying cryptic taxa. For example, a recent DNA analysis of sugarbeet root aphid showed that samples identified as *Pemphigus betae* based on gall morphology in fact belong to three species, one of which is undescribed (Foottit *et al.* 2010).

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## Chapter 13 Black Flies (Diptera: Simuliidae) of the Prairie Grasslands of Canada

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Mating pair of *Cnephia dacotensis*, the only obligatorily autogenous species of black fly from the Prairies Ecozone of Canada. Photo courtesy of Stephen A. Marshall.

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**Abstract.** Only 18 of Canada's 165 species of black flies are considered residents of the prairie grasslands. Topography and climate influence the quality and quantity of breeding sites, but host availability may also play a role in influencing species richness. Most species that dwell on the prairies are widely distributed, occurring in two or more ecozones. Only *Simulium johannseni* and *Simulium meridionale*, whose distributions fall largely within the Great Plains region, could be considered prairie-adapted species. Outbreaks of prairie black flies today tend to be localized and episodic, causing occasional discomfort to humans and domesticated animals. In general, the nuisance factor is minor compared with that in northern woodland areas. The role of prairie black flies in the transmission of disease agents, especially to wildlife, is not well understood.

**Résumé.** Seules 18 des 165 espèces de mouches noires (simulies) qui existent au Canada sont réputées être des espèces résidentes des prairies. La topographie et le climat influent sur la qualité et sur le nombre des sites de reproduction, mais la disponibilité des hôtes influence aussi probablement la diversité des espèces. La plupart des espèces qui vivent dans les prairies sont largement réparties, occupant au moins deux écozones. Seuls *Simulium johannseni* et *Simulium meridionale*, dont l'aire de répartition coïncide largement avec la région des Grandes Plaines, peuvent être considérés comme des espèces adaptées aux prairies. Les pullulations de mouches noires dans les prairies ont aujourd'hui tendance à être localisées et épisodiques, devenant à l'occasion une source d'inconfort pour les humains et les animaux domestiques. En règle générale, le facteur de nuisance est mineur si on le compare à celui qui existe dans les zones boisées du nord. Le rôle des mouches noires des prairies dans la transmission d'agents pathogènes—en particulier aux animaux sauvages—reste mal connu.

## Introduction

Black flies are best known as blood-sucking pests of birds and mammals, including humans. Less appreciated is the beneficial role they play in running-water food webs (Adler *et al.* 2004). The Simuliidae are a relatively small family of flies with about 2,140 extant species recognized worldwide (Adler and Crosskey 2013). The immature stages occupy every conceivable running-water habitat, from tiny headwater trickles to mighty rivers and from hot springs to glacier meltwaters—anywhere there is freely flowing water. Only the polar regions and high mountain areas are uninhabited by members of the family. It is not surprising, therefore, that black flies are also represented in the grasslands of Canada.

Characterizing black flies from the full range of Canadian grasslands habitats presents a number of challenges. Neither the adults nor immature stages have a close association with grasses, except as oviposition sites and attachment substrata for larvae and pupae. Furthermore, the fragmented nature of grasslands habitats across Canada—in combination with the strong dispersal capabilities of adults—means that a majority of Canada's 165 species have the potential to be encountered in such habitats. This chapter explores whether the nature of grasslands has any marked influence on black fly community assembly; coverage is therefore restricted to the largest contiguous tract of grasslands in Canada—the prairie grasslands of Alberta, Saskatchewan, and Manitoba.

The Canadian prairie grasslands are a continuation of the Great Plains region of the United States, which extend south to Texas in a broad expanse of relatively flat land between the Rocky Mountains and the Mississippi River (Wishart 2004). Published records of black flies suggest that the Great Plains fauna is meagre, although the intensity of research varies greatly throughout the region. Taking Nebraska as an example of a well-known area that falls more or less entirely within the Great Plains, only 18 species have been recorded from that state so far (Pruess and Peterson 1987; Adler and Crosskey 2013). In contrast, Mono County, California—which has just one-twenty-fifth the land area of Nebraska—supports 55–60 species of black flies in a mosaic of different stream habitats ranging from desert to high mountain elevations (Adler in Hershey *et al.* 1995). Such marked regional differences suggest that stream habitat heterogeneity is positively correlated to species richness. What attributes of the Great Plains limit black fly species richness?

## Ecological Setting

Among the most important determinants of black fly species distribution is the availability of suitable breeding sites. Accordingly, it is important to understand the attributes of prairie streams and their potential impact on black fly development. Topographical and climatic factors likely impose the greatest influence on breeding-site availability. The immature stages require running water for their development; both larvae and pupae attach themselves to submerged substrates and therefore require specific substrate and flow conditions. The generally flat terrain and aridity of the prairies influences both the quality and quantity of breeding sites. The Canadian prairies are situated within three major drainage basins, two originating in the Rocky Mountains (the Saskatchewan and Missouri rivers) and one originating on the Great Plains of North Dakota and Minnesota (the Red River). While rivers originating in the mountains are relatively cool, clear, and rapidly flowing near their sources, they rapidly transform as they empty onto the prairies (Rosenberg *et al.* 2005). As the gradient declines, the river channel assumes a more meandering course, with few areas of rapid current. The ability of the current to transport bed materials (gravel, sand, silt) also changes. Organic and inorganic particles that were once entrained in the current begin to settle, and the once rocky riverbed becomes covered by sediments. This limits the amount of substrate available for colonization by larvae and pupae, as they typically cannot attach themselves to heavily silted surfaces (Crosskey 1990). With much of the stream bottom rendered unsuitable for attachment, larvae and pupae are confined to siltation-resistant substrata such as trailing grasses (Pruess 1989) or submerged branches, greatly limiting the ability of black flies to colonize prairie streams. Although the slower current causes much of the larger-sized particles to settle, the finest materials continue to be carried in the current. Consequently, prairie streams are typically turbid (cloudy).

Another limiting factor is the relative scarcity of tributaries feeding the three major rivers, a product of the gently undulating terrain and low annual precipitation, which averages only 454 mm across the Canadian prairie grasslands (McGinn 2010). Furthermore, many tributaries are intermittent, drying shortly after snowmelt in spring. Depending on nutrient inputs (e.g., from surrounding agriculture), dissolved oxygen can also decline in slow-moving sections, especially during winter (Rosenberg *et al.* 2005), further limiting survival of aquatic organisms.

While topography and climate on the prairies produce generally unfavourable conditions for black flies, other attributes actually promote larval development. With little or no overhanging riparian vegetation, prairie streams have greater exposure to sunlight than do forested streams, with concomitant increases in water temperature and primary productivity (e.g., Vannote *et al.* 1980); however, high turbidity can limit light penetration and primary productivity if sediment levels are too high. Temperature is the most important factor influencing the development of black fly larvae (Merritt *et al.* 1982; Ross and Merritt 1988), and the increased production of diatoms and filamentous algae has the potential to promote larval growth. Primary production is further enhanced by the input of nutrients from the naturally fertile prairie soils (Rosenberg *et al.* 2005). In addition to these natural phenomena, the development of irrigation systems has markedly extended the breeding sites of black flies, both seasonally and geographically, in areas that were previously too arid to produce streams except briefly during spring runoff or flash floods (Fredeen and Shemanchuck 1960).

In summary, prairie streams are influenced by a unique set of factors that influence both the quality and quantity of watercourses available for colonization by black flies.

While some of these attributes are favourable for development (i.e., relatively warm water, abundance of nutrients), others (i.e., slow water current, lack of suitable substrata for larval and pupal attachment) are not. On balance, the negative aspects evidently outweigh the positive, as simuliid species richness on the Great Plains is low relative to that of most other ecozones in North America.

### **Annotated Checklist of Black Flies from the Canadian Prairie Grasslands**

Listed here are 18 species of black flies that are considered residents of the grasslands of the Canadian Prairies Ecozone of Alberta, Saskatchewan, and Manitoba (as defined by Shorthouse (2010) and Shorthouse and Larson (2010); see also Table 1). The list was compiled with reference to the distribution maps of North American black flies in Adler *et al.* (2004). Species were considered residents if distributional records fell decisively within the grasslands of the Canadian Prairies Ecozone. Species whose ranges fell predominantly in adjacent areas (i.e., the Aspen Parkland of the Prairies Ecozone, the Boreal Plains Ecozone, and the Montane Cordillera Ecozone), but only peripherally onto the prairie grasslands, were excluded.

