Terrestrial isopods (Isopoda: Oniscidea) in Alberta: species diversity, symbionts, and population structure

by

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Abstract

Terrestrial isopods (Isopoda: Oniscidea), also known as sowbugs or woodlice, are one of the few groups of crustaceans that include members fully adapted to a terrestrial lifestyle. Sowbugs are readily transported by human activity, and many species have been introduced worldwide. Potential impacts of sowbugs on areas to which they are introduced include altering decomposition through feeding on organic matter, competition with native species, and co-introduction of symbionts (including parasites). However, the study of sowbugs has been largely overlooked in Canada, especially in the Prairie Provinces: only a single published study mentions the presence of sowbugs in this area. The goal of this study was to document a neglected component of Alberta's biodiversity and to provide a foundation for understanding the potential impact of introduced sowbugs in this region. I first conducted a survey of sowbug species in Alberta, with additional collections from British Columbia, Saskatchewan, Ontario, and Newfoundland, and compiled an updated list of the sowbugs found in Canada. All nine species in Alberta are non-native and originate from Europe or Asia; one of these species (*Nagurus cristatus* (Dollfus) (Trachelipodidae)) has never been recorded from Canada. To assess the potential impact of introduced sowbugs through co-introduction of symbionts, I examined collected sowbugs for associated symbiotic species and compiled a list of all previously-recorded metazoan symbionts of sowbugs. I recovered nematodes, acanthocephalans, and mites from sowbugs in Alberta and British Columbia, including eight symbiont species never recorded previously from sowbugs. Sowbug-associated mites include the first record of *Bakerdania elliptica* (Krczal) (Neopygmephoridae) from North America. Sowbug and symbiont identifications are both supported by molecular data (COI barcodes, partial 18S) and include the

first sequences for one sowbug and one symbiont species. Finally, I investigated the population structure of the sowbug *Porcellio spinicornis* Say in Alberta using genomic markers (ddRADseq) to explore the history and routes of entry of introduced sowbugs in the province and to assess the long-held hypothesis that greenhouses are sites of sowbug introduction. I found that sowbugs in Alberta likely originate from at least three introductions, most probably from other North American populations. Genetic evidence is consistent with anecdotal reports that sowbugs in Alberta are a recent introduction. Sowbug populations within Edmonton were remarkably homogenous, and likely originated from the same source. Evidence for greenhouses as primary introduction sites was inconclusive, but at least one greenhouse population originated via introduction from another site within Edmonton. Overall, it is unlikely that sowbugs currently pose a threat to Alberta's ecology, economy, or human health. However, given the probable recency of sowbug introduction, sowbug populations in Alberta should be monitored to detect evidence of range expansion outside of urban sites of introduction. Additional surveys of sowbugs in Alberta and sowbug-associated symbionts globally may uncover many additional species records and symbiotic associations.

Preface

A version of chapter 2 will be submitted for publication with plural pronouns and the following authors: Stormer, H.G., Pike, T.M., Sperling, F.A.H. and Proctor, H.C. I was responsible for sample collection (in part), molecular data collection and analysis, and writing the manuscript (including the literature review). F.A.H. Sperling was responsible for molecular training and resources and also provided methodological advice. T. Pike was responsible for sample collection (in part). H.C. Proctor was the supervisory author and was involved with sample collection (in part), study design, and manuscript composition.

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Chapter 1.

General introduction

1.1. Routes of entry and impact of introduced species

In the past 200 years, tens of thousands of species have been transported by human activity to areas in which those species did not already occur at the time of their introduction (Seebens *et al*. 2017). Such species are referred to as "introduced species" (Falk-Petersen *et al*. 2006). Detecting the presence of introduced species and assessing and monitoring their impact is of great concern, as introduced species have the potential to negatively affect the economy, environment, and human health (Pyšek and Richardson 2010; Keller *et al*. 2011). However, there has been recent debate over whether all introduced species should be viewed as inherently detrimental (Warren 2023; Pereyra *et al*. 2024). Some introduced species may have an overall neutral or beneficial impact (Schlaepfer *et al*. 2011; Boltovskoy *et al*. 2018; Vimercati *et al*. 2020; Sax *et al*. 2022). For example, introduced species may increase populations of native species by acting as a food source (Twardochleb and Olden 2016; Rosa *et al*. 2021) or may exert an overall neutral impact on the survival of native species by filling empty niches rather than competing (Arnan *et al*. 2021), or by a balance of negative and positive effects on native species. For example, Thieltges (2005) found that introduced limpets growing on the shells of native mussels resulted in reduced growth of the mussels, but also acted as a form of protection from predation by sea stars, which avoided the limpet-fouled mussels. Even introduced species that spread rapidly may not necessarily exert negative effects on populations of native species (Ricciardi and Cohen 2007). Rather than calling for action against a species simply because it is non-native, some have advocated that species should be assessed primarily on their impact rather than their origin

(reviewed in Warren 2023). Given that effects of introduced species can vary, it is important assess whether a particular species exerts any effects deemed to be detrimental prior to committing resources to eradicate or manage that species. Many assessment schemes are available to evaluate the impact of introduced species (reviewed in Vimercati *et al*. 2020). Completing such an assessment typically requires detailed knowledge of the biology and ecology of an introduced species, including whether it competes with, predates, or hybridizes with native species, and whether it has co-introduced parasites or pathogens (Blackburn *et al*. 2014; Nentwig *et al*. 2016).

If an introduced species is determined to be undesirable, preventing further introduction is essential to managing its spread. This requires knowledge of how and where the species is introduced. There are many potential means by which a species may be introduced to a new area (Hulme *et al*. 2008; Harrower *et al*. 2018). These include arrival with ships in ballast or via hull fouling (e.g. crabs: Costello *et al.* 2022), import of a species as a pet that is later released intentionally (e.g. reptiles: Stringham and Lockwood 2018) or unintentionally (e.g. birds: Nishida and Kitamura 2024), deliberate introduction of a species for biocontrol of an unwanted species (e.g. ladybeetles: Snyder *et al*. 2004), or deliberate introduction as a landscaping component (e.g. ornamental plants: Niemiera and Holle 2009). Introduction of one species may also lead to co-introduction of another, including parasitic species (Bojko *et al*. 2021) and species associated with plants (Bella 2013). Introduced populations may originate from an area to which a species is native (primary introduction) or from other introduced populations (secondary introductions) (Michaelides *et al*. 2015). The route(s) of introduction for a particular species can sometimes be determined with historical data (e.g. dates and locations of appearance of a species) and/or with molecular data (e.g. population structure, genetic diversity). Historical

data on the presence or absence of a species in particular areas can be used to determine the probable initial site(s) of introduction and to track range expansion of a species (Pyšek and Prach 1995), while molecular data can provide a variety of information about an introduced species (Welles and Dlugosch 2019), including the probable source population(s) (Kolbe *et al*. 2004), the role of passive dispersal within the introduced range (Roberts and Weeks 2011), the initial site(s) of introduction (Acevedo-Limón *et al*. 2020), whether particular populations likely originated via primary or secondary introduction (Pérez-Portela *et al*. 2012) or from one or multiple introductions (Cao *et al*. 2017), and the approximate size of a founding population (Zhang *et al*. 2022). Molecular data can also be used in a broader context to answer questions about the biology and ecology of a species, such as its capability to recover genetic diversity after a population bottleneck (e.g. the cricket *Metrioptera roeselii* (Hagenbach) Kaňuch *et al*. 2021) and how a species disperses through a landscape (e.g. the snake *Vipera berus* (Linnaeus) François *et al*. 2021).

1.2. Sowbugs as introduced species

Terrestrial isopods (Isopoda: Oniscidea), also known as woodlice or sowbugs, are one of the few groups of crustaceans with members fully adapted to life on land (Richardson and Araujo 2015). Their ability to live on land is enabled by numerous behavioural, physiological, and morphological adaptations, including a tendency to aggregate, an enclosed brood pouch (marsupium) in which young develop, and, in some species, a covered respiratory surface with spiracles (Hornung 2011). Over 3700 species have been described (Schmalfuss 2004; Sfenthourakis and Taiti 2015), with greatest species richness in the Mediterranean region and other areas with temperate climates (Sfenthourakis and Hornung 2018). Sowbugs have been introduced worldwide through human activity (Hatch 1947; Jass and Klausmeier 2000;

Schmalfuss 2004; Szlavecz *et al*. 2018). Although sowbugs are sometimes imported as pets (e.g. Jungle Jewel Exotics 2023) or as pet food (Cochard *et al*. 2010), most of these introductions are likely unintentional. Sowbugs can be transported in shipments of building materials, gravel, soil, and potted plants (McQueen 1976; Slabber and Chown 2002). It has been suggested that greenhouses may be sites of primary introduction (Hatch 1947; Vilisics and Hornung 2009; Cochard *et al*. 2010; De Smedt *et al*. 2017). There are several reasons why introduced sowbugs may be a concern. Firstly, they may complete with native sowbug species. The introduction of *Hyloniscus riparius* (Koch) into eastern Russia and its subsequent spread and rise in abundance has led to concerns that it may cause declines in populations of native sowbug species (Gongalsky *et al*. 2013). Secondly, sowbugs may act as crop pests under some circumstances. Sowbugs typically feed on dead organic matter (both plant and animal) (Kensley 1974; Zimmer 2002) but may sometimes act as predators (Edney *et al*. 1974) or feed on living plant material (Saska 2008; Johnson *et al*. 2012). When sowbug density is high, damage to plants in greenhouses and fields can be substantial (Messelink and Bloemhard 2007; Johnson *et al*. 2012; Souty-Grosset and Faberi 2018). The role of sowbugs as agricultural pests has been reviewed previously (Souty-Grosset and Faberi 2018) and is linked to the rise of no-till farming practices that allow populations of sowbugs to grow to large numbers. Crops damaged by sowbug feeding include canola, soybeans, sunflowers, and cereal crops, and localities affected include Argentina, Australia, South Africa and the midwestern United States (Souty-Grosset and Faberi 2018). Thirdly, introduction of sowbugs may lead to co-introduction of parasites or pathogens. Sowbugs host a variety of parasitic taxa that use vertebrates as intermediate and/or final hosts, including nematodes (Carreno 2008), acanthocephalans (Vakarenko and Lisitsina 2001; Dimitrova 2009), and trematodes (Pinto *et al.* 2014), which may impact wild and domesticated populations of

vertebrates. Even if sowbugs do not bring novel parasitic taxa, they may amplify levels of parasitism in native hosts if they are able to host native parasitic taxa (Young *et al*. 2017). Finally, sowbugs may affect nutrient cycling through their contribution to decomposition in feeding on dead organic matter (Zimmer 2002; Des Marteaux *et al*. 2020). An example of this type of impact may be seen in the changes in plant communities and decline in native plant species as a result of the burrowing and feeding activity of introduced earthworms in North America (Bohlen *et al*. 2004).

While sowbugs have the potential to negatively impact areas to which they are introduced, introduced sowbugs are sometimes thought to pose few detrimental impacts due to their association with urban areas (Cochard *et al*. 2010) and limited competition with other species (Sfenthourakis and Hornung 2018). Even when present in non-urban areas, negative impact may not be evident. For example, sowbugs were determined to present little risk to tallgrass prairie ecosystems due to their low abundance and preference for dead leaves rather than native plant seeds (Singer *et al.* 2012). Economic impact may similarly be minimal: although several species of sowbugs have been recorded from fields of corn, soy, and wheat in Ontario (Belaoussoff *et al*. 1998) there appears to be no evidence that sowbugs act as crop pests in this area. Finally, concerns about competition with native species of sowbugs are unwarranted if areas to which sowbugs are introduced lack native terrestrial isopods. For example, the Prairie Provinces of Canada (Alberta, Saskatchewan, Manitoba) are thought to lack native sowbug species due to past glaciation that would have removed any existing native species (Jass and Klausmeier 2000). However, Alberta is home to a native cave-dwelling aquatic isopod, *Salmasellus steganothrix* Bowman, which is thought to have survived glaciation due to its

troglobitic nature (Clifford and Bergstrom 1976; Holsinger *et al*. 1983) and so it may be possible that native terrestrial isopod species survived in similar refugia.