#### **Family Simuliidae Newman 1834**

##### **Subfamily Simuliinae Newman 1834**

##### **Tribe Simuliini Newman, 1834**

#### **Genus *Cnephia* Enderlein, 1921**

##### **1. *Cnephia dacotensis* (Dyar and Shannon, 1927)**

*Distribution:* Alberta to Quebec south to Kansas.

*Grasslands Records:* There are numerous records of this species throughout the southern grasslands of Manitoba (Crosskey 1994), Saskatchewan (Fredeen 1985*a*), and Alberta (Currie 1986).

*Biological Information:* Populations of *C. dacotensis* have ranges that extend west only as far as the foothills of the Rocky Mountains, which evidently serve as a barrier to dispersal into the grasslands of south-central British Columbia. The immature stages occur abundantly in streams enriched by pastures and feedlots, especially at the outlets of impounded water (Adler *et al.* 2004). Females are obligatorily autogenous (i.e., do not blood-feed), their mouthparts not being armed with serrations and teeth and thus being incapable of piercing skin.

#### **Genus *Ectemnia* Enderlein, 1930**

##### **2. *Ectemnia invenusta* (Walker, 1848)**

*Distribution:* Alberta to Quebec, south to Georgia.

*Grasslands Records:* The distribution of *E. invenusta* on the Canadian prairies is uncertain, as females—the most frequently encountered life stage—are structurally similar to those of the closely related species *E. taeniatifrons*. The only known record of *E. invenusta* so far is a single pharate pupa collected from the South Saskatchewan River in southwestern Alberta (Currie 1986). It is possible that certain records of *E. taeniatifrons* from Manitoba are actually *E. invenusta* (Wood in Crosskey 1994).

*Biological Information:* The immature stages of *E. invenusta* typically live in deep, rapidly

**Table 1.** Black flies (Diptera: Simuliidae) of the prairie grasslands of Canada, with distributional data and feeding habits. Abbreviations for distribution: AB = Alberta, SK = Saskatchewan, MB = Manitoba. Abbreviations for feeding habits: A = autogenous, O = ornithophilic, M = mammalophilic.

Taxon	Distribution	Feeding Habit
Subfamily SIMULIINAE Newman, 1834		
Tribe SIMULIINI Newman, 1921		
<b>CNEPHIA</b> Enderlein, 1921		
<i>Cnephia dacotensis</i> (Dyar and Shannon, 1927)	AB, SK, MB	A
<b>ECTEMNIA</b> Enderlein, 1930		
<i>Ectemnia invenusta</i> (Walker, 1848)	AB	O
<i>Ectemnia taeniatifrons</i> (Enderlein, 1925)	AB, SK, MB	O
<b>SIMULIUM</b> Latreille, 1802		
Subgenus <b>BOREOSIMULIUM</b> Rubtsov and Yankovsky, 1982		
JOHANNSENI species group		
<i>Simulium johannseni</i> Hart in Forbes, 1912	AB, SK, MB	O
Subgenus <b>BYSSODON</b> Enderlein, 1925		
MERIDIONALE species group		
<i>Simulium meridionale</i> Riley 1887	AB, SK, MB	O
Subgenus <b>EUSIMULIUM</b> Roubaud, 1906		
<i>Simulium pilosum</i> (Knowlton and Rowe, 1934)	AB	O
Subgenus <b>PSILOPELMIA</b> Enderlein, 1921		
ESCOMELI species group		
<i>Simulium bivittatum</i> Malloch, 1914	AB, SK	M
<i>Simulium griseum</i> Coquillett, 1898	AB, SK	M
Subgenus <b>PSILOZIA</b> Enderlein, 1936		
vittatum species complex		
<i>Simulium tribulatum</i> Lugger, 1897	AB, SK, MB	M
<i>Simulium vittatum</i> Zetterstedt, 1838	AB, SK, MB	M
Subgenus <b>ASPATHIA</b> Enderlein, 1935		
METALLICUM species group		
<i>Simulium hunteri</i> Malloch, 1914	AB, SK	M
<i>Simulium piperi</i> Dyar and Shannon, 1927	AB, SK	M
Subgenus <b>SIMULIUM</b> s.s.		
JENNINGSI species group		
<i>Simulium luggeri</i> Nicholson and Mickel, 1950	AB, SK, MB	M
MALYSHEVI species group		
arcticum species complex		
<i>Simulium vampirum</i> Adler, Currie and Wood, 2004	AB	M
NOELLERI species group		
<i>Simulium decorum</i> Walker, 1848	AB, SK, MB	M
TUBEROSUM species group		
tuberosum species complex		
<i>Simulium tuberosum</i> (Lundström, 1911)	AB, SK, MB	M
VENUSTUM species group		
venustum species complex		
<i>Simulium venustum</i> Say, 1823	AB, SK	M
verecundum species complex		
<i>Simulium rostratum</i> (Lundström, 1911)	AB, SK, MB	M

flowing streams and rivers. Larvae hatch in the fall and develop throughout the winter. The adults are among the earliest black flies to emerge in spring (Wolfe and Peterson 1959; Davies *et al.* 1962). Females are known to bite ruffed grouse, wild and domestic ducks, and Canada geese (Bennett 1960; Tarshis and Herman 1965; Tarshis 1972).

### 3. *Ectemnia taeniatifrons* (Enderlein, 1925)

*Distribution:* Alberta and Manitoba, south to Kansas.

*Grasslands Records:* This species is widely but sparsely distributed throughout the three Prairie Provinces.

*Biological Information:* Ecological details are similar to those described above for *E. invenusta*. Hosts include ring-necked pheasants, ruffed grouse, chickens, and domestic turkeys (Anderson and DeFoliart 1961). Females are attracted to humans and, in Saskatchewan, are reported to occasionally bite people (Fredeen 1985a). Although Fredeen (1985a) reports that adults are pests of mammals, the females possess bifid tarsal claws, a character associated with bird feeding. Consequently, birds are more likely to be the primary hosts of *E. taeniatifrons*.

## Genus *Simulium* Latreille, 1802

### Subgenus *Boreosimulium* Rubtsov and Yankovsky, 1982 *johannseni* species group

#### 4. *Simulium johannseni* Hart in Forbes, 1912

*Distribution:* Alberta and Manitoba, south to Texas and Georgia.

*Grasslands Records:* *Simulium johannseni* is distributed widely, if not abundantly, across the prairie grasslands of Canada.

*Biological Information:* Immature stages occur typically in large-size streams and rivers throughout their range, with larvae hatching shortly after ice breakup in spring (Fredeen 1981; Westwood and Brust 1981; Currie 1986). The female tarsal claw is bifid and adapted for ornithophily, and gallinaceous birds such as ring-necked pheasants, domestic turkeys, and chickens are among the known hosts (Anderson and DeFoliart 1961). However, females are also attracted to mammals and are known to occasionally bite horses, cattle, and humans (Westwood and Brust 1981). Even in the absence of blood feeding, females can be a significant pest of humans and other mammals due to their swarming and probing activities (Adler *et al.* 2004).

### Subgenus *Byssodon* Enderlein, 1925 *meridionale* species group

#### 5. *Simulium meridionale* Riley 1887

*Distribution:* Alberta and Manitoba, south to California and Alabama.

*Grasslands Records:* The immature stages of *S. meridionale* inhabit all the major drainage basins of the Canadian prairies.

*Biological Information:* This multivoltine species breeds in meandering rivers with sandy or alluvial substrata (Fredeen 1981; Adler *et al.* 2004). Although the tarsal claws of females are adapted for ornithophily, blood meals are taken from both avian and mammalian hosts. Ring-necked pheasants, mourning doves, starlings, purple martins, tree swallows, bluebirds, chickens, and domesticated turkeys are among the confirmed avian hosts (Anderson and Defoliart 1981; Gaard 2002; Adler *et al.* 2004; Currie and Hunter

2008). Outbreaks of *S. meridionale* are of major concern to poultry operations, with deaths attributed to exsanguination reported in Saskatchewan (Fredeen 1981). Females are also pests of mammals. They are attracted to moose and can be a nuisance to horses, cattle, and humans (Pledger *et al.* 1980; Westwood and Brust 1981; Peterson and Kondratieff 1995). In addition to their status as bloodsucking pests, females of *S. meridionale* are vectors of *Leucocytozoon smithi* and equine encephalitis virus to poultry (Anderson and DeFoliart 1961; Anderson *et al.* 1961; Fredeen 1981; Pinkovsky *et al.* 1981).

### **Subgenus *Eusimulium* Roubaud, 1906**

#### **6. *Simulium pilosum* (Knowlton and Rowe, 1934)**

*Distribution:* Transcontinental.

*Grasslands Records:* Most historical records of “*Simulium aureum* Fries” from the Canadian prairies are probably *S. pilosum*. This species is unquestionably more common across the prairies than suggested by the distributional map in Adler *et al.* (2004). The apparent absence of *S. pilosum* from Saskatchewan and Manitoba probably reflects the lack of cytological screening in those provinces (see the next section, Biological Information).

*Biological Information:* *Simulium pilosum* is one of five North American species referable to the *Simulium aureum* species complex. As only some of these species can be distinguished morphologically in one or two life stages, most of the historical literature refers to them collectively as “*S. aureum*” (a strictly Palearctic species), or the “*S. aureum* complex.” In general, species in the complex can be distinguished reliably only through examination of the giant polytene chromosomes of larvae (Leonhardt 1985). Specific host records for *S. pilosum* are unknown because females of the *S. aureum* complex are undistinguishable morphologically. However, members of the complex are predominantly ornithophilic, with a diversity of hosts in the Galliformes, Anseriformes, Columbiformes, Ciconiiformes, Strigiformes, and Passeriformes. Females are vectors of several species of *Leucocytozoon* and are probable vectors of *Trypanosoma confusum* (Adler *et al.* 2004).

### **Subgenus *Psilopelmia* Enderlein, 1921 *escomeli* species group**

#### **7. *Simulium bivittatum* Malloch, 1914**

*Distribution:* Southern Alberta and Saskatchewan south to Mexico.

*Grasslands Records:* In Canada, this species occurs almost exclusively in the grasslands of Alberta and Saskatchewan.

*Biological Information:* The immature stages of *S. bivittatum* live in irrigation canals and rivers in the prairie grasslands of Alberta and Saskatchewan. Females attack a wide variety of large mammals, including horses, cattle, sheep, pigs, and humans (Fredeen and Shemanchuck 1960; Fredeen 1981). Occasional severe outbreaks of this multivoltine species have forced residents of Saskatoon, Saskatchewan, and Medicine Hat, Alberta, indoors (Fredeen 1981).

#### **8. *Simulium griseum* Coquillett, 1898**

*Distribution:* Southern Alberta and Saskatchewan south to California and New Mexico.

*Grasslands Records:* As with *S. bivittatum*, the Canadian distribution of this species is almost exclusively within the grasslands ecoregions of the Prairies Ecozone of Alberta and Saskatchewan.



*Biological Information:* The immature stages of this species are often found together with those of *S. bivittatum* in rivers and irrigation canals, although in relatively larger numbers in the latter habitat (Fredeen and Shemanchuk 1960). Overwintering is in the egg stage, with larvae of this multivoltine species occurring throughout the ice-free period (Currie 1986; Pruess and Peterson 1987). Feeding preferences are similar to those of *S. bivittatum*, with females attacking large mammalian hosts such as horses, cattle, sheep, pigs, and humans (Fredeen 1981); however, they are also known to attack smaller-sized mammals (black-tailed jackrabbits) in California (Ryckman 1961). Prior to the construction of a hydroelectric dam on the South Saskatchewan River in 1968, outbreaks of *S. griseum* were substantial enough to drive people indoors in Saskatchewan (Fredeen 1977a).

**Subgenus *Psilozia* Enderlein, 1936**  
***vittatum* species complex**

**9. *Simulium tribulatum* Lugger, 1897**

*Distribution:* Transcontinental.

*Grasslands Records:* This species, along with its cryptic sister species *Simulium vittatum*, are among the most abundant and commonly encountered black flies on the Canadian prairies.

*Biological Information:* The immature stages of members of the *S. vittatum* species complex occupy an enormous variety of running-water habitats, ranging from tiny trickles to large (>300 m wide) rivers. Optimal habitats include nutrient-rich streams coursing through pasture lands, especially at the outlets of lakes and other sources of impounded water (Adler *et al.* 2004). In addition to their ability to thrive in different kinds of watercourses, the larvae are tolerant of extreme ranges in temperature (0 °C–33 °C), oxygen tension, current velocity, pH, and salinity (Adler *et al.* 2004). They also exhibit the greatest tolerance of any North American species to organic and industrial pollutants. Members of the *S. vittatum* complex can overwinter in either the egg or larval stages and have up to four generations per year on the prairies (Abdelnur 1968; Fredeen 1981). Adults fly from April or May through October (Currie 1986). Hosts include a wide variety of ungulates, including cattle, horses, sheep, elk, moose, and deer (Knowlton and Rowe 1934; Fredeen 1973; Merritt *et al.* 1978; Pledger *et al.* 1980). Other less frequently attacked hosts include pigs and domestic geese, ducks, chickens, and turkeys (cf. Adler *et al.* 2004 for review). Females of the *S. vittatum* complex are vectors of vesicular stomatitis virus to mice (Mead *et al.* 1999, 2000), domestic swine (Mead *et al.* 2004; Smith *et al.* 2009), and domestic cattle (Mead *et al.* 2009).

**10. *Simulium vittatum* Zetterstedt, 1838**

*Distribution:* Transcontinental.

*Grasslands Records:* *Simulium vittatum* and its cryptic sister species *S. tribulatum* are among the most abundant and frequently encountered black flies on the Canadian prairies.

*Biological Information:* See entry for *S. tribulatum*.

**Subgenus *Aspathia* Enderlein, 1935**  
***metallicum* species group**

**11. *Simulium hunteri* Malloch, 1914**

*Distribution:* Southern Alaska and Yukon west to South Dakota, south to Mexico.

*Grasslands Records:* This species occurs marginally on grasslands ecoregions in the Prairies Ecozone, with records only from the foothills of the Rocky Mountains (Alberta)

and Cypress Hills (Saskatchewan). The Cypress Hills population is isolated from the nearest foothills population by almost 300 km.

*Biological Information:* The immature stages of this widely distributed Cordilleran species live in predominantly cool small-sized streams. Overwintering is probably in the egg stage, with larvae first appearing in June. Adults fly until well into September (Currie 1986). Adult females are known to bite cattle (Malloch 1914), humans (Peterson 1956; Currie 1997), and blue grouse (Williams *et al.* 1980).

#### 12. *Simulium piperi* Dyar and Shannon, 1927

*Distribution:* A common and widely distributed species in western North America, from southern British Columbia and Saskatchewan south to Mexico.

*Grasslands Records:* This species occurs mainly in the Montane Cordillera Ecozone of Canada, with grasslands records near the foothills of the southern Rocky Mountains and Cypress Hills. The Cypress Hills population—which represents the only record of this species from Saskatchewan—is isolated from the nearest foothills population by a distance of nearly 300 km.

*Biological Information:* This multivoltine species occurs in small-sized streams throughout its range. Outlets of beaver ponds and other small bodies of impounded water are especially favourable habitats (Currie 1986). Ungulates such as horses, cattle, and sheep are among the primary hosts of females (Hearle 1932; Jones 1961).

#### Subgenus *Simulium* Latreille, 1802 *jenningsi* species group

#### 13. *Simulium luggeri* Nicholson and Mickel, 1950

*Distribution:* Southern Northwest Territories south to Oklahoma, east to New Hampshire and South Carolina.

*Grasslands Records:* *Simulium luggeri*, the most northern and western member of the *S. jenningsi* species group, is distributed widely in the three Canadian Prairie Provinces.

*Biological Information:* Cytological studies reveal that *Simulium luggeri* is likely a complex of at least two species: one eastern and one western (Moulton and Adler 1995; Adler and Mason 1997). Both entities are included under the name *S. luggeri* pending further study (Adler *et al.* 2004; Adler and Crosskey 2013). The immature stages occur in relatively warm large-sized rivers throughout their range. Larvae and pupae are present from May until November on the Canadian prairies, with three to five generations per year depending on location (Depner 1971; Fredeen 1981; Westwood and Brust 1981; Currie 1986). Females attack a wide variety of mammalian hosts, including ungulates (cattle, horses, elk, pigs, and sheep), humans, and dogs (Anderson and Defoliart 1961; Fredeen 1985*b*; Mason and Kusters 1990). Massive outbreaks of *S. luggeri* in east-central Saskatchewan during the 1970s and 1980s had a severe economic impact on cattle farmers in the vicinity of breeding sites (Fredeen 1977*a*, 1984, 1985*b*); however, population levels were subsequently controlled by using the biological control agent *Bacillus thuringiensis* var. *israelensis* (*Bti*) (Khachatourians 1990).

#### *malyschevi* species group *arcticum* species complex

#### 14. *Simulium vampirum* Adler, Currie and Wood, 2004

*Distribution:* Southernmost Northwest Territories, Alberta, and Saskatchewan.