Even if introduced sowbugs are found to pose little risk of negative impact in a particular area, there are several reasons why these populations may still be of interest. Documenting the existence of introduced populations of sowbugs not only contributes to the knowledge of the biodiversity in a region, but also broadens knowledge of global sowbug species distributions. Determining these distributions is the first step to understanding how sowbug species may be impacted by climate change (Sfenthourakis and Hornung 2018) and is also of interest for conservation purposes. Some species of sowbugs have declined due to habitat loss (Harding 2016) while others may be negatively affected by climate change (Sfenthourakis and Hornung 2018), and some species have extremely restricted distributions (Dutton and Pryce 2018; Reboleira *et al*. 2022). Knowing whether these species have established healthy populations elsewhere may impact conservation management decisions. Secondly, examination of introduced species may also lead to the discovery of cryptic species. Detailed investigation of populations of the sowbug *Porcellionides pruinosus* (Brandt) in North America revealed that at least two species were present (Garthwaite and Sassaman 1985). Many species of introduced sowbugs have been documented in North America via citizen science observations (e.g. iNaturalist (https://www.inaturalist.org/) and BugGuide (https://bugguide.net/node/view/15740) and while sowbug species in these photos can often be identified by general appearance (Gregory 2022), features that may differentiate closely-related species (e.g. male pleopod and pereiopod morphology) are typically not visible in these observations (pers. obs., HS). Populations of introduced sowbugs from many areas of North America may also never have been compared molecularly with their European counterparts. Molecular genetic analysis of introduced

populations may also be used to assess long-held assumptions about the routes and history of sowbug introductions. While greenhouses are often assumed to be primary sites of introduction based on the diversity and abundance of introduced species at these sites (Hatch 1949; Cochard *et al*. 2010; De Smedt *et al*. 2017), this assumption has never been assessed with molecular evidence. Finally, introduced sowbug populations may also act as useful research models: sowbugs can be used to test hypotheses about phenotypic plasticity (Lardies and Bozinovic 2008) or traits impacting resilience to adverse climate conditions (Hassall *et al*. 2018).

1.3. Existing knowledge of Canadian sowbugs

Despite the importance of documenting and studying introduced sowbugs for the purposes of assessing negative impacts and out of interest in the populations themselves, the sowbug fauna across a large part of Canada has been mostly overlooked. Based on my review of the literature, research up to this point has focused primarily on the biology and ecology of coastal populations of native species (e.g. Carefoot *et al.* 2000; Ziegler *et al*. 2000; Zimmer *et al*. 2001; Wright *et al*. 2003) and documentation of species on the eastern and western coasts and parts of southern Ontario and Québec (see Chapter 2). Sowbugs in the Prairie Provinces of Canada (Alberta, Saskatchewan, and Manitoba) have been especially neglected (Snyder 2014; Floate *et al*. 2017). Until very recently, no sowbug species had been documented from this area in peer-reviewed literature, and at the time of this writing only a single published journal article mentions the existence of sowbugs in the Prairie Provinces (Li 2022), listing only one species from a single site in Alberta. Expanding beyond peer-reviewed literature provides considerably more information: citizen science websites document several sowbug species from the Prairie Provinces (iNaturalist 2023a-c; BugGuide 2023a-c) and the Barcode of Life Data System (BOLD) includes a single COI barcode from a sowbug from Calgary (SDP795001-18, *Porcellio*

spinicornis Say). All species listed in these sources are introduced European species, and it appears that the distributions are centered around cities (iNaturalist 2024d). However, data obtained from citizen science may be spatially biased towards populated areas (Dickinson *et al*. 2010) and so it is unclear whether these species may also be found outside of urban areas. Sowbug-associated symbionts are even more poorly documented: no records exist from the Prairie Provinces, and the only record of a sowbug symbiont from Canada is the nematode *Caenorhabditis remanei* (Rhabditidae) from unidentified terrestrial isopods in Ontario (Dey *et al*. 2012). It is also unclear when sowbugs first arrived in the Prairie Provinces and what the route(s) of introduction may have been. Anecdotal evidence from long-term residents suggests a very recent arrival of sowbugs in Alberta in the 1970s (pers. obs., Heather Proctor; pers. comm., John Acorn) with sowbugs first appearing in city gardens (Acorn and Sheldon 2000). This date is broadly consistent with the first record of sowbugs from areas surrounding the Prairie Provinces: the earliest sowbug record from Ontario is 1871 (Stuxberg 1873); from British Columbia, 1905 (Richardson 1905); from Minnesota, 1932 (Arcangeli 1932); and from Montana, 1939 (Hatch 1939).

1.4. Research objectives

The following chapters comprise an investigation of the diversity, distribution, symbionts, and population structure of sowbugs in Alberta. In Chapter 2 I present the first survey of sowbugs in Alberta with additional records from other parts of Canada (British Columbia, Saskatchewan, Ontario, and Newfoundland). I include an updated checklist of the terrestrial isopods of Canada, encompassing new collections from this study and records from published literature, collections in research institutions and museums (E.H. Strickland Entomological Museum teaching collections (University of Alberta); Global Biodiversity Information Facility

(GBIF)), and citizen science initiatives (iNaturalist; BugGuide; this study). Sowbugs from Alberta were predicted to be European in origin rather than native and to include representatives of the top ten most common sowbug species in North America (Jass and Klausmeier 2000).

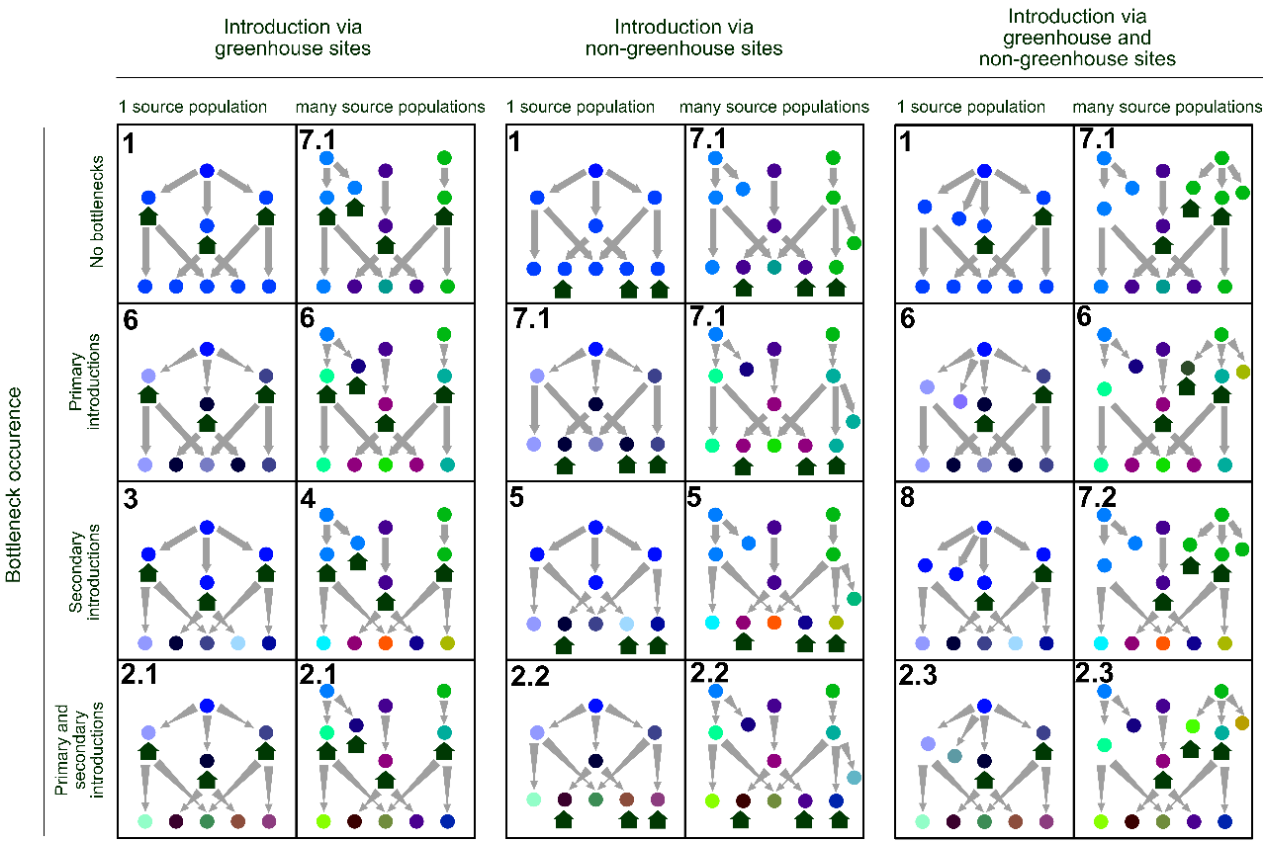
In Chapter 3 I survey symbionts associated with sowbugs in Canada, with the goal of determining whether introduced sowbugs may pose a threat to native biodiversity via introduction of parasitic or pathogenic taxa or amplification of populations of native parasitic/pathogenic taxa (Young *et al*. 2017). The survey focuses primarily on sowbug populations in Alberta, with additional records from British Columbia. Parasitic symbionts were predicted to be European in origin and to have a direct life cycle (i.e. only one host species required), as parasites with complex life cycles may lack a host when introduced to a new environment (Torchin *et al*. 2002, 2003; Lymbery *et al*. 2014). I include a review of the sowbug metazoan symbiome (i.e. all metazoan taxa recorded in a symbiotic association with a sowbug species), with additional records from non-metazoan taxa (viruses, fungi, bacteria).

In Chapter 4 I investigate the population structure of *Porcellio spinicornis* in Edmonton, Alberta, using double digest restriction-site associated DNA sequencing (ddRADseq), including individuals collected from greenhouses and from several parts of southern Alberta. Analyses focus on assessing the role of greenhouses in the introduction of sowbugs and the involvement of passive vs active dispersal in sowbug range expansion. I also compare species richness in greenhouses vs non-greenhouse sites. Due to the frequently high abundance and diversity of sowbugs in greenhouses (Hatch 1947; Korsós *et al*. 2002; De Smedt *et al*. 2017), I hypothesized that greenhouses play a major role in primary introduction of sowbugs in Alberta, and that they should have higher genetic diversity and species richness than non-greenhouse sites (Fig. 1.1). There are many possible patterns of differentiation among sowbug populations in different areas

depending on whether bottlenecks occur during primary and/or secondary introduction, whether there are few or many source populations (Fig. 1.1), and the relative importance of passive vs active dispersal in establishing new populations. I expected that sowbug populations in Alberta overall and within Edmonton likely came from multiple sources, and so predicted that populations would be dissimilar regardless of location or city of origin.

1.5. Figures

Figure 1.1 (next page): Expected patterns of genetic diversity and differentiation in populations of sowbugs when primary introduction of sowbugs occurs to greenhouses (), to non-greenhouse sites (no greenhouse symbol), or to both, and when bottlenecks are associated with primary introduction, secondary introduction, both, or neither. Arrows indicate introduction of individuals from a population (represented by a circle) to create a new population; narrowed arrows indicate a bottleneck associated with the introduction. Different coloured circles indicate populations that differ genetically. Numbers in the figure refer to the different introduction scenarios described in the table. Note that these diagrams only show primary and secondary introductions.