*Grasslands Records:* *Simulium vampirum* is found in irrigation canals in southern Alberta and is the only member of the *Simulium arcticum* species complex that breeds in the prairie grasslands of Canada (Procnier and Shemanchuk 1983).

*Biological Information:* The *Simulium arcticum* complex includes at least nine reproductively isolated sibling species (i.e., “cytospecies”) and a number of additional chromosomally distinct forms that may or may not represent valid species (i.e., “cytotypes”) (Adler *et al.* 2004). *Simulium vampirum*—one of the nine reproductively isolated cytospecies—is without question the most notorious member of the complex. Massive outbreaks of this species were responsible for mortality in livestock and wildlife in northern Alberta and Saskatchewan up until the 1980s, after which control measures such as treatment with methoxychlor and other larvicides successfully reduced population sizes (Adler *et al.* 2004). The immature stages of *S. vampirum* typically occur in the rapids of large silty rivers, such as the North Saskatchewan, Athabasca, and Slave rivers of northern Alberta and Northwest Territories; the species is included here because it is also found in irrigation canals in southern Alberta (Procnier and Shemanchuk 1983). Larvae can be found from April to September, representing a single generation with up to three cohorts (Procnier 1984; Procnier *et al.* 1984; Anderson and Shemanchuk 1987). Females are major pests of cattle and other large ungulates in the northern part of their range; however, the problem is not as severe in the south—perhaps a consequence of southern populations managing just one cohort before flow is terminated in irrigation canals (Procnier 1984). Ungulates, including cattle, horses, pigs, sheep, bison, moose, caribou, elk, and white-tailed deer, are among the primary targets of blood-seeking females. Humans and other animals (including chickens) may be attacked during severe outbreaks (Rempel and Arnason 1947; Fredeen 1969, 1977b; Shemanchuk 1988; Adler *et al.* 2004).

### ***noelleri* species group**

#### **15. *Simulium decorum* Walker, 1848**

*Distribution:* Transcontinental.

*Grasslands Records:* This widely distributed species occurs abundantly at suitable sites throughout the grasslands of Alberta, Saskatchewan, and Manitoba.

*Biological Information:* *Simulium decorum* is a habitat specialist whose immature stages live almost exclusively in the food-rich outflows of impounded water. Larvae and pupae can be found in huge numbers in such habitats, thickly festooning submerged twigs and trailing vegetation. Overwintering eggs hatch after ice breakup, with pupae first appearing in late May on the Prairies (Currie 1986). The number of generations annually varies according to location, with up to four recorded in southern Manitoba (Westwood and Brust 1981). Adults have been collected well into October in Alberta (Currie 1986). Females are autogenous for the first gonotrophic (feeding and egg laying) cycle, but most nulliparous and parous females (no egg development having occurred, and egg development having occurred, respectively) are capable of taking a blood meal (Simmons and Edman 1981). Females seek blood meals primarily from large mammalian hosts, including cattle, horses, moose, deer, and bears (Davies and Peterson 1956; Davies *et al.* 1962; Fredeen 1973; Addison 1980; Pledger *et al.* 1980). Other hosts include small mammals such as rabbits (Mokry *et al.* 1981), humans (Davies and Peterson 1956; Currie and Adler 1986), and birds (Bennett 1960). *Simulium decorum* has been implicated in the transmission of legworm (*Onchocera cervipedis*) to moose (Pledger *et al.* 1980) and in the mechanical transmission of tularemia (rabbit fever) to rabbits (Philip and Jellison 1986).

***tuberosum* species group**  
***tuberosum* species complex**

**16. *Simulium tuberosum* (Lundström, 1911)**

*Distribution:* Holarctic. Transcontinental at northern latitudes, extending southward into the United States along mountain chains.

*Grasslands Records:* *Simulium tuberosum* occurs commonly in grassland streams throughout Alberta, Saskatchewan, and Manitoba.

*Biological Information:* *Simulium tuberosum* s.s. is one of at least nine sibling species of the *S. tuberosum* complex recognized in North America. Because most ecological studies were undertaken when the complex was treated as a single species, the available literature must be interpreted with caution. The immature stages live in a wide variety of running-water habitats, although large-sized streams and rivers are evidently preferred (McCreadie *et al.* 1995). In Alberta, smaller-sized streams inhabited by the larvae of *S. tuberosum* are often organically enriched (Adler 1986). The immature stages can be found from spring until fall, suggesting that there is more than one generation per year. Members of the *S. tuberosum* complex feed primarily on small mammals, such as squirrels, rabbits, and foxes. Reports of bloodsucking from larger-sized mammals are probably based on misidentifications (Adler *et al.* 2004).

***venustum* species group**  
***venustum* species complex**

**17. *Simulium venustum* Say 1823**

*Distribution:* Transcontinental.

*Grasslands Records:* *Simulium venustum* occurs only marginally on the grasslands of the Prairies Ecozone.

*Biological Information:* *Simulium venustum* s.s. is one of 10 species of the *S. venustum* complex recognized in the Nearctic region. As a prodigious biter of humans and domestic animals, this species is among the most feared (and loathed) black flies in North America. As with members of the *S. tuberosum* complex, most ecological studies were undertaken when the complex was treated as a single species. Accordingly, much of the previous literature must be interpreted carefully. *Simulium venustum* is one of the most widely distributed and common black flies in North America; however, the most favourable habitats are medium-sized streams in northern and eastern woodlands (Adler *et al.* 2004). This univoltine species occurs only spottily on the grasslands, their scarcity perhaps related to the dearth of suitable breeding sites. Additionally, females attack hosts more in forested habitats than in open areas (Martin *et al.* 1994), which further reduces the probability of attacks on the grasslands. In addition to its status as a bloodsucking pest, *S. venustum* is implicated as a vector of the filarial nematode *Dirofilaria ursi* to American black bears in Ontario (Addison 1980).

***verecundum* species complex**

**18. *Simulium rostratum* (Lundström, 1911)**

*Distribution:* Holarctic. Transcontinental in Canada and the northern United States.

*Grasslands Records:* *Simulium rostratum* is among the most commonly encountered black flies on the Canadian prairies.

*Biological Information:* *Simulium rostratum* is one of two species in the *S. verecundum* species complex and the only one to occur on the Canadian prairie grasslands. Members

of this complex are morphologically similar to those of the *S. venustum* complex, and so much of the ecological literature is muddled. The immature stages live in variously sized low-gradient streams throughout their range, but are especially prevalent in enriched flows such as the outlets of ponds and lakes. This multivoltine species overwinters in the egg stages, with larvae present from spring until fall. There are few reliable bloodsucking records for this species, but females evidently have a preference for larger-sized ungulates such as horses, cattle, and deer (Adler *et al.* 2004).

### Diversity Patterns and Ecology

The 18 species here considered residents of the Canadian prairies represent less than 11% of the Canadian simuliid fauna. Species richness for the region is exactly the same as that recorded for Nebraska, although only 12 species are shared between the two areas. This suggests that the black fly fauna of the Great Plains is far from uniform, perhaps reflecting differences in geographical history and local topography. Nonetheless, the relative paucity of species is consistent with observations from other regional studies on the Great Plains Simuliidae (e.g., Fredeen 1958; Snyder and Huggins 1980; Pruess and Peterson, 1987; Mock and Adler 2002). In comparison, Yukon, which has about the same land area as the Canadian Prairies Ecozone, supports about three times the number of species (55)—despite being considerably farther north (Currie 1997). The higher species richness in Yukon is related, in part, to its unique geographical history. However, the terrain is also considerably more complex than the prairie landscape, and the resulting mosaic of breeding habitats is likely a major factor behind higher species richness in the Yukon.

Diversity in the prairie grasslands is also low at the generic level. The 18 prairie grasslands resident species are distributed among just three of 13 genera recognized in North America (Table 1). This number is low relative to the 11 genera recorded from the Canadian Prairie Provinces as a whole, reflecting the absence of mountain- and woodland-adapted genera. But as in other regions of North America, the prairie fauna is dominated numerically by species of *Simulium s.l.*, which constitute 83% of all black flies known from the region. This figure is high compared with the North American fauna, in which *Simulium s.l.* constitutes about 60% of all species. The only other genera present on the Canadian prairies are *Cnephia* (one species) and *Ectemnia* (two species), both well adapted for life in lowland streams and rivers.