Pattern	Occurs with primary introduction to greenhouse sites (G), non-greenhouse sites (NG), or both?	Occurs with primary or secondary bottlenecks?	Differentiation between greenhouse and non-greenhouse populations	Differentiation among greenhouse populations	Differentiation among non-greenhouse populations	Genetic diversity in greenhouse (G) vs non-greenhouse (NG) populations
1	G, NG, G+NG	None	Low	Low	Low	G = NG
2.1	G	1°+2°	High	High	High	G > NG
2.2	NG	1°+2°	High	High	High	G < or = NG
2.3	G + NG	1°+2°	High	High	High	G > or = NG
3	G	2°	High	Low	High	G > NG
4	G	2°	High	Varies	High	G > NG
5	NG	2°	High	High	Varies	G < or = NG
6	G, G+NG	1°	Varies	High	Varies	G = NG
7.1	G, NG, G+NG	None, 1°	Varies	Varies	Varies	G = NG
7.2	G+NG	2°	Varies	Varies	Varies	G > or = NG
8	G+NG	2°	Varies	Low	Varies	G > or = NG

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Chapter 2.

Distribution and diversity of terrestrial isopods (Isopoda: Oniscidea) in Canada, with new records from Alberta

2.1. Introduction

Isopods (Peracarida: Isopoda) are a morphologically and ecologically diverse group of crustaceans that inhabit a variety of freshwater, marine, and terrestrial environments (Schmidt 2008; Wilson 2008; Poore and Bruce 2012). Terrestrial isopods belong to the suborder Oniscidea (Schmidt 2008) and are also known as woodlice or sowbugs. With over 3700 species, sowbugs form the largest isopod suborder (Schmalfuss 2004; Sfenthourakis and Taiti 2015) and are one of the few groups of crustaceans with fully terrestrial members (Richardson and Araujo 2015). Sowbugs are found worldwide in a range of different habitats, including caves, deserts, shorelines, ant nests, and urban areas (Hornung 2011; Szlavecz *et al.* 2018). The highest species diversity occurs in the Mediterranean region and other areas with temperate climates (Sfenthourakis and Hornung 2018).

Sowbugs are both ecologically and economically important. As sowbugs primarily feed on plant detritus, they are involved in the process of decomposition and can alter the structure of microbial communities in leaf litter (Zimmer 2002; Des Marteaux *et al*. 2020). Some species also feed on seeds (Saska 2008), dead animal matter (Kensley 1974), or live plants (Johnson *et al.* 2012). The latter behavior may result in damage to crops in fields and greenhouses if sowbug populations reach large numbers (Messelink and Bloemhard 2007; Souty-Grosset and Faberi

2018). The role of sowbugs as agricultural pests has been previously reviewed (Souty-Grosset and Faberi 2018); targeted crops include canola, soybeans, sunflowers, and cereal crops, and localities affected include Argentina, Australia, South Africa and the midwestern United States. Sowbugs also act as intermediate hosts for parasites that have wild or domesticated vertebrates as final hosts. These include the nematode genera *Acuaria* and *Dispharynx*, which infect birds (Carreno 2008) and the acanthocephalan *Plagiorhynchus cylindraceus* (Goeze) (Dimitrova 2009) which infects a wide variety of birds and mammals (Llanos-Soto *et al*. 2019).

Sowbugs were first documented in Canada in 1859, when *Porcellio scaber* Latreille was recorded from coastal British Columbia (GBIF 699124508, Museum of Comparative Zoology, Harvard University). The first review of sowbugs to include species recorded from Canada was published almost 50 years later (Richardson 1905) and listed six species from Canada. This was followed by a review of sowbugs from Canada and Alaska in which 10 species were listed (Johansen 1926). A decade later the number of sowbugs from Canada had grown to 14 species (Van Name 1936), then to 15 (Hatch 1947) and later to 16 (Leistikow and Wägele 1999). The most recent review of sowbugs found north of Mexico lists 25 species from Canada (Jass and Klausmeier 2001). Many of these species are non-native and originate from Europe (Leistikow and Wägele 1999; Jass and Klausmeier 2001). Except for the troglobitic *Ligidium elrodii* (Packard) (Schultz 1970), native sowbugs in the northern part of North America are limited to coastal habitats (Jass and Klausmeier 2000, 2001). Past glaciation over much of northern North America would likely have removed any existing native sowbugs in this area (Jass and Klausmeier 2000). However, the existence of a native cave-dwelling aquatic isopod in Alberta that apparently survived glaciation (Clifford and Bergstrom 1976; Holsinger *et al*. 1983) suggests that troglobitic sowbugs could also have hypothetically survived glaciation.

Published records of sowbugs in Canada have been geographically limited to the eastern and western coast and localities near the Great Lakes, and records prior to 1980 are scarce. No published sowbug records exist from northern Canada (Yukon, Northwest Territories, Nunavut) and as of 2014 there were no records from any of the Prairie Provinces (Alberta, Saskatchewan, Manitoba) (Snyder 2014). The first and only published record of a sowbug from the Prairie Provinces was *Trachelipus rathkii* (Brandt) from a single site in Edmonton, Alberta (Li 2022). Despite the scarcity of published records of sowbugs from Alberta, Saskatchewan, and Manitoba, sowbugs have been present in this area for at least two decades: citizen science websites such as iNaturalist and BugGuide include many unambiguous photographs of sowbugs from Alberta, Saskatchewan, and Manitoba (iNaturalist 2023a-c; BugGuide 2023a-c) and there are many unpublished GBIF records that also list sowbugs from this area (GBIF 2023a-m). Including these sources, the earliest record of a sowbug from the Prairie Provinces is *Porcellio spinicornis* Say from Edmonton, Alberta that was observed in 2005 (BugGuide 33837).

There are several possible reasons why few published records exist for sowbugs from the Prairie Provinces. Firstly, this area has never been surveyed specifically for sowbugs (Floate *et al*. 2017). A variety of types of pitfall traps can effectively capture sowbugs (Siewers *et al*. 2014) and so surveys designed to assess arthropod diversity in the Prairie Provinces using pitfall traps (Floate *et al*. 2017) would likely have captured sowbugs if they were present. However, sowbugs may have been overlooked or unreported if they were not among the taxa of interest. Secondly, arthropod surveys may have failed to capture sowbugs because arthropod surveys in the Prairie Provinces have typically covered natural or semi-natural area rather than urban areas (Snyder 2014; Floate *et al*. 2017). Introduced species of sowbugs are common in urban areas (Cochard *et al.* 2010; Szlavecz *et al*. 2018), and in regions where the climate is unfavorable, buildings

provide warm refugia (Wright 1997). If sowbugs are only abundant in urban areas in the Prairie Provinces, this would reduce the likelihood of encountering them in surveys of natural areas. Similarly, sowbugs in urban areas in eastern Russia are thought to have been present long before the populations were first reported, since soil arthropod surveys had focused on undisturbed areas (Gongalsky and Kuznetsova 2021). Finally, sowbugs may be a very recent introduction to the Prairie Provinces. Anecdotal evidence from long-time residents of Alberta suggests sowbugs were absent from the province until the late 1970s (pers. obs., HP; pers. comm., John Acorn).

Initial introductions of sowbugs to North America may have occurred through transport of soil ballast on ships (Lindroth 1957), and present-day introduction may take place through sale of sowbugs as pet food (Cochard *et al*. 2010), as pets themselves (e.g., Jungle Jewel Exotics 2023), through shipment of building materials (Slabber and Chown 2002) and gravel (McQueen 1976), or via shipment of soil, plants, and other gardening supplies to greenhouses and gardens (Hatch 1947; Jass and Klausmeier 2000; Vilisics and Hornung 2009; Cochard *et al*. 2010; De Smedt *et al*. 2017). The importance of the latter route is suggested by the abundance and species richness of sowbugs in greenhouses. Sowbugs were present in 66/67 greenhouses examined in North America in the Pacific Northwest (Hatch 1947) and 7/7 greenhouses surveyed in Britain (Gregory and Lugg 2020). Greenhouses also typically have high species richness (De Smedt *et al*. 2017) even when compared to natural areas such as parks and forests (Korsós *et al*. 2002). Some species of sowbugs may be entirely restricted to greenhouses in colder parts of their non-native range (Hatch 1947; Rapp 2001; Schmalfuss 2004; Gregory 2014).

This study is the first targeted survey of sowbugs in Alberta and includes new collections from four other Canadian provinces (British Columbia, Saskatchewan, Ontario, and Newfoundland). These collections include the first Canadian record of *Nagurus cristatus*

(Dollfus) (reported in Stormer and Proctor 2022) and the first molecularly-supported record of a sowbug from Saskatchewan. I support my identifications with COI barcode sequences for eight sowbug species and provide a partial 18S sequence for *Nagurus cristatus.* An updated list of the species of sowbugs found in Canada is also provided, along with brief descriptions of the habitat each species occupies in Canada and the date of the first Canadian record. This study will help to guide researchers and naturalists in their identification of sowbugs found in Canada and promote additional research pertaining to the origin and ecological impact of sowbugs in this area.

2.2. Methods

2.2.1. Canadian records of terrestrial isopods

To compile a list of sowbug species previously recorded from Canada, I performed literature searches in Google Scholar and Web of Science using combinations of the keywords “isopod”, “terrestrial”, “sowbug”, “woodlice”, and “Canada”, with names of Canadian provinces and territories. All published records containing at least one species-level identification of a sowbug species from a Canadian locality were included in the dataset. I cited the original publication for each record whenever possible; if a publication listed a record without citing another source for the record, I assumed the record originated with that publication. In addition to published literature, I compiled all records of sowbugs from Canada available on iNaturalist (https://www.inaturalist.org/) and BugGuide (https://bugguide.net/node/view/15740) up to 10 December 2023, and records form GBIF up to 18 January 2023 (GBIF 2023a-m). I obtained GBIF records by searching for each family in Oniscidea with the following filters applied: location = Canada; basis of record = material sample or preserved specimen. These filters exclude records from iNaturalist and limit records mostly to those originating from collections in museums and research institutions. To visualize species distributions, I used Google Maps to assign GPS coordinates to GBIF records and published records that lacked coordinates by using locality information listed in the source (e.g. descriptions, maps, province). Coordinates were placed in the center of the most precise locality possible given the information listed in the source. When the locality was identified only as a province, the coordinates were set to the center of the province. I created a distribution map for each species using QGIS v 3.14.16 (QGIS.org 2023).

2.2.2. Sowbug collections

I collected sowbugs from in Alberta from 2021-2023, with smaller opportunistic collections from British Columbia and Ontario. Collecting efforts in Alberta focused on the greater Edmonton area. Sowbugs from Newfoundland collected from 2011-2023 were contributed by D. Langor, L. Lafosse, D. Harrison, and A. Pretty, with collections from provincial parks conducted under permits to D. Langor (Survey of insects of Newfoundland and Labrador (2011-2013); Survey of terrestrial invertebrates of NL 2022-24). Additional sowbugs were collected from Alberta, British Columbia, and Saskatchewan by R. Palmer, B. Tonn, C. Paszkowski, H. Carcamo, B. Grappone, H. Beck, C. Goater, D. Floate, L. Pollett, P. Perry, B. Wingert, K. Kent, C. Crooks, G. Pohl, C. Davis, D. Edwards, K. Hudson, H. Kastelic, G. and L. Jackson, K. Van Slyke (Van Slyke 2023), C. Kolt, and J. Sperling. As the goal of these collections was to maximize the number of species encountered rather than to perform an exhaustive survey, I chose collection sites based on their similarity to published descriptions of sowbug habitat rather than their geographic location. I used Google maps to look for sites with suitable habitat (e.g. rock piles, mulch, wooded areas with fallen logs). I collected sowbugs in the spring, summer, and fall from a variety of urban areas, disturbed natural areas (e.g. nature trails in residential areas), and relatively undisturbed natural areas (e.g. trails in rural areas). In addition to outdoor collections, I searched for sowbugs in greenhouses in the Edmonton area with permission from greenhouse managers. Collection methods were similar across all types of collection sites: I hand-collected sowbugs by turning over gravel and mulch and by lifting items on the ground, and obtained smaller sowbugs from Tullgren funnel extractions from leaf piles and soil. I also assessed the use of a UV flashlight and thermal imaging camera as an aid to visual search for sowbugs. Although sowbugs placed on a white paper background were visible using both methods when placed on a

flat table (glowing slightly under UV light, or visible as a spot of differing temperature), neither method was sensitive enough to detect sowbugs in a more complex environment such as a leaf pile. All collected sowbugs were temporarily housed alive in containers with a damp paper towel until they were identified, after which they were euthanized with carbon dioxide gas, photographed, and preserved in 95% ethanol for DNA extraction or in 70% as morphological vouchers. My collections were augmented by specimens deposited in the E.H. Strickland Entomological Museum teaching collections (University of Alberta) and photos of sowbugs taken by the public via a citizen science initiative for this study. As well as publishing requests for photos and specimens in the Biological Survey of Canada newsletter (Stormer and Proctor 2021, 2022) I posted instructions on Facebook groups belonging to nature and gardening clubs in Alberta to request participants to submit photographs of sowbugs with locality and habitat information (I did not request the precise locality or personal information). Characteristics or habitus that allow sowbug identification to a particular species or genus are usually visible in photographs (personal observation, HS; Gregory 2022). Sowbugs collected by colleagues were obtained either by hand collection or with pitfall traps, and most were received after the sowbugs were preserved in 70% ethanol. Representative sowbugs collected for this study are deposited in the E.H. Strickland Entomological Museum collections (University of Alberta) under accession numbers UASM407002 - UASM407369.

To gather additional information pertaining to the entry of sowbugs into Canada and the species that may be present, I requested Canadian Food Inspection Agency (CFIA) import records for sowbugs imported to Canada from 2015 onwards. Records prior to 2015 were not available electronically.

2.2.3. Identification

I identified all sowbug specimens and photographs morphologically with keys and by comparison to species descriptions (Sars 1898; Van Name 1936, 1940; Hopkin 1991; Vandel 1960,1962; Schultz 1982, 1984b; Ferrara and Schmalfuss 1985; Garthwaite and Sassaman 1985; Garthwaite and Lawson 1992; Bilton 1992, 1997; Schmidt 1997; Schmidt 2003; Shultz 2018; Gregory 2019). For each morphologically-identified species, I sequenced the cytochrome c oxidase subunit I (COI) barcode region from 3-5 individuals (Appendix A Table A1), and chose individuals to maximize intraspecific morphological variation and the geographic distance among sampling sites. I extracted sowbug DNA with a DNeasy Blood and Tissue Kit (Qiagen) according to the manufacturer's instructions, but with the following modifications: (1) tissue was ground with a pestle after adding buffer ATL; (2) incubation time was 3 hours after adding proteinase K; (3) 4 µl of RNAse A was added after incubation. For PCR and sequencing I used the primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and either HC02198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') or IsoCoiRint (5'-GCYCCYGCYAAWACAGGKARDGA-3') (Folmer *et al*. 1994; Dimitriou and Sfenthourakis 2022). The latter primer is designed specifically for sowbugs and usually resulted in successful amplification of samples that produced a poor sequence with the LCO1490/HC02198 primer pair. PCR reactions contained 5 µl of template DNA, 0.5 µl of each primer (10 µM concentration), 10 µl of AccuStart II GelTrack® PCR SuperMix (Quantabio) and 4 µl of water for a total volume of 20 µl. When using the LCO1490/HC02198 primer pair, the amplification conditions consisted of initial denaturation at 94˚C for 3 minutes, followed by 35 cycles of 94˚C for 45 seconds, 48˚C for 45 seconds, and 72˚C at 60 seconds, and a final extension at 72˚C for 7 minutes. Amplification with LCO1490/IsoCoiRint followed the "strict"

protocol in Dimitriou and Sfenthourakis (2022). I assessed amplification success with gel electrophoresis, cleaned amplified DNA with a column-based PCR cleanup kit (Truin Science KTS1115) and submitted the samples to the University of Alberta Molecular Biology Service Unit (MBSU) for bidirectional Sanger sequencing. To create consensus sequences for each sample I manually trimmed and aligned the forward and reverse reads in JalView (Waterhouse *et al*. 2009) and searched for matching sequences in both BOLD (Ratnasingham and Hebert 2007) and NCBI BLAST (Altschul *et al*. 1990) using default settings. All sowbug COI sequences obtained in this study are deposited in GenBank under accession numbers PP995851 - PP995894.

To assess confidence in species identifications resulting from COI sequencing, I constructed a maximum likelihood phylogeny for each sowbug family from which I had obtained sequences. Each phylogeny contained all COI sequences from this study and from GenBank (https://www.ncbi.nlm.nih.gov/nucleotide/) that belonged to that family. The outgroups for these phylogenies consisted of the longest COI sequences available from GenBank for every species-level taxon in Ligiidae and Tylidae, with the phylogenies rooted on Ligiidae. I did not include *Ligia* (Ligiidae) as an outgroup because its inclusion in Oniscidea is debated (Dimitriou *et al*. 2019; Tabacaru and Giurginca 2021). I aligned and trimmed the sequences for each family using MAFFT (Nakamura *et al*. 2018) and constructed each phylogeny with IQ-TREE version 2.2.2.7 (Nguyen *et al*. 2015). I used ModelFinder (Kalyaanamoorthy *et al*. 2017) to test substitution models and choose the model with the lowest Bayesian information criterion (BIC) score for each phylogeny (-m MFP). Phylogenies were assessed with ultrafast bootstrap (Hoang *et al*. 2018) using 5000 replicates (-B 5000) and allowing up to 5000 bootstrap iterations (-nm 5000).

Finally, I used FigTree (Rambaut 2009) and TreeGraph2 (Stöver and Müller 2010) to format and annotate the phylogenies for viewing.

2.2.4. Possible NUMT

The COI sequences I obtained from *Nagurus cristatus* may represent nuclear mitochondrial pseudogenes (NUMTs), in which case they would likely be nonfunctional. To look for evidence of non-functionality, I added these sequences to a dataset of 25 additional COI sequences from GenBank consisting of 19 sowbug species (terrestrial isopods) and 6 non-terrestrial isopod species. I included three non-isopod peracarid outgroups consisting of two species of amphipod and the mysid *Hemimysis margalefi* Alcaraz *et al*. (GenBank HE614276.1) and rooted the phylogenies on *H. margalefi*. I manually aligned and trimmed the dataset in JalView (Waterhouse *et al*. 2009) and constructed a maximum likelihood tree using MEGA6 (Tamura *et al*. 2013). I then used MEGA6 to convert the nucleotide sequences to amino acid sequences, construct a pairwise distance matrix from the amino acid sequences, and build a neighbor-joining tree using the pairwise distance matrix. I also used the pairwise distance matrix to calculate the average amino acid dissimilarity for each sequence included in the matrix.

To attempt to obtain the "true" *Nagurus cristatus* COI sequence, I used Poly Peak Parser (Hill *et al*. 2014) to subtract the possible NUMT sequence from the mixed templates that had resulted from attempting to sequence the COI barcode region from *N. cristatus* using LCO1490/IsoCoiRint primers. I also constructed two pairs of *Nagurus*-specific COI primers with Primer3 (Ye *et al*. 2012) as implemented in Primer-BLAST (https://www.ncbi.nlm.nih.gov/tools/primer-blast/) using a COI sequence from *Nagurus carinatus* (Dollfus) (GenBank ON212542.1) as the template. These primer pairs are Nag_3_F/Nag_3_R (5'-GGGGCTCTTGGGACTTCATT-3',

5’-TAGCCCCGGCTAAAACAGGA-3’) and Nag_9_F/Nag_9_R (5’-CGGAGTTAGGTCAAGCTGGT-3’, 5’-TAGCCCCGGCTAAAACAGG-3’). The PCR reaction volume and components were the same as described previously for COI sequencing from the other sowbug species. Amplification conditions for the *Nagurus* primers Nag_3_F/Nag_3_R were intended to limit non-specific amplification, and consisted of denaturation at 94˚C for 3 minutes, followed by 5 cycles of 94˚C for 45 seconds, 62˚C for 45 seconds, and 72˚C for 60 seconds; 5 cycles of 94˚C for 45 seconds, 60˚C for 45 seconds, and 72˚C for 60 seconds; 10 cycles of 94˚C for 45 seconds, 58˚C for 45 seconds, and 72˚C for 60 seconds; 10 cycles of 94˚C for 45 seconds, 55˚C for 45 seconds, and 72˚C for 60 seconds; and a final extension at 72˚C for 7 minutes. For the Nag_9_F/Nag_9_R primers I used an alternative amplification protocol consisting of denaturation at 94˚C for 3 minutes, followed by 15 cycles of 94˚C for 45 seconds, 55˚C for 45 seconds, 72˚C for 60 seconds; 15 cycles of 94˚C for 45 seconds, 52˚C for 45 seconds, 72˚C for 60 seconds; and a final extension at 72˚C for 7 minutes. I assessed amplification success as described previously.

2.2.5. Sowbug 18S phylogeny

If the COI sequences obtained from *N. cristatus* represent the “true” COI sequence, this would suggest that *N. cristatus* is extremely diverged from other sowbugs, which should be reflected in its nuclear genome. I used the primers 18SA1_mod (5’-CTGGTTGATCCTGCCAGTCATATGC-3’) (Raupach *et al*. 2009) and 18S700R (5’-CGCGGCTGCTGGCACCAGAC-3’) (Dreyer and Wägele 2001) to amplify a 620 bp section of the 18S gene. Amplification conditions followed a touchdown PCR protocol developed by Dimitriou *et al*. (2018). I assessed amplification success and obtained final sequences as

described previously. *Nagurus cristatus* partial 18S sequences obtained in this study are deposited in GenBank under accession numbers PQ001581- PQ001583.

To construct a phylogeny to compare partial 18S sequences in *Nagurus cristatus* and other sowbugs, I compiled a dataset of 18S sequences by searching GenBank (https://www.ncbi.nlm.nih.gov/nucleotide/) for "18S and FAMILY" for all 39 extant sowbug families (Ahyong *et al*. 2011; Javidkar *et al*. 2015; Sfenthourakis and Taiti 2015) and added the longest sequence for each species to the dataset. I also added the longest sequence for each genus that did not have any representatives identified to species-level. I aligned these sequences with MAFFT (Nakamura *et al*. 2018) using the E-INS-I alignment algorithm, which is recommended for RNA polymerase sequences (https://mafft.cbrc.jp/alignment/software/algorithms/algorithms.html) and constructed a maximum likelihood phylogeny with IQ-TREE (Nguyen *et al*. 2015) using the process described previously for the sowbug COI sequences. I also constructed a second phylogeny using an alternative alignment produced with the MAFFT L-INS-I alignment algorithm. Both trees were rooted on Ligiidae. As for the COI phylogenies, I did not include *Ligia* as an outgroup.

2.3. Results

2.3.1. Sowbug collections

My colleagues and I searched for sowbugs in 118 sites in Alberta (15 of them greenhouses), 15 sites in British Columbia, 22 in Newfoundland, two in Ontario, and one in Saskatchewan (Fig. 2.1). Additionally, I received 47 citizen science observations from Alberta and examined 17 Alberta-collected sowbugs from the E.H. Strickland Entomological Museum. Of the 118 sites in Alberta that were surveyed for sowbugs, 79 had sowbugs present (66.95%), including 11 of the 15 greenhouse sites (73.33%). In total, I identified 2382 sowbugs to the level of species, with 14 species and eight families represented in the examined material (Fig. 2.2). Nine of the 14 occur in Alberta: *Cylisticus convexus* (De Geer), *Trachelipus rathkii* (Brandt), *Nagurus cristatus* (Dollfus), *Armadillidium nasatum* (Budde-Lund), *Armadillidium vulgare* (Latreille), *Porcellionides pruinosus* (Brandt), *Porcellio spinicornis* Say, *Porcellio dilatatus* Brandt and *Porcellio scaber* Latreille. Species composition appeared to differ between Alberta, British Columbia, and Newfoundland: sowbugs in Newfoundland and British Columbia consisted primarily of *Oniscus asellus* Linnaeus and *Porcellio scaber*, while *Porcellio spinicornis* and *Trachelipus rathkii* made up the majority of samples from Alberta (Fig. 2.1).