The black flies of the Canadian prairies grasslands consist mainly of species that occur in other ecozones, including a combination of widespread species (e.g., *Simulium pilosum*, *S. tribulatum*, *S. vittatum*, *S. tuberosum*, *S. decorum*, *S. venustum*), predominantly Cordilleran species (*S. hunteri*, *S. piperi*), and predominantly northern woodlands species (*S. vampirum*). While no species of black fly is restricted to the Great Plains, at least two—*S. johannseni* and *S. meridionale*—have the great bulk of their ranges within that grasslands-dominated region. If any black flies could be considered characteristic of North American grasslands, it would be these. Special comment is warranted about *S. bivittatum* and *S. griseum*, both members of the subgenus *Psilopelmia*. While most North American species of this subgenus are restricted to the American Southwest, *S. bivittatum* and *S. griseum* have their ranges extended much farther north into southern Alberta and Saskatchewan. These species are distributed widely in both grasslands and intermountain valley habitats in the western United States and cannot, therefore, be considered strictly grasslands specialists. Nonetheless, these species evidently thrive in such habitats and are known in Canada exclusively from the prairie grasslands of Alberta and Saskatchewan.

Because widely distributed species are typically tolerant of a wide range of environmental conditions, it is perhaps not surprising that such species dominate the prairie grasslands simuliid fauna. In contrast, relatively few species are specially adapted for life on the prairies. Consequently, because of the generally unfavourable conditions of grasslands for supporting black flies, the Canadian prairies support the lowest species richness of any major ecozone in Canada outside the High Arctic.

Since most species require access to avian and/or mammalian hosts for blood meals, one other factor that might influence black fly species richness and distribution is host availability. Ecozones differ in the quality and quantity of potential hosts, although it is unclear how such differences affect simuliid community assembly. Feeding preferences remain an understudied aspect of black fly ecology, with no host information whatsoever for about 60% of North American black flies (Adler *et al.* 2004). Even for the 40% of species with one or more host records, the information is strongly biased toward domesticated birds and mammals. Nonetheless, it seems possible that prevalence of grasslands-adapted hosts on the Canadian prairies—along with absence of woodland- and mountain-adapted hosts—could exert some influence on black fly community assembly. Unfortunately, intensive studies of prairie black flies did not begin until the mid-20<sup>th</sup> century, at which point much of the native flora and fauna had already been affected by agriculture. In the absence of historical baseline data, we can only speculate about the composition of prairie black flies prior to the arrival of settlers.

Only one species of black fly on prairie grasslands—*Cnephia dacotensis*—is entirely independent of host availability. Females are obligatorily autogenous and so do not take blood meals. All other prairie black flies are anautogenous (i.e., are capable of blood feeding), although some of these (e.g., *S. decorum*, members of the *S. vittatum* species complex) are facultatively autogenous in the first gonotrophic cycle (Davies and Györkös 1990). Among the anautogenous component, five are classified as predominantly ornithophilic species, whereas 12 are classified as primarily mammalophilic species. The percentage of ornithophilic to mammalophilic species is about 30:70, somewhat lower than for North American fauna as a whole (i.e., 37:63) (Adler *et al.* 2004).

Black flies are notorious pests of humans, livestock, and wildlife in locations where they are abundant. However, they are evidently not as problematical to wild and domestic animals on the prairie grasslands as they are in northern woodland areas. For example, *Simulium vampirum*, by far the most noxious species in western Canada, is a major pest of cattle in northern Alberta, Saskatchewan, and the southernmost Northwest Territories. Although this species also occurs in the irrigation areas in southwestern Alberta, it has never been considered a pest, perhaps owing to the episodic nature of irrigation and its effect on life history (Proconier 1984). However, it is also possible that irrigation canals simply cannot support the same enormous populations of *S. vampirum* as are found in large northern rivers. Suboptimal breeding conditions might also explain the relatively benign presence of *S. venustum* on the Canadian prairies. Among the most serious bloodsucking pests of humans and other mammals in North America, *S. venustum* breeds in staggeringly large numbers on the Canadian Shield. In contrast, the species occurs only spottily on the prairie grasslands and, even then, occurs in comparatively low numbers. Nonetheless, pest species such as *S. luggeri*, *S. bivittatum*, and *S. griseum* occasionally develop in sufficient numbers to cause discomfort to humans and domesticated animals. While present-day conditions on the grassland prairies are generally unfavourable for supporting large populations of black flies, anecdotal evidence suggests that pest species were once more prominent. For example, during Lewis and Clark's trek across the Great Plains in

1805, Captain Meriwether Lewis was moved to write that gnats, prickly pear cactuses, and mosquitoes were the “great trio of pests equal to any three curses that ever poor Egypt labored under” (Duncan and Burns 1997).

One important aspect of black fly biology that has been virtually unstudied on the prairies is their role in transmission of disease agents. The North American black fly fauna as a whole is known to transmit at least 10 species of protozoa, four filarial nematodes, an indeterminate number of viruses, and a bacterium (cf. Adler *et al.* 2004 for review). How many of these disease agents are transmitted by prairie-dwelling populations is unknown, as there have been few attempts to screen either the flies or their prospective hosts on the prairies. Evidence is accumulating that avian-borne diseases in particular are a threat to rare and endangered birds (e.g., Adler *et al.* 2007; King and Adler 2012). Unfortunately, blood-feeding records are unknown for many prairie-inhabiting bird species such as Sage grouse (*Centrocercus urophasianus* (Bonaparte)), Piping plover (*Charadrius melodus* (Ord)), Burrowing owl (*Athene cunicularia* (Molina)), Ferruginous hawk (*Buteo regalis* (Grey)), and Peregrine falcon (*Falco peregrinus* Tunstall). Along similar lines, there are no blood-feeding records whatsoever for several endangered species of prairie-dwelling mammal, including the black-footed ferret (*Mustela nigripes* Audubon & Bachman) and swift fox (*Vulpes velox* (Say)). Given that none of the above-mentioned species is immune to attacks by black flies, this is clearly an area that warrants further study.

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## Chapter 14

# Biting Flies (Culicidae, Ceratopogonidae, Tabanidae) of the Prairies Ecozone

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**Abstract.** This chapter lists 81 species of biting flies from the families Culicidae, Ceratopogonidae (genus *Culicoides*), and Tabanidae for the Canadian Prairies. Twenty-five species of Culicidae are listed, including one species of Anophelinae and 25 species of Culicinae. Twenty-six species of *Culicoides* are listed. This group has been the least intensively studied in Canadian grasslands, and this is undoubtedly an underestimate of the number of species present. Thirty species of Tabanidae are listed, including seven species of Chrysopsinae and 23 species of Tabaninae. All three families are readily captured using a variety of trapping methods. Identification of the Culicidae and Tabanidae is facilitated by the availability of excellent identification resources. Identification of the genus *Culicoides* is hampered by the lack of a unified key for western Canada. Despite this, there are many opportunities for investigators to increase knowledge of these groups in Canadian grasslands.

**Résumé.** Ce chapitre présente une liste des 81 espèces de mouches piqueuses appartenant aux familles des culicidés, des cératopogonidés (genre *Culicoides*) et des tabanidés présentes dans les prairies canadiennes. Cette liste renferme 25 espèces de culicidés, y compris une espèce de la sous-famille des anophélinés et 25 espèces de la sous-famille des culicinés, ainsi que 26 espèces du genre *Culicoides*. Ces diptères forment le groupe le moins étudié des prairies canadiennes, et la liste proposée sous-estime donc sans doute le nombre réel d'espèces présentes dans cette région. La liste compte 30 espèces de tabanidés, y compris sept espèces de chrysopsinés et 23 espèces de tabaninés. Tous ces insectes sont faciles à recenser à l'aide de diverses méthodes de capture. Les ressources documentaires disponibles facilitent l'identification des culicidés et des tabanidés. Par contre, l'identification des espèces du genre *Culicoides* est compliquée par l'absence d'une clé unifiée pour l'ouest du Canada. Malgré tout, les chercheurs jouissent de nombreuses occasions pour approfondir leur connaissance des diptères appartenant à ces groupes dans les prairies canadiennes.

### Introduction

Biting flies are notorious for their impact on human health and welfare, and on the fitness and performance of domestic animals and wildlife. Canada is renowned for its diversity of species of biting flies, representing four families and including mosquitoes, no-see-ums, black flies, horse flies, and deer flies. All species of these families in Canada rely upon the availability of aquatic habitats for their success. Although grasslands are better known for their terrestrial ecosystems, there is considerable variety in aquatic habitats interspersed throughout the Prairies Ecozone (Shorthouse 2010; Wrubleski and Ross 2011), which are essential components for most of these biting flies. Many species have very specific

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habitat requirements. Black fly larvae and pupae are found only in running water and, although they are an important element in many areas of grasslands in Canada, they are considered elsewhere in this volume (see Chapter 13).