2.3.2. Molecular identification

I obtained 44 COI barcode sequences from 13 sowbug species representing 7 families, including specimens from Alberta, Saskatchewan, British Columbia, and Ontario (Appendix A Table A1). All sequences except five matched a species-level record from BOLD or GenBank with >99% identity. For all sequences except *Nagurus cristatus* and one *Onscisus asellus*, the closest match was to the species determined by morphological identification. For the three *N. cristatus*

sequences, the closest match was *Hemimysis margalefi* (Mysida: Mysidae) in GenBank (78.8 - 79.3% identity) and *Mongoloniscus vannamei* (Arcangeli) (Isopoda: Agnaridae) in BOLD (80.03 - 80.13% identity). The two *Oniscus asellus* sequences matched to *O. asellus* in BOLD with 82.53 - 94.58% identity, but in GenBank they matched to different species: one of the sequences matched to *O. asellus* with 96.3% identity, and the other matched *Armadillidium vulgare* with 81.3% identity. The *Porcellionides pruinosus* sequence matched with 97.5% identity to *P. pruinosus* in GenBank and 97.7% identity to *P. pruinosus* in BOLD. The poor matches for *O. asellus* and *P. pruinosus* were likely due to a high level of sequence noise that resulted in many unresolved bases (Appendix A Fig. A1).

In the COI phylogenies constructed for each sowbug family, almost all sequences for each species of interest (including those obtained in this study) were placed in a single monophyletic clade with >95% ultrafast bootstrap support (Fig. 2.3a-g). The exception was *Nagurus cristatus*. No other sequences were available for this species besides the ones obtained in this study, and these sequences were placed in a polytomy with Tylidae and the rest of Trachelipodidae rather than clustering with *Nagurus carinatus* (Fig. 2.3f). Another exception was *Porcellionides pruinosus,* which was paraphyletic due to *Porcellionides myrmecophilus* (Stein) forming a well-supported clade within the *P. pruinosus* clade (Fig. 2.3e). It was not possible to assess whether *Cylisticus convexus* could be differentiated from other Cylisticidae using COI, as no other cylisticids had publicly available COI sequences.

2.3.3. Possible NUMT

Excluding unresolved bases, all *Nagurus cristatus* sequences were identical. When analyzed together with a variety of terrestrial and aquatic isopods and other Peracarida, the *N. cristatus* sequences formed a clade between the *H. margalefi* outgroup and the rest of Peracarida rather

than appearing in the clade containing all other sowbugs (Appendix A Fig. A2). In the phylogeny constructed with only Trachelipodidae COI sequences, *Nagurus cristatus* was placed in a polytomy with the Tylidae outgroup and the rest of Trachelipodidae rather than clustering with *Nagurus carinatus* (Fig. 2.3f). The *N. cristatus* sequences did not exhibit a long branch compared to the other sowbugs in either of the phylogenies.

My *Nagurus cristatus* COI sequences contained a high level of noise when produced with the LCO1490/HC02198 primer pair, suggesting that two or more templates were present. Amplification with LCO1490/IsoCoiRint resulted in an unreadable sequence with even more noise. Elevated noise may result from coamplification of a "true" mitochondrial COI barcode and a nuclear mitochondrial pseudogene (NUMT) (Moulton *et al*. 2010). My attempts to extract the "true" barcode from the mixed template using Poly Peak Parser (Hill *et al*. 2014) did not result in a clear sequence. NUMTs may contain stop codons, but not always (Moulton *et al*. 2010). Conversion of the nucleotide sequences to amino acid sequences did not reveal stop codons in *N. cristatus* or in any of the other peracarid sequences in the dataset. The neighbor-joining tree constructed by pairwise comparison of amino acid sequences showed evidence of sequence divergence for *N. cristatus*, which had a slightly longer branch than other Trachelipodidae included in the tree (Appendix A Fig. A3). *Nagurus cristatus* also had the highest average amino acid sequence dissimilarity (0.136 amino acid substitutions per site) of any sowbug species in the dataset (Appendix A Fig. A4). The second-highest average dissimilarity was 0.125 substitutions per site for *Protracheoniscus pokarzhevskii* Gongalsky & Turbanov (GenBank MH400723.1).

2.3.4. Sowbug 18S phylogeny

All three *Nagurus cristatus* yielded identical 18S sequences excluding unresolved bases. The closest GenBank match to the consensus of the three sequences was *Philoscia muscorum* (Scopoli) (Isopoda: Philosciidae) (GenBank AJ287058.1) which matched with 91.03% identity. The *N. cristatus* 18S sequences did not cluster with other Trachelipodidae in the 18S phylogeny as expected, but instead were contained in a clade with Scyphacidae, Porcellionidae, and *Levantoniscus* (Fig. 2.4). There were two other unexpected placements of taxa traditionally included in the Trachelipodidae: (1) *Levantoniscus* clustered with Porcellionidae, and (2) *Porcellium* was placed in Cylisticidae. Four other unexpected placements included (1) *Tylos punctatus* Holmes & Gay placed with Ligiidae instead of with *Tylos europaeus* Arcangeli; (2) two Philosciidae spp. placed with Platyarthridae; (3) two *Spherillo* spp. placed with *Tylos* instead of in Armadillidae; (4) *Trichorhina tomentosa* (Budde-Lund) placed as an outgroup to Paraplatyarthridae, Philosciidae and Armadillidae rather than in Platyarthridae. The placement of the *T. punctatus* sequence is likely due to poor sequence alignment, as the *Tylos* sequences did not align well with the rest of the dataset. Using an alternative alignment algorithm (L-INS-I) resulted in both *Tylos* sequences clustering together with *Spherillo* (Appendix A Fig. A5).

2.3.5. Canadian records of terrestrial isopods

The following section contains a list of 31 well-documented species and four species with dubious records (numbers 32 - 35) of terrestrial isopods (Isopoda: Oniscidea) that have been reported from Canada in published literature, unpublished records (GBIF), citizen science observations (iNaturalist, BugGuide, citizen science initiative for this study), and new collections from this study. A summary of species recorded from each province and territory and species

distribution maps can be found in Table 2.1 and Fig. 2.5. Enlarged distribution maps are also available for each species (Appendix A Fig. A6).

Notes:

1. Records are listed in alphabetical order by family, then genus, then species. All the families included in this list belong to the infraorder (a.k.a. "section") Crinocheta (Dimitriou *et al*. 2019) except for Ligiidae (Diplocheta) and Trichoniscidae (Synocheta).
2. Recent molecular evidence suggests Ligiidae is polyphyletic, with *Ligia* more closely related to marine isopods (Dimitriou *et al.* 2019). This would exclude *Ligia* from Oniscidea, and *Ligidium* and other genera formerly in Ligiidae would be assigned to the new family 'Ligidiidae' (Dimitriou *et al.* 2019). These changes would mean *Ligia* is not a terrestrial isopod, and so should not be included in this review, and that *Ligidium* should be listed under the family Ligidiidae instead of Ligiidae. However, both of these changes are debated on the grounds that they do not match morphological evidence that supports the monophyly of Oniscidea (Tabacaru and Giurginca 2021). As *Ligia* has traditionally been considered part of Oniscidea, it is included in this list for continuity with older lists of sowbugs. For the same reason the name 'Ligiidae' is used in the old sense throughout this paper (i.e. including both *Ligia* and *Ligidium*).
3. 'New collections' refer to specimens collected and examined for this study. Unaccessioned specimens from the E.H. Strickland Entomological Museum teaching collections (University of Alberta) which were examined and identified for this study are also listed under "New collections", since to the best of my knowledge these records have not been previously published. Records associated with specimens from the E.H. Strickland Entomological Museum teaching collections are referenced as "Strickland".

4. Species records generated by citizen science can provide valuable data and may result in a broader picture of the distribution of a species than published literature, and so records of sowbugs from iNaturalist and BugGuide are included when available. However, these records do not undergo peer review and do not typically include vouchers deposited in museums or other publicly accessible collections. Records of sowbugs from localities supported solely by iNaturalist and/or BugGuide are listed separately under the heading "Unpublished Canadian Distribution". Citations for records from iNaturalist and BugGuide can be found in Appendix B.
5. GBIF records that list localities outside of those covered by published literature were assumed to represent unpublished records (i.e. pertaining to specimens not connected with a publication) unless associated literature could be found. I attempted to find an associated publication in these cases. Since unpublished GBIF records may not have been peer reviewed, records without associated literature are listed under the "Unpublished Canadian Distribution" section. To avoid duplication of records, I did not include published GBIF records under the "Unpublished Canadian Distribution" section, since these records are listed under the "Published Canadian Distribution" section with their associated publication.
6. Records from the citizen science initiative associated with this study are listed under the "Unpublished Canadian Distribution" section, as the species were identified only from photographs rather than examination of specimens. These records are referenced as "Cit. Sci.".

7. Synonyms listed for each species only include synonyms used by the referenced sources. These synonyms are listed so records may be found more easily in the original sources. The sources in which a synonym is used are listed below the synonym.
8. Collection localities are written as they appear in the original source, except when the name was known to be outdated (e.g. Queen Charlotte Islands = Haida Gwaii; Britain Island = Cape Breton) or was likely a misspelling (e.g. Ferrar Point = Ferrer Point; Comax = Comox; Tolfino = Tofino).
9. The "First Canadian Record" is the earliest collection date for a species in Canada, including both published and unpublished sources (i.e. citizen science records). The date of collection for published records was considered equivalent to the publication date unless otherwise specified in the publication (e.g. records without a collection date in a publication from 1929 were assumed to have been collected in 1929).
10. Similar habitat types are listed separately whenever they may not be identical (e.g. 'sand' and 'beach' are not combined, since sand may occur in areas other than beaches).
11. Determining the specific native locality (or localities) for each species is outside the scope of this review, and so the native range is indicated broadly for most species (e.g. "Europe" instead of "southwestern Europe with the exclusion of the following areas…").

(1) Alloniscidae: *Alloniscus*: *Alloniscus perconvexus* Dana, 1854

First Canadian record: 1926, Vancouver Island, BC (GBIF 1898275934).

Published Canadian distribution: BC: Coastal (Austin 1985), Tofino (Hatch 1947), Ferrer Point (Vancouver Island) (Schultz 1984a).

Unpublished Canadian distribution: BC: Vancouver Island (iNaturalist 2023d).

Canadian Habitat: Marine littoral (Austin 1985); creates burrows in wet beach sand (Hatch 1947; Schultz 1984a).

Origin: Native to the Pacific coast of North America (Leistikow and Wägele 1999; Schmalfuss 2004; Hatch 1947; Schultz 1984a; Jass and Klausmeier 2001).

(2) Armadillidiidae**:** *Armadillidium*: *Armadillidium nasatum* Budde-Lund, 1885

= *Armadillidium quadrifrons* Stoller, 1902

(Spencer 1942)

The occurrence of this species in New Brunswick is currently supported by only a single iNaturalist record (iNaturalist 130920223). The photo is indistinct, and while the coloring somewhat resembles *Armadillidium nasatum*, the isopod appears to have uropods that extend well past the end of the telson. This is not consistent with the short, spade-like uropods found in *Armadillidium* species, but both the coloration and the uropods would match the general appearance of *Porcellio scaber* (Hopkin 1991). There are no other records of this species in New Brunswick.

First Canadian record: 1914, London, ON (Ross 1914).

Published Canadian distribution: BC: Langley Prairie (Hatch 1947, 1949), Fraser Valley (Spencer 1942), **ON**: London (Judd 1965), Ottawa (Rafi and Thurston 1982); **QC**: Québec City (Hatch 1947).

Unpublished Canadian distribution: BC: Chilliwack, Victoria (GBIF 2023h; iNaturalist 2023e); **AB:** Red Deer (iNaturalist 2023f); **ON:** South of Ottawa (BugGuide 2023d; iNaturalist 2023g); **QC:** Montreal (iNaturalist 2023j); **NB**: Moncton (iNaturalist 2023i); **NS:** Truro, Halifax (iNaturalist 2023h).