We focus on mosquitoes (Culicidae), no-see-ums (Ceratopogonidae), deer flies, and horse flies (Tabanidae) known to inhabit aquatic or moist organic habitats in prairie grasslands in Alberta, Saskatchewan, and Manitoba. Mosquito larvae and pupae are specialists found only in standing water, often in temporary aquatic habitats (Wood *et al.* 1979). Larvae of no-see-ums (*Culicoides* spp.) inhabit a wide variety of wetland or moist organic habitats (Kettle 1977). Most species of deer flies and horse flies in prairie grasslands inhabit permanent and semi-permanent wetlands, but some are found in running water (Teskey 1990). Given the impact of these biting flies on livestock production as a nuisance and as vectors of disease-causing agents, it is surprising that so little attention has been paid to them on the Prairies. Our objective is to highlight biting fly species that inhabit the Canadian prairie grasslands and to identify gaps in our knowledge about these groups.

### Criteria for Inclusion

We have chosen to include those species of Culicidae, Ceratopogonidae, and Tabanidae that are known to reproduce and are established in the Canadian prairie grassland regions of Alberta, Saskatchewan, and Manitoba (region identified in Shorthouse and Larson 2010). Some species are restricted to these grassland regions, while others are habitat generalists and have extensive ranges that happen to include prairie grasslands. Some species of biting flies might have considerable dispersal capacity, carried on strong southerly winds, for example, from distant locations. Unless there is evidence that a species is a permanent resident of our selected study area, it is not included here.

### Family Culicidae

Species records were extracted from a variety of published sources, including Rempel (1950, 1953), Wood *et al.* (1979), and regional studies of mosquitoes associated with particular grassland habitats (Shemanchuk 1959, 1969; Shemanchuk *et al.* 1963; Scholefield *et al.* 1981; Lysyk 2010). Three subfamilies are represented in the Culicidae, of which two, the Anophelinae and Culicinae, occur in the Prairie region.

*Anopheles earlei* is the only representative of the Anophelinae that occurs in the Prairies Ecozone. This species is widespread but relatively rare in grasslands (Rempel 1950). Adult females overwinter in subterranean environments such as mammal burrows (Shemanchuk 1965). Adults emerge from burrows in the spring and lay eggs singly on standing water (Anderson and Galloway 1988).

The subfamily Culicinae has three tribes with representatives in Canadian grasslands. The tribe Culicini is represented by one species, *Culex tarsalis*. This species also overwinters as adult females in mammalian burrows (Shemanchuk 1965) and lays eggs in rafts on grassy pools of permanent and semi-permanent standing water. *Culex tarsalis* is common in grasslands and feeds readily on birds, large mammals, and humans. It is the principal vector of Western equine encephalitis virus (Shemanchuk and Morgante 1968) and West Nile virus (Turell *et al.* 2005) in western North America. The tribe Culisetini includes two representatives in the Canadian grasslands. *Culiseta alaskaensis* has been reported in grasslands (Strickland 1938; Shemanchuk 1959; Lysyk 2010) but is relatively uncommon; this species tends to be more abundant farther north. *Culiseta inornata* is widely distributed

and may be among the most abundant mosquito species near areas inhabited by livestock (Lysyk 2010). It feeds preferentially on large mammals such as cattle and horses, and has been implicated as a vector of a variety of pathogens (Shemanchuk and Morgante 1968). Both of these *Culiseta* species also overwinter as adults and lay eggs as rafts on the surface of standing water. Larvae of *Cs. inornata* do best at lower temperatures (Brust and Hanec 1967), and egg rafts are more often laid in shaded pools.

The tribe Aedini in the prairie grasslands, represented by the genera *Ochlerotatus*, *Aedes*, *Coquillettidia*, and *Psorophora*, includes at least 21 species, most of which oviposit on the soil and organic matter on the margins of temporary aquatic habitats (except *Coquillettidia*; see below). The eggs are the overwintering stage and hatch under suitable conditions when submerged by snowmelt or summer flood water (Dixon and Brust 1972). Most of these species are univoltine, their only generation developing in snowmelt pools in the spring, while some (e.g., *Oc. spencerii*, *Oc. sticticus*, *Ae. cinereus*) produce batches of mixed diapausing and non-diapausing eggs (Brust 1968), or are multivoltine (e.g., *Oc. campestris*, *Oc. dorsalis*, *Oc. melanimon*, *Ae. vexans*) (Tauthong and Brust 1977; Wood *et al.* 1979). *Aedes vexans* is a multivoltine flood-water species, which, under ideal conditions, can produce many generations in a summer, emerging in extraordinary numbers and causing severe stress to humans and other animals. These *Ochlerotatus* and *Aedes* species are well adapted to grassland habitats where drought is a common phenomenon; their eggs may lay dormant for many years in the absence of sufficient snowmelt water or rainfall (e.g., Gjullin *et al.* 1950).

The most common aedine species in grasslands are *Ae. vexans*, *Oc. dorsalis*, *Oc. campestris*, *Oc. melanimon*, *Oc. spencerii*, *Oc. flavescens*, and *Oc. nigromaculis* (Shemanchuk 1959; Lysyk 2010). *Ochlerotatus sticticus* occurs sporadically on the Prairies but can be abundant. It oviposits in wooded areas along the flood plains near large rivers (Trpis *et al.* 1973) and occurs in large numbers during years of heavy rainfall (Lysyk 2010). The remaining 11 species occur sporadically in grassland areas; they live more typically on the periphery of true grassland habitats, being considered primarily woodland, parkland, or northern species. Some are rarely collected species throughout their range and their status in grasslands remains to be confirmed. *Ochlerotatus euedes* and *Oc. implicatus* are widespread (Scholefield *et al.* 1981), but were not detected in recent surveys in grasslands in Alberta (Lysyk 2010). *Ochlerotatus fitchii*, *Oc. increpitus*, and *Oc. cataphylla* were considered ubiquitous in southern Alberta by Scholefield *et al.* (1981), but as woodland species by Rempel (1950). *Ochlerotatus cataphylla* was collected in grasslands by Shemanchuk (1959, 1969) and Lysyk (2010), although in low numbers. *Ochlerotatus increpitus* is a rarely collected species (Rempel 1950). *Ochlerotatus impiger* typically occurs in alpine, northern boreal, and tundra habitats (Wood *et al.* 1979), but a few specimens were captured in grasslands by Scholefield *et al.* (1981) and Lysyk (2010); its true status as a member of the grasslands fauna remains to be determined. *Ochlerotatus intrudens* is a rare species in foothills and mountains (Scholefield *et al.* 1981), and only two specimens were identified in recent surveys (Lysyk 2010); its inclusion as part of the grassland mosquito fauna is tentative. *Aedes cinereus* is primarily a woodland species that occurs along the northern edge of the grasslands (Rempel 1950; Scholefield *et al.* 1981) and is rarely present in grasslands (Shemanchuk 1959, 1969). *Ochlerotatus riparius* was reported in earlier studies (Shemanchuk 1959; Shemanchuk *et al.* 1963). However, these records may refer to *Oc. euedes* (Wood *et al.* 1979), as these were not recognized as separate species at the time (Enfield 1977). *Ochlerotatus canadensis* occurs in woodlands (Rempel 1950) but also in open prairie pools (McLintock 1944).

There is only one record for *Psorophora signipennis* in Canada (Rempel 1953). The status of this multivoltine, flood-water mosquito is not known in the Canadian Prairies, but it was the opinion of Wood *et al.* (1979) that it is likely to be more widely distributed in Canada, but has been overlooked because of its resemblance to species that have similar coloration but are more numerous.

*Coquillettidia perturbans* is exceptional among representatives of Aedini in that it is restricted to permanent ponds and sloughs with abundant emergent vegetation. Eggs are laid in rafts attached to the undersides of floating vegetation. Larvae and pupae are found in the mud at the bottom, where they tap into the roots and stems of aquatic plants to obtain oxygen. *Coquillettidia perturbans* has one generation per year in Canada and overwinters as larvae. Because of the requirement for permanent standing water that is sufficiently deep to prevent larvae from freezing into the substrate, this species is not well suited to drought-prone central grassland regions. They are found on the eastern and northern peripheral areas of the Prairies Ecozone (McLintock and Rempel 1963; Wood *et al.* 1979).