Canadian Habitat: Common in greenhouses (Spencer 1942; Hatch 1947, 1949) but also found in garbage dumps and on grassy plains near creeks (Judd 1965).

New collections: AB: Edmonton, Westerose.

New collections - Habitat: AB: In greenhouses under rocks and concrete debris resting on damp soil, under pots sitting on rocks and gravel, and in damp concrete drainage channels; in the vicinity of greenhouses under cinder blocks, under boards and wooden debris on gravel and landscape fabric, under wooden pallets resting on grass, under pots on mulch, grass, and damp landscape fabric; under rocks near buildings in urban areas.

Origin: Native to Europe, and introduced to North America (Hatch 1949; Lindroth 1957; Leistikow and Wägele 1999; Jass and Klausmeier 2000; Schmalfuss 2004). Canadian Food Inspection Agency import records from 2015-2022 list a shipment of 60 *Armadillidium* sp. from the United States to British Columbia in 2022 (CFIA 2022).

(3) Armadillidiidae**:** *Armadillidium*: *Armadillidium vulgare* (Latreille, 1804)

First Canadian record: 1914, London, ON (Ross 1914).

Published Canadian distribution: BC: Coastal BC (Austin 1985), Southwestern BC (Spencer 1942), Burnaby, Langley Prairie (Hatch 1947), Victoria (Hatch 1947; Edney 1964), Vancouver (Hatch 1947; Taylor and Carefoot 1993); **ON**: Kingston, Toronto, Ottawa (Walker 1927), London (Ross 1914; Judd 1965), Ottawa (Rafi and Thurston 1982), Lake Erie (Dexter *et al.* 1988); **QC:** Montreal (Orstan *et al.* 2008).

Unpublished Canadian distribution: BC: South of Kamloops (BugGuide 2023e; GBIF 2023h; iNaturalist 2023k); **AB**: Edmonton, Calgary, Lethbridge, Medicine Hat, Barrhead (BugGuide 2023f; GBIF 2023h; iNaturalist 2023l; Cit. Sci.); **SK**: Saskatoon (iNaturalist 2023m); **ON**: South of Ottawa (BugGuide 2023g; GBIF 2023h; ; iNaturalist 2023r); **QC**: South of Québec City (BugGuide 2023h; iNaturalist 2023n); **NB**: Nackawic, Fredericton, Saint John, Sackville, Shediac, Moncton (BugGuide 2023i; iNaturalist 2023o); **NS**: Glace Bay, Antigonish, Truro, Windsor, Halifax, Lower Sackville, Elmsdale, Digby, Prospect (iNaturalist 2023p); **PEI**: Charlottetown, Souris (iNaturalist 2023q).

Canadian Habitat: Common in greenhouses throughout its distribution (Walker 1927; Spencer 1942; Hatch 1947; Judd 1965; Rafi and Thurston 1982), but has also been found in garbage dumps, fields, and riverside wooded slopes (Judd 1965); in dry conditions (Dexter *et al.* 1988); in leaf litter, under shrubs, and under boards (Taylor and Carefoot 1993); and associated with buildings (Walker 1927; Taylor and Carefoot 1993; Orstan *et al.* 2008). Austin (1985) lists this species as "supralittoral".

New collections: BC: Parksville, Qualicum Beach, Lake Country; **AB:** Edmonton (Strickland; this study), Lethbridge, Coaldale, Drumheller.

New collections - Habitat: BC: Under rotting logs; in urban areas; **AB:** In urban yards; under rocks, mulch, gravel and pots in urban areas; on moss in a greenhouse by an artificial waterfall; in riparian poplar forest in urban areas; in ornamental planters inside a large building; inside a school.

Origin: Native to the Mediterranean, introduced to North America (Lindroth 1957; Leistikow and Wägele 1999; Schmalfuss 2004; Jass and Klausmeier 2001). An individual observed in 1927 in Toronto, Ontario was associated with imported vegetables, which were thought to be a potential route of sowbug introduction (Walker 1927). Canadian Food Inspection Agency import records from 2015-2022 list a shipment of 60 *Armadillidium* sp. from the United States to British Columbia in 2022 (CFIA 2022).

(4) Cylisticidae: *Cylisticus*: *Cylisticus convexus* (De Geer, 1778)

= *Porcellio convexus* De Geer, 1778

(Underwood 1886)

First Canadian record: 1876, Niagara, ON (Stuxberg 1876).

Published Canadian distribution: BC: Kamloops (Hatch 1947); **AB**: Edmonton (Stormer and Proctor 2022); **ON:** Niagara (Stuxberg 1876; Underwood 1886), Belleville, Brockville, Lake Simcoe, Toronto, Humber Valley (Walker 1927), Lake Erie (Walker 1927; Dexter *et al.* 1988), Bois Blanc Island (Hatch 1939), London (Judd 1963, 1965), Ottawa (Rafi and Thurston 1982); **QC:** Hemmingford (Walker 1927); **NB**: Fredericton

(Wallace 1919), Shediac (Johansen 1929); **NS:** Pictou (Johansen 1929), Sable Island (Wright 1989), Grosses Coques, Gilbert's Cove (Bousfield 1962); **NL**: St. John's (Van Name 1936; Palmén 1951), Corner Brook, Curling, Gaultois, Holyrood, Ramea Island, Spaniard's Bay (Palmén 1951).

Unpublished Canadian distribution: BC: Kamloops, Kelowna (GBIF 2023i; iNaturalist 2023t); **AB**: Edmonton, Calgary, Lethbridge, Camrose (iNaturalist 2023s; Cit. Sci.); **MB**: Winnipeg (iNaturalist 2023u); **ON**: Toronto, Kingston, Sudbury, Ottawa, Tweed, Guelph, Echo Bay, Sault Ste. Marie, Batchawana Bay (BugGuide 2023k; GBIF 2023i; iNaturalist 2023w); **QC**: Rivière-du-Loup, Montreal, Chénéville, Gatineau (GBIF 2023i; iNaturalist 2023x); **NB**: Moncton (BugGuide 2023j); **NS**: Halifax, Brighton, Lockeport (GBIF 2023i; iNaturalist 2023v); **PEI**: Stanley Bridge (GBIF 2023i); **NL**: Grand Falls, Grand Bank (GBIF 2023i).

Canadian Habitat: Under decaying bark and stones (Wallace 1919); under stones and vegetation associated with brooks, pastures and buildings (Palmén 1951; Judd 1965); in garbage dumps (Palmén 1951; Judd 1965; Rafi and Thurston 1982); under rocks in a field (GBIF 1318946951); in grassland, by harbours (Palmén 1951); under debris on beaches and salt marshes (Bousfield 1962); in wooded areas (Judd 1963, 1965; Rafi and Thurston 1982); in damp areas (Dexter *et al.* 1988); on golfing greens and lawns, in marshes (Judd 1965); in greenhouses (Judd 1965; Rafi and Thurston 1982); under boards (Wright 1989).

New collections: AB: Edmonton; Calgary; **ON:** Port Hope; **NL**: Fortune.

New collections - Habitat: AB: In urban areas under damp places associated with cinderblocks, mulch, rocks, bricks, concrete rubble, compost bins, plastic raised bed

pieces, basketball hoop base, leaves, and piles of soil; indoors in basements; in greenhouses under rocks, pots sitting on damp gravel and concrete, and in damp concrete drainage channels; in the vicinity of greenhouses under wooden pallets and in wet leaf litter; **ON**: Under bricks bordering an urban garden bed; **NL**: Under rocks in vacant lot.

Origin: Native to Europe and Asia, introduced to North America (Hatch 1947; Lindroth 1957; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004).

Note: This species typically exhibits a dark brown coloration, but a population in the Biological Sciences greenhouse (University of Alberta) consisted almost entirely of pale-colored individuals (Appendix A Fig. A7). Other species of *Cylisticus* (e.g. *Cylisticus esterelanus* Verhoeff) exhibit similar depigmentation (Gabiot *et al*. 2020). However, the greenhouse population did not appear to be morphologically different from *Cylisticus convexus* with typical coloration from other sites in Alberta, and COI from a depigmented individual was 100% identical to *C. convexus* from Germany (GenBank MN810826.1), and was >99% identical to COI from *C. convexus* collected for this study from other sites in Alberta and from Ontario. When a few individuals were kept in a container with dead leaves (food) and soil, the coloration gradually darkened over several weeks until it resembled the typical coloration for this species, and offspring of these individuals exhibit the typical dark coloration for this species (pers. obs. H.S.). There appear to be no published records of atypical coloration in *C. convexus*, although captive populations of a cylisticid resembling *C. convexus* include a "pied" form (e.g. https://www.smug-bug.com/available-animals/Cylisticus-convexus-Ukraine-pied-p192556903).

(5) Detonidae: *Armadilloniscus*: *Armadilloniscus holmesi* Arcangeli, 1933

First Canadian Record: 1985, BC (Austin 1985).

Published Canadian distribution: BC (Austin 1985).

Unpublished Canadian distribution: BC: Calvert Island (GBIF 2023j).

Canadian Habitat: Marine littoral (Austin 1985).

Origin: Found along the North American Pacific coast, including Mexico and the United States, and also in Japan (Van Name 1936; Hatch 1947; Leistikow and Wägele 1999; Schmalfuss 2004). The North American population is thought to be native (Jass and Klausmeier 2001). The coast of British Columbia would therefore represent the northernmost edge of the distribution of this species in North America.

(6) Detonidae: *Detonella*: *Detonella papillicornis* (Richardson, 1904)

= *Trichoniscus papillicornis* Richardson, 1904

(Fee 1926)

First Canadian Record: 1926, Hammond Bay, BC (Fee 1926).

Published Canadian distribution: BC: Hammond Bay (Fee 1926).

Unpublished Canadian distribution: BC: Roller Bay, Calvert Island, Long Beach (GBIF 2023j; iNaturalist 2023y).

Canadian Habitat: Found in tide pools (Fee 1926).

Origin: In addition to British Columbia, this species has also been recorded from Alaska, Washington, Japan, Russia, and the Kuril Islands (Hatch 1947; Leistikow and Wägele 1999; Schmidt 2000, 2002; Schmalfuss 2004). The North American population of this species is thought to be native (Jass and Klausmeier 2001).

(7) Halophilosciidae: *Littorophiloscia: Littorophiloscia richardsonae* (Holmes & Gay, 1909)

First Canadian Record: 1955, Vancouver Island, BC (Taiti and Ferrara 1986).

Published Canadian distribution: BC: Vancouver Island (Taiti and Ferrara 1986).

Unpublished Canadian distribution: BC: Cape Scott (Vancouver Island) (iNaturalist 2023z).

Canadian Habitat: Coastal regions (Taiti and Ferrara 1986).

Origin: Native to the Pacific coast of North America (Van Name 1936; Taiti and Ferrara 1986; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004).

(8) Halophilosciidae: *Littorophiloscia: Littorophiloscia vittata* (Say, 1818)

First Canadian Record: 1958, Sandy Cove, NS (Bousfield 1962).

Published Canadian distribution: NS: Eel Pond, Gilbert Point (Taiti and Ferrara 1986), Sandy Cove (Bousfield 1962).

Unpublished Canadian distribution: NS: Wolfville (iNaturalist 2023aa).

Canadian Habitat: In a culvert near a pond (Taiti and Ferrara 1986); under *Fucus* (brown algae) and pebbles on rocky beach (Bousfield 1962).

Origin: Native to the Atlantic coast of North America (Van Name 1936; Taiti and Ferrara 1986; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004).

(9) Ligiidae: *Ligia: Ligia occidentalis* (Dana, 1853)

There are over 570 iNaturalist observations from the southern coast of British Columbia (Vancouver area) depicting a species of *Ligia* that has been identified as *Ligia occidentalis* (iNaturalist 2023ab). The distribution of *L. occidentalis* only extends as far north as California (Hurtado *et al*. 2010; Markow and Pfeiler 2010; Santamaria *et al*. 2016). If *L. occidentalis* occurs in the Vancouver area, this would leave a gap of ~700 km between the population in Vancouver and the population in California, assuming the gap is due to true absence and not simply to a lack of records. This gap could be explained by *L. occidentalis* having dispersed along the coast as far north as Vancouver and then disappearing from Washington and Oregon, or by introduction of *L. occidentalis* to the Vancouver area through human activity or drifting materials. However, since members of the genus *Ligia* are very morphologically similar (Van Name 1936), the unusual distribution raises the question of whether the identification of *Ligia occidentalis* in Vancouver is correct. Two other *Ligia* species occur on the Pacific coast of the United States: *L. pallasii* Brandt and *L. exotica* Roux (Jass and Klausmeier 2000, 2001). *Ligia pallasii* has eyes positioned further apart than *L. occidentalis* and *L. exotica* (gap between the eyes is 2x the horizontal width of the eye vs. 1x in *L. exotica*) and has uropod bases with the length greater than the width, vs. the length almost equal to the width in *L. pallasii* (Van Name 1936; Hiebert 2015). Observations from Vancouver clearly depict individuals with rectangular uropod bases and eyes positioned close together (e.g. iNaturalist 124337301; iNaturalist 65124102) which suggests the species is not *L.*

pallasii. Separating *L. exotica* from *L. occidentalis* is difficult: Van Name (1936) noted the high similarity between the two species and distinguished them based on the blunt ("obtuse") telson in *L. occidentalis* vs the pointed ("sharply angular") telson in *L. exotica*. Jackson (1922) separated the two based on antenna length in males, with "antennae shorter than [the] thorax" (= not reaching past the end of the pereion?) in *L. occidentalis*, but longer than the thorax in *L. exotica*. It is difficult to determine the sex of individuals in iNaturalist observations because the ventrally located male pleopods are frequently not visible, but most individuals in the Vancouver population appear to have antennae shorter than the pereion, which would be consistent with *L. occidentalis* (e.g. iNaturalist 133177246; 64380999; 59713259; 196728721; 182838263; 185499188). However, many individuals from the same area also appear to have pointed telsons (iNaturalist 168222896; 64380999; 56817582; 59713259; 146628166), which would be consistent with *L. exotica* rather than *L. occidentalis*. It is possible that more than one species of *Ligia* is present, or that antennae length and telson shape cannot reliably distinguish between *L. exotica* and *L. occidentalis*.

Members of the Vancouver *Ligia* population may be a separate species even if they appear to morphologically match *L. occidentalis*. Based on molecular genetic analyses, populations of *L. 'occidentalis'* on the south Pacific coast of North America were found to represent a cryptic species complex whose members cannot be differentiated morphologically (Hurtado *et al*. 2010; Markow and Pfeiler 2010; Santamaria *et al*. 2016). Therefore, it is possible that the northern populations of *L. 'occidentalis'* found in British Columbia may also be a morphologically cryptic undescribed species. Molecular and

morphological comparison of Vancouver and southern populations of *L. occidentalis* would help resolve the identity of the Vancouver population.

First Canadian Record: 2010, Vancouver, BC (iNaturalist 91588288)

Published Canadian distribution: No records.

Unpublished Canadian distribution: BC: On the south coast of Vancouver Island and around the Vancouver area (iNaturalist 2023ab; BugGuide 2023l).

Canadian Habitat: There are no published records of Canadian habitat for this species.

Origin: Native to the southern Pacific coast of North America (Van Name 1936; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004).

(10) Ligiidae: *Ligia: Ligia oceanica* (Linnaeus, 1767)

The Canadian distribution of this species is likely limited to the east coast. GBIF lists a single record of *L. oceanica* from British Columbia based on a specimen collected by Bousfield in 1955 that is currently deposited in the Canadian Museum of Nature Crustacea Collection (GBIF 1804350972). Bousfield later lists *L. oceanica* from Nova Scotia (Bousfield 1962) but there appear to be no published records from British Columbia. Either Bousfield collected a specimen in British Columbia and did not publish the collection record, or the locality listed for the GBIF record is incorrect.

First Canadian Record: 1958, Sandy Cove, NS (Bousfield 1962).

Published Canadian distribution: NS: Sandy Cove (Bousfield 1962).

Unpublished Canadian distribution: BC: Albert Head (GBIF 2023e); **NB:** Grand Manan, Kent Island, White Head, Sandy Cove Beach, Cape Saint Mary's (iNaturalist 2023ac); **NS:** West coast (iNaturalist 2023ad; GBIF 2023e).

Canadian Habitat: On rocky beach under *Fucus* (brown algae) and rocks (Bousfield 1962).

Origin: Native to Europe, introduced to North America (Van Name 1936; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004).

(11) Ligiidae: *Ligia: Ligia pallasii* Brandt, 1833

= *Ligyda pallasii* (Brandt)

(Richardson 1905; Fee 1926; Johansen 1926; Walker 1927)

= *Lygia dilatata* Stimpson

(Smith 1879)

First Canadian Record: 1878, Victoria, BC (Smith 1879).

Published Canadian distribution: BC: Victoria (Smith 1879; Richardson 1905; Johansen 1926), Lowe Inlet (Richardson 1904, 1905), Ucluelet (Johansen 1926), Brandon Islands, Prince Rupert (Walker 1927), Jesse Island (Fee 1926), Calvert Island, Haida Gwaii (= Queen Charlotte Islands) (Hatch 1947), Port Renfrew (Carefoot 1973, 1979), Botanical Beach (Carefoot 1984), Bamfield (Taylor and Carefoot 1993; Pennings *et al*. 2000), Vancouver (Taylor and Carefoot 1993), Seppings Island (Carefoot *et al*. 2000; Ziegler *et al*. 2000; Zimmer *et al*. 2001; Zimmer *et al*. 2002; Taiti *et al*. 2003; Wright *et al.* 2003).

Unpublished Canadian distribution: BC: Coastal (BugGuide 2023m; iNaturalist 2023ae; GBIF 2023e).

Canadian Habitat: On rocky shore under flat rocks (Walker 1927); on large rocks (Fee 1926); in gaps in rocky cliffs (Carefoot 1973); associated with seaweed (Carefoot 1979); on cobble beaches (Zimmer *et al*. 2001, 2002); under boulders next to cliffs (Carefoot *et al*. 2000; Wright *et al.* 2003); on logs (GBIF 1319700864).

Origin: Native to the Pacific coast of North America (Van Name 1936; Hatch 1947; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004).

(12) Ligiidae: *Ligidium: Ligidium elrodii* (Packard, 1873)

= *Ligidium hypnorum* (Cuvier, 1792)

(Underwood 1886; Richardson 1905)

= *Ligidium longicaudatum* (Stoller, 1902)

(Walker 1927; Judd 1965)

There are few early records from Ontario of a species that was identified as *Ligidium hypnorum* (Underwood 1886; Richardson 1905). *Ligidium hypnorum* is a European species (Schmalfuss 2004) and early records of this species from North America were later believed to represent *L. longicaudatum* (Johansen 1926; Walker 1927; Van Name 1936). *Ligidium longicaudatum* was eventually synonymized with *L. elrodii* (Schultz 1970). Therefore, early records of *L. hypnorum* from Canada likely represent *L. elrodii*.

First Canadian Record: 1876, Niagara, ON (Stuxberg 1876).

Published Canadian distribution: ON: Niagara (Underwood 1886; Richardson 1905), Lake Simcoe, Credit River, Richmond Hill (Walker 1927), London (Judd 1965).

Unpublished Canadian distribution: ON: Walsingham, Richmond Hill, Norfolk (GBIF 2023e, iNaturalist 2023af, BugGuide 2023n).

Canadian Habitat: Under pebbles beside streams; on wet moss in a swamp; under dead leaves and humus in damp woods (Walker 1927); on creek banks, in damp wooded areas (Walker 1927; Judd 1965).

Origin: Recorded only from northeastern North America (Leistikow and Wägele 1999; Schmalfuss 2004). Jass and Klausmeier (2001) list five entries for *L. elrodii*: *L. elrodii* is listed as an "immigrant to Canada and the U.S.", but four subspecies of *L. elrodii* are listed as native to this area (p. 10). The statement that *L. elrodii* is an immigrant is likely an error, as the absence of records of this species from any other part of the world suggests it is native to North America.

(13) Ligiidae: *Ligidium: Ligidium gracile* (Dana, 1854)

= *Ligidium tenue* Budde-Lund, 1885

(Johansen 1926)

First Canadian Record: 1913, Departure Bay, BC (Walker 1927).

Published Canadian distribution: BC: Coastal (Johansen 1926), including Departure Bay, Prince Rupert (Walker 1927), Massett (Jackson 1923), Vancouver (Spencer 1942; Fee 1926), Victoria (Fee 1926), Haney (Hatch 1947), Harrison Hot Springs, Sooke (Arcangeli 1932).

Unpublished Canadian distribution: BC: Coastal (iNaturalist 2023ag; GBIF 2023e).

Canadian Habitat: Under pebbles at brook edge (Walker 1927); under dead leaves and logs in damp wooded areas (Walker 1927; Fee 1926); in woods in urban areas (Spencer 1942); along the coast (Johansen 1926).

New collections: BC: French Beach.

New collections – Habitat: BC: Under rocks near seaside cliffs.

Origin: Native to the Pacific coast of North America (Van Name 1936; Hatch 1947; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004).

(14) Oniscidae**:** *Oniscus: Oniscus asellus* Linnaeus, 1758

= *Oniscus vicarius* Stuxberg, 1872

(Stuxberg 1873; Underwood 1886)

First Canadian Record: 1871, Niagara, ON (Stuxberg 1873).

Published Canadian distribution: BC: Stanley Park, West Point Grey, (Spencer 1942), Vancouver (Spencer 1942; Taylor and Carefoot 1993), Burnaby, Langley Prairie, North Vancouver, Fernie (Hatch 1947); **ON:** Ottawa (Rafi and Thurston 1982), Niagara (Stuxberg 1873; Underwood 1886; Richardson 1905), Toronto (Walker 1927), London (Ross 1914; Judd 1965), Lake Erie (Dexter *et al.* 1988), Copper Cliff, Little Current (Alikhan 1995); **QC:** Québec City (Johansen 1926), Hemmingford (Walker 1927); **NB:** Shediac (Johansen 1929); **NS:** Black Rock, Mabou, Lord's Cove (Bousfield 1956b), Bay of Fundy, Pictou (Johansen 1929), Grosses Coques (Bousfield 1962), Halifax (Hatch

1947), Sable Island (Bousfield 1970; Wright 1989); Kejimkujik National Park (Wright 1995); **NL:** St. John's (Stuxberg 1873; Palmén 1951), Brigus Junction, Burgeo, Cape Broyle, Gaultois, Grand Bruit, Hare Bay, Holyrood, Kitty's Brook, Norris Arm, Pass Island, Placentia, Portugal Cove, Pushthrough, Recontre West, Renews, Rose Blanche, Spaniards Bay, St. Albans, Trepassey, Villa Marie, Waterford Bridge, Whitbourne (Palmén 1951)**.**

In 1949 this species was absent from the western coast of Newfoundland despite thorough sampling (Palmén 1951).

Unpublished Canadian distribution: BC: South of Prince Rupert (BugGuide 2023o; GBIF 2023g; iNaturalist 2023ah); **ON**: South of Sault Ste. Marie (BugGuide 2023s; GBIF 2023g; iNaturalist 2023al); **QC**: South of Rimouski (BugGuide 2023t; GBIF 2023g; iNaturalist 2023an); **NB:** Beresford, Bathurst, Miramichi, Fredericton, Moncton, Sackville, Saint John, Grand Manan, Simpsons Island, Bocabec, Campobello Island, Albert County (BugGuide 2023p; iNaturalist 2023ai); **NS:** Widely distributed (BugGuide 2023r; iNaturalist 2023ak); **PEI:** Charlottetown, Summerside, North Wiltshire (iNaturalist 2023am); **NL:** Avalon Peninsula, Saint-Pierre, Marystown, Clarenville, Gander, Corner Brook (BugGuide 2023q; GBIF 2023g; iNaturalist 2023aj).