### **Ceratopogonidae: Genus *Culicoides***

Extensive surveys of the family Ceratopogonidae have not been conducted in Canadian grasslands. The number of published surveys is quite small and work has focused on the genus *Culicoides*. This is the only genus treated here, with the understanding that many additional members of other ceratopogonid genera likely occur on the prairie grasslands. Downes (1958) published a list of several species collected in Canadian grasslands and referenced several undescribed species. The most extensive survey published to date was conducted near feedlots and grasslands in southern Alberta (Lysyk 2006), and the 14 species reported account for much of the species list in Table 1. Additional species are included on the basis of records from Borkent and Grogan (2009), with other additions from the literature.

The subgenus *Culicoides* contains the greatest number of species in the Canadian Prairies. Five members of the subgenus *Culicoides* were recorded in southern Alberta (Lysyk 2006) (Table 1). We added *C. lahontan* and *C. paraimpunctatus* on the basis of recent collections, bringing the total to seven species.

Two species in the subgenus *Monoculicoides* have been identified in southern Alberta. These are *Culicoides gigas* and *C. sonorensis* (Downes 1958; Lysyk 2006). The latter species has undergone extensive nomenclatural revision (e.g., Downes 1978; Holbrook *et al.* 2000) and was originally reported in Alberta as *Culicoides variipennis albertensis* (Wirth and Jones 1957), but has since been synonymized with *C. sonorensis* (Wirth and Morris 1985). The nomenclatural change has caused some confusion concerning the geographical distribution of *C. sonorensis*, which is important as a vector of the viruses that cause bluetongue and epizootic haemorrhagic disease in ruminants. *Culicoides variipennis* and *C. occidentalis* are likely present in Canadian grasslands, but have not yet been reported. Downes (1958) reported an as yet undescribed species of *Monoculicoides*, and we have collected specimens of that same species in southern Alberta.

The remaining subgenera are each represented by relatively few species. Two species in the subgenus *Avaritia* likely occur in Canadian grasslands. *Culicoides obsoletus* was collected feeding on cattle in central Alberta (Shemanchuk 1978) and is primarily a woodland species, but occasional specimens have been collected in grasslands (Curtis 1941). *Culicoides chiopterus* is widespread, but only rarely collected. Larvae of both species develop in animal manure, and *C. obsoletus* also develops in a wide range of moist organic

material (Jamnback and Wirth 1963). Two species in the subgenus *Beltranmyia* have been reported from grasslands, of which *Culicoides crepuscularis* is widespread and abundant. Species in the subgenus *Diphaomyia* have not been reported in western Canada; however, *Culicoides haematopotus* is abundant in North Dakota (Anderson and Holloway 1993) and likely occurs in Canadian grasslands. Two species in the subgenus *Selfia* have been collected in southern Alberta (Lysyk 2006). *Culicoides denningi* is noteworthy, as it is common along rivers and irrigation canals (Fredeen 1969). Species in the subgenus *Sylvaticulicoides* have not been reported from Canadian grasslands; however, *C. biguttatus* has been collected in British Columbia (Curtis 1941) and we have collected this species recently in Alberta. Three members of the *palmerae* species group are present (Lysyk 2006) (Table 1). Other unplaced *Culicoides* include *C. unicolor* (Curtis 1941), *C. stonei*, and *C. travisi*. The latter two species have recently been collected in southern Alberta.

### Family Tabanidae: Deer Flies and Horse Flies

Adult deer flies and horse flies are large, mobile, diurnal flies. The females of most species take blood from mammalian hosts and inflict a painful bite. Eggs are usually laid in distinctive masses on the undersides of leaves and stems of emergent vegetation in and along the margins of aquatic and semi-aquatic habitats. Egg masses of the largest horse flies may contain 700–800 eggs (Teskey 1990). Hatching larvae drop from the egg mass into the water or onto the wet soil, and live in the substrate. It is time-consuming and exhausting to collect tabanid larvae. However, Teskey (1969) published descriptions of many species of tabanids occurring in Canada, and with them, accounts of associated habitats in which various species were found. All species in Canada overwinter as larvae in the substrate and after one or more years, pupate and emerge as adults at characteristic times during the season. Adults may be present from May until late summer.

The list of species recorded for Canadian grasslands in Table 1 was derived from the many records in Teskey (1990), previously published surveys (Cameron 1926; Hanec and Bracken 1964), and unpublished records (TDG, unpublished data). In Canada, tabanids typically reach their greatest abundance in wooded areas where there are numerous wetland habitats. Therefore, it is not surprising that many surveys (Thomas 1970; McElligott and Galloway 1991) have been conducted in Aspen Parkland areas, where intense fly activity may have a deleterious impact on pastured animals (e.g., Ralley *et al.* 1993) and wildlife. Many species found in grasslands are habitat generalists, and this can be extrapolated from information gathered in other ecozones. There is a decided lack of recent information on seasonal activity and species composition of tabanids in prairie grasslands in Canada. This is unfortunate, as these flies are important pests and potential vectors of disease-causing agents, such as equine infectious anaemia.

The subfamily Chrysopsinae is represented by seven species in the genus *Chrysops*, five of which were recorded by Cameron (1926). Most of these are widely distributed species that extend their range into the prairie grassland region where suitable ponds and sloughs are available. *Chrysops aestuans* (reported by Cameron (1926) as *Chrysops moerens* Walker) has larvae that are found in slow-moving water as well as in alkaline ponds (Teskey 1990). *Chrysops discalis* is the only grassland specialist, where its larvae are found at the margins of alkaline lakes and sloughs in the Prairie Provinces and in the dry grassland regions of southern British Columbia (Teskey 1990).

There are 19 species of Tabaninae listed in Table 1. The genus *Haematopota* is represented by one species in prairie grasslands, *H. americana*. This species is widely



distributed in Canada, and, although the larvae are found in many different habitats, they do inhabit prairie sloughs (Teskey 1990). *Atylotus calcar* is the sole member of this genus in western Canada. This species was likely identified by Cameron as *Tabanus insuetus* (Teskey 1990). *Atylotus calcar* has been found most often at the margins of alkaline sloughs (Teskey 1990).

Seventeen species of *Hybomitra* are included in our list for Canadian grasslands. Among them, only *Hybomitra pediontis* and *H. rhombica* might be considered true grassland species. Most of the other species are widely distributed and seem to be habitat generalists, with records scattered throughout the Prairies. Many of these are associated with woodland ponds and wetlands within the Prairies Ecozone.

Three species of *Tabanus* are included in Table 1 that are based on Cameron (1926) and Hanec and Bracken (1964). None of these species is restricted in their distribution to prairie grasslands, but are widely distributed in southern Canada. The black horse fly, *Tabanus atratus*, is also included here following recent observations associated with tallgrass prairie in southeastern Manitoba.

## Conclusions

The biting flies examined in this chapter are among the most important pests of humans, domestic animals, and wildlife in western Canada. Generally speaking, the females of most species are not difficult to collect. They are attracted to suitable hosts, including the entomologists who study them. Mosquitoes and no-see-ums can be collected by using CO<sub>2</sub>-baited traps or light traps. A diversity of female tabanids can be collected in large numbers in Manitoba horse fly traps. There are excellent identification keys for mosquitoes (Wood *et al.* 1979; Thielman and Hunter 2007) and tabanids (Teskey 1990), and so the resulting trap catches can be processed with reasonable reliability. Ceratopogonids as a group are challenging to identify. There is still no key specifically designed to assist in the identification of species in western Canada. Despite there being many records for most of the species included here, serious gaps still exist in our understanding of the grassland fauna. Most of the research effort has been conducted in areas peripheral to prairie grassland habitats, or in urban areas where biting flies affect human comfort and where there is risk of pathogen transmission and deleterious impact on human health. Provinces spend large amounts of money on vector surveillance, but invest relatively little in basic field research. In addition, the number of veterinary entomologists and vector ecologists working in the field has fallen significantly during the last 20 years.

As a result, our knowledge about the distribution and abundance of biting flies in prairie grasslands is deficient. The Ceratopogonidae, in particular, have been largely ignored. This especially applies to the blood-feeding *Culicoides*, where, with few exceptions, records are widely scattered, sparse, and poorly consolidated. There are, no doubt, many new records and undescribed species to be collected. There is also a great need for study in the core areas of the grasslands, especially in southeastern Alberta, southern Saskatchewan, and southwestern Manitoba. Many of the records that are available are decades old, and there is no doubt that the prairie landscape has changed and continues to change. The extent to which current faunal assemblages resemble those reported 50 years ago is underappreciated. In addition, gaps in our knowledge of these biting flies identified several decades ago by Laird *et al.* (1982) still apply. Many challenges are left open to the next generation of entomologists, and many rewarding opportunities await.