Canadian Habitat: Occupies a wide variety of environments. In urban areas, this species has been found in greenhouses (Ross 1914; Spencer 1942; Hatch 1947; Judd 1965), under stones, leaves, and boards around buildings (Walker 1927; Palmén 1951; Rafi and Thurston 1982; Wright 1989; Taylor and Carefoot 1993), in gardens (Ross 1914; Spencer 1942; Rafi and Thurston 1982), in basements (Ross 1914), on lawns and golfing greens (Judd 1965), in dumps and garbage cans (Judd 1965), in association with railway stations

(Palmén 1951), and in woods near urban areas (Alikhan 1995). Outside of urban areas this species has been found in ravines and wooded areas (Ross 1914; Palmén 1951; Judd 1965; Dexter *et al.* 1988; Wright 1995), by river banks (Judd 1965) and lakes (Wright 1995), along the coast (Palmén 1951), under debris on beaches (Bousfield 1962), in fields and marshes (Judd 1965), in moss and lichens (Wright 1995), and under debris on shorelines (Bousfield 1956b).

New collections: BC: Prince George, Vancouver, Parksville, Qualicum Beach, Bamfield; **NL**: Channel-Port aux Basques, J.T. Cheeseman Provincial Park, Barachois Pond Provincial Park, Pasadena, Pynn's Brook, Notre Dame Provincial Park, St. John's, Butter Pot Provincial Park, La Manche Provincial Park, Mount Moriah.

New collections - Habitat: BC: In yards and under wet decaying logs in urban areas; under planters and pots associated with buildings; climbing up the outside walls of cabins at night; **NL:** Under rocks in disturbed open areas; in vegetation at the edges of forests and roadsides; in gravel, sand, and moss on river banks; in mixed and conifer forests.

Origin: Native to Western Europe, introduced to North America (Van Name 1936; Hatch 1947; Lindroth 1957; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004).

The presence of this species only at railway stations in the northern part of Newfoundland in 1949 suggests that it could be dispersed by train (Palmén 1951). This species and others are thought to have been introduced to Kejimkujik National Park, Nova Scotia through farming activity (Wright 1995). Walker (1927) noted that this species was rare in Toronto, Ontario in 1915 but had become common by 1927. He noted that it was found

only in urban environments and concluded that the species must have arrived in Toronto recently. Similarly, Spencer (1942) noted that the species was uncommon in Vancouver, British Columbia in 1929 but had become very abundant by 1942.

Note: This species typically exhibits a dark grey pigmentation, but a single orange individual was present in each of two populations in British Columbia in collections made for this study (Appendix A Fig. A7). Orange-colored individuals of species with typically dark coloration have been documented in several families of terrestrial isopods, including Armadillidae, Armadillidiidae, Detonidae, Philosciidae, Porcellionidae, Platyarthridae, and Trachelipodidae (Sutton 1972; Johnson 1976; Sassaman and Garthwaite 1980; George 1986; Garthwaite 1988; Negishi *et al*. 1994). There appear to be no published records of an orange form of *Oniscus asellus* or other Oniscidae. However, orange *O. asellus* have been documented by terrestrial isopod enthusiasts and are kept as pets, with captive-bred populations thought to have originated from British Columbia (Smug Bug 2021).

(15) Philosciidae: *Philoscia*: *Philoscia muscorum* (Scopoli, 1763)

First Canadian Record: 1958, Grosses Coques, NS (Bousfield 1962).

Published Canadian distribution: NS: Grosses Coques (Bousfield 1962), Kejimkujik National Park (Wright 1995).

McAlpine & Oldham (2011) state that this species has been recorded from Ontario by Rafi and Thurston (1982), but I was unable to find mention of this species or any synonyms in this source.

Unpublished Canadian distribution: BC: Kelowna, on the south coast of Vancouver Island and around the Vancouver area (BugGuide 2023u; GBIF 2023k; iNaturalist 2023ao); **ON:** South of Ottawa (GBIF 2023k; iNaturalist 2023as); **QC:** Montreal (iNaturalist 2023au); **NB**: South of Moncton (BugGuide 2023v; iNaturalist 2023ap); **NS:** Widely distributed (iNaturalist 2023ar); **PEI**: Widely distributed (iNaturalist 2023at); **NL:** St. John's **(**iNaturalist 2023aq).

Canadian Habitat: On gravel beach under beach drift (Bousfield 1962), under rocks and logs in wooded areas (Wright 1995).

New collections: BC: Qualicum Beach, Parksville. **ON:** Port Hope.

New collections - Habitat: BC: From urban yard. **ON**: Under logs and bark by disturbed creek-side trail.

Origin: Native to Europe, introduced to North America (Van Name 1936; Hatch 1947; Lindroth 1957; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004). Van Name (1936) thought this species could have been introduced to North America via imported plants. This species and others are thought to have been introduced to Kejimkujik National Park, Nova Scotia via farming activity (Wright 1995).

(16) Platyarthridae: *Platyarthrus*: *Platyarthrus hoffmannseggii* Brandt, 1833

First Canadian Record: 2016, Chateauguay, QC (BugGuide 1309899).

Published Canadian distribution: No records.

Unpublished Canadian distribution: ON: Toronto, Mississauga, Kingston, Hamilton, Guelph, St. Thomas (iNaturalist 2023av); **QC:** Montreal, Québec City, Rimouski, Chateauguay (BugGuide 2023w; iNaturalist 2023aw).

Canadian Habitat: This species is found in association with ants (Harding and Sutton 1985). There are no published records of Canadian habitat for this species.

Origin: Introduced to North America, native to Europe, Africa, and Asia (Lindroth 1957; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004). Lindroth (1957) proposed that this species was introduced to North America via soil ballast in ships.

(17) Porcellionidae: *Porcellio*: *Porcellio dilatatus* Brandt, 1831

First Canadian Record: 1946, Burnaby, BC (Hatch 1947).

Published Canadian distribution: BC: Burnaby (Hatch 1947); **NS:** Sable Island (Bousfield 1970); **NL:** Corner Brook, St. John's (Palmén 1951).

Unpublished Canadian distribution: No records.

Canadian Habitat: In greenhouses (Hatch 1947; Palmén 1951), near railway stations (Palmén 1951).

New collections: AB: St. Albert.

New collections - Habitat: AB: In a greenhouse under boards and buckets resting on a mix of damp soil and gravel.

Origin: Native to Europe, introduced to North America (Hatch 1947; Lindroth 1957; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004).

(18) Porcellionidae: *Porcellio*: *Porcellio laevis* Latreille, 1804

Several Canadian records of this species are questionable. Thompson (1932) identified a species from Ontario as "probably" *P. laevis*, but no illustrations or additional notes are provided to confirm the identification. It is not possible to tell what characteristics were used to identify the *P. laevis* that Dexter *et al*. (1988) record from Ontario, as the cited key (Hatchett 1947) does not include *P. laevis,* and additional literature used to identify collected sowbugs is not cited. The authors state that the *P. laevis* specimens were missing at the time the article was written. Unpublished records are also doubtful: the GBIF record of *P. laevis* from Nova Scotia does not include a photograph of the specimen (GBIF 1317217230), and a single iNaturalist record of *P. laevis* from New Brunswick is indistinct, so it is difficult to be certain about this identification (iNaturalist 180828685). However, the collections by Belaoussoff *et al*. (1998) from Ontario likely do represent *P. laevis*, as the authors created a key that mentions the characteristically smooth dorsal surface of this species.

First Canadian Record: 1927, Nova Scotia (GBIF 1317217230).

Published Canadian distribution: ON: Big Chicken Island (Dexter *et al.* 1988), Brantford (Thompson 1932), Ayr, Drumbo (Belaoussoff *et al*. 1998).

Walker (1927) searched for sowbugs in British Columbia, New Brunswick, Ontario, and Québec, but was unable to find *P. laevis* despite specifically searching for it. Van Name (1936) did not know of any Canadian records of this species.

Unpublished Canadian distribution: NB: Dunlop (iNaturalist 2023ax); **NS**: Locality not specified (GBIF 2023c).

Canadian Habitat: In corn, soy, and wheat fields (Belaoussoff *et al*. 1998). Thompson (1932) documented an enormous population of sowbugs in Ontario associated with a garbage dump and basements; however, the identification of these species as *P. laevis* is questionable (see above). The GBIF record from Nova Scotia (GBIF 1317217230) is recorded on an accession card from the Smithsonian National Museum of Natural History which says the specimens were found "in soil about roots of plants", as a transfer associated with the "Fed. Hort. Bd" (presumably referring to the Federal Horticulture Board). The card also includes the note "Boston #3655". Possibly the specimens were recovered from a shipment of plants between Boston and Nova Scotia, but it is not clear which location represents the receiving end.

Origin: Native to Europe and Northern Africa, introduced to North America (Van Name 1936; Hatch 1947; Lindroth 1957; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004). Human-mediated dispersal to new areas via plant shipment has been documented (see above).

(19) Porcellionidae: *Porcellio*: *Porcellio scaber* Latreille, 1804

= *Asellus groenlandicus* Kroter

(Packard 1867)

First Canadian Record: 1859, Gulf of Georgia, BC (GBIF 699124508).

Published Canadian distribution: BC: Coastal (Fee 1926; Spencer 1942), Departure Bay (Walker 1927), Victoria (Richardson 1905; Walker 1927; Arcangeli 1932; Hatch 1947), Agassiz (Arcangeli 1932; Hatch 1947), Goldstream (Hatch 1939), Fraser Valley (Spencer 1942), Burnaby, North Vancouver, Haida Gwaii, Salmon Arm, Langley Prairie (Hatch 1947), Sooke (Hatch 1947; Arcangeli 1932), Vancouver (Hatch 1947; Edney 1964; Taylor and Carefoot 1993), Salt Air, Enderby, Peachlands (Edney 1964), Comox, Taylor Bay, Gabriola Island (Richardson 1905); **ON:** Niagara (Stuxberg 1876; Underwood 1886), Toronto (Walker 1927; Bhella *et al*. 2006), Belleville, Long Point (Walker 1927), London (Judd 1965), Ottawa (Rafi and Thurston 1982); Lake Erie (Dexter *et al.* 1988), Ayr, Drumbo (Belaoussoff *et al*. 1998); **QC:** Magdalen Islands (Richardson 1905), Anticosti Island (Johansen 1924); **NB:** Widely distributed (Wallace 1919), St. Andrews (Walker 1927); **NS:** Cape Breton Island (Richardson 1905), Bay of Fundy, Truro (Johansen 1929), Moosehead, Poulamon, Black Rock, Big Pond, North Pond, Mabou (Bousfield 1956b), West Light, Sable Island (Bousfield 1970; Wright 1989), Kejimkujik National Park (Wright 1995); **PEI:** Tyne Valley (Johansen 1929); **NL:** Grand Manan (Richardson 1905), St. John's (Johansen 1926; Palmén 1951), Biscay Bay, Brigus Junction, Burgeo, Cape Broyle, Codroy Pond, Come by Chance, Corner Brook, Cow Head, Curling, Deer Lake, Eddie's Cove, Gambo, Gaultois, Glenburnie, Grand Bruit, Grand Falls, Hare Bay, Holyrood, Kippen's River, Kitty's Brook, Lomond, Millertown, Norris Arm, Pass Island, Placentia, Port Aux Basques, Port Saunders, Portugal Cove, Pushthrough, Ramea Island, Rencontre West, Renews, Rose Blanche,

South Branch, Spaniard's Bay, Spruce Brook, St. Albans, St. David's, Steady Brook, Stephenville, Trepassey, Villa Marie, Waterford Bridge, Whitbourne, Woody Point (Palmén 1951), Hopedale, Square Islands (Packard 1867), Salmonier (Avalon Peninsula), Campbell's Creek, Witless Bay