**Table 1.** Biting flies (Culicidae, Ceratopogonidae genus *Culicoides*, and Tabanidae) of the Prairies Ecozone.

Family: Subfamily: Tribe	Species
Culicidae: Anophelinae	<i>Anopheles earlei</i> Vargas, 1943
Culicidae: Culicinae: Culicini	<i>Culex tarsalis</i> Coquillett, 1896
Culicidae: Culicinae: Culisetini	<i>Culiseta alaskaensis</i> (Ludlow, 1906) <i>Culiseta inornata</i> (Williston, 1839)
Culicidae: Culicinae: Aedini	<i>Ochlerotatus campestris</i> (Dyar & Knab, 1907) <i>Ochlerotatus canadensis</i> (Theobald, 1901) <i>Ochlerotatus cataphylla</i> (Dyar, 1916) <i>Ochlerotatus dorsalis</i> (Meigen, 1830) <i>Ochlerotatus euedes</i> (Howard, Dyar & Knab, 1913) <i>Ochlerotatus fitchii</i> (Felt & Young, 1904) <i>Ochlerotatus flavescens</i> (Müller, 1764) <i>Ochlerotatus impiger</i> (Walker, 1848) <i>Ochlerotatus implicatus</i> (Vockeroth, 1954) <i>Ochlerotatus increpitus</i> (Dyar, 1916) <i>Ochlerotatus intrudens</i> (Dyar, 1919) <i>Ochlerotatus melanimon</i> (Dyar, 1924) <i>Ochlerotatus mercurator</i> (Dyar, 1920) <i>Ochlerotatus nigromaculis</i> (Ludlow, 1906) <i>Ochlerotatus riparius</i> (Dyar & Knab, 1907) <i>Ochlerotatus spencerii</i> (Theobald, 1901) <i>Ochlerotatus sticticus</i> (Meigen, 1838) <i>Aedes cinereus</i> Meigen, 1818 <i>Aedes vexans</i> (Meigen, 1830) <i>Coquillettidia perturbans</i> (Walker, 1856) <i>Psorophora signipennis</i> (Coquillett, 1904)
Ceratopogonidae: Ceratopogoninae: Culicoidini	
Subgenus <i>Avaritia</i>	<i>Culicoides chiopterus</i> (Meigen, 1830) <i>Culicoides obsoletus</i> (Meigen, 1818)
Subgenus <i>Beltranmyia</i>	<i>Culicoides crepuscularis</i> Malloch, 1915 <i>Culicoides wisconsinensis</i> Jones, 1956
Subgenus <i>Culicoides</i>	<i>Culicoides cockerellii</i> (Coquillett, 1901) <i>Culicoides frohnei</i> Wirth & Blanton, 1969 <i>Culicoides gregsoni</i> Wirth & Blanton, 1969 <i>Culicoides lahontan</i> Wirth & Blanton, 1969 <i>Culicoides neomontanus</i> Wirth, 1976 <i>Culicoides paraimpunctatus</i> Borkent, 1995 <i>Culicoides yukonensis</i> Hoffman, 1925
Subgenus <i>Diphaomyia</i>	<i>Culicoides haematopotus</i> Malloch, 1915
Subgenus <i>Monoculicoides</i>	<i>Culicoides gigas</i> Root & Hoffman, 1937 <i>Culicoides occidentalis</i> Wirth & Jones, 1957

- Culicoides sonorensis* Wirth & Jones, 1957  
*Culicoides variipennis* (Coquillett, 1901)  
*Culicoides* (*Monoculicoides*) (undescribed sp.)
- Subgenus *Selfia* *Culicoides denningi* Foote & Pratt, 1954  
*Culicoides jamesi* Fox, 1946
- Subgenus *Sylvaticulicoides* *Culicoides biguttatus* (Coquillett, 1901)
- Subgenus unplaced – *palmerae* group *Culicoides davisi* Wirth & Rowley, 1971  
*Culicoides palmerae* James, 1943  
*Culicoides wirthi* Foote & Pratt, 1954
- Subgenus unplaced – *piliferus* group *Culicoides unicolor* (Coquillett, 1905)
- Subgenus unplaced – *stonei* group *Culicoides stonei* James, 1943
- Subgenus unplaced – miscellaneous *Culicoides travisi* Vargas, 1949
- Tabanidae: Chrysopsinae: Chrysopsini *Chrysops aestuans* Van der Wulp, 1867  
*Chrysops ater* Macquart, 1850  
*Chrysops discalis* Williston, 1880  
*Chrysops excitans* Walker, 1850  
*Chrysops fulvaster* Osten Sacken, 1877  
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*Chrysops mitis* Osten Sacken, 1877
- Tabanidae: Tabaninae: Haematopotini *Haematopota americana* Osten Sacken, 1877
- Tabanidae: Tabaninae: Tabanini *Atylotus calcar* Teskey, 1983  
*Hybomitra affinis* Kirby, 1837  
*Hybomitra arpadi* (Szilady, 1923)  
*Hybomitra astuta* (Osten Sacken, 1876)  
*Hybomitra criddlei* (Brooks, 1946)  
*Hybomitra enigmatica* Teskey, 1982  
*Hybomitra epistates* Osten Sacken, 1878  
*Hybomitra frontalis* Walker, 1848  
*Hybomitra illota* (Osten Sacken, 1876)  
*Hybomitra lasiophthalma* Macquart, 1838  
*Hybomitra liorhina* (Philip, 1936)  
*Hybomitra lurida* ((Fallén, 1817)  
*Hybomitra nitidifrons nuda* (McDunnough, 1921)  
*Hybomitra opaca* (Coquillett, 1904)  
*Hybomitra osburni* (Hine, 1904)  
*Hybomitra pediontis* (McAlpine, 1961)  
*Hybomitra rhombica* (Osten Sacken, 1876)  
*Hybomitra tetrica* (Marten, 1883)  
*Tabanus atratus* Fabricius, 1775  
*Tabanus marginalis* Fabricius, 1805  
*Tabanus reinwardtii* Weidemann, 1828  
*Tabanus similis* Macquart, 1850
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# Arthropods of Canadian Grasslands (Volume 3): Biodiversity and Systematics, Part 1

Edited by Héctor A. Cárcamo and Donna J. Giberson

*Arthropods of Canadian Grasslands (Volume 3): Biodiversity and Systematics – Part 1* is the third volume in the series that provides an overview of Canada's grasslands and its associated insects, mites, spiders and their close relatives.

Volume 1, *Ecology and Interactions in Grassland Habitats* (Shorthouse and Floate 2010), reviews the ecological attributes and interactions of arthropods in natural grasslands. Volume 2, *Inhabitants of a Changing Landscape* (Floate 2011), focuses on the anthropogenic effects on grasslands and their arthropod fauna, with an emphasis on agroecosystems.

Volume 3, *Biodiversity and Systematics – Part 1*, opens with an overview of the biogeography of arthropods of Canadian grasslands and provides a taxonomic summary, including checklists of selected taxa of Myriapoda (e.g. millipedes and centipedes), Arachnida (mites and spiders), Collembola and Insecta. Volume 4, *Biodiversity and Systematics – Part 2*, will continue the taxonomic review of another 11 insect groups.

With the publication of *Arthropods of Canadian Grasslands*, the Biological Survey of Canada hopes to increase awareness of the plight of Canada's grasslands, to draw attention to its associated arthropods and to provide a baseline reference to support future studies of arthropods in these environments.

**Héctor A. Cárcamo** is a research scientist with Agriculture and Agri-Food Canada (AAFC), in Lethbridge, Alberta. His main research focus is the development of ecological strategies to manage insect pests of prairie field crops, particularly biological control with parasitoids. Additional research topics include biodiversity studies of carabid beetles and spiders.

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**Front cover images:** Red Deer River valley west of Bindloss, Alberta (Photo: Mark Oliver). Boxed figures from left to right: (1) male dwarf sheet spider, *Hypselistes florens* (Erigoninae); (2) mating pair of *Cnephia dacotensis* (Simuliidae), the only obligatorily autogenous species of black fly from the Prairies Ecozone of Canada; (3) Whitcomb's beauty, *Stirellus bicolor* (Van Duzee), a leafhopper monophagous on little bluestem in tallgrass prairie; (4) a millipede (Myriapoda) nr. *Oriulus venustus* (Parajulidae); (5) scanning electron micrograph of *Bryobia* n. sp. 1 (*praetostia* sp. complex) (Tetranychidae); (6) the Damsel fly, *Coenagrion angulatum* (Prairie Bluet), female. Photo credits: (1) T. Murray; (2) S. Marshall; (3) M.J. Hatfield; (4) B. Snyder; (5) F. Beaulieu; (6) J. Acorn

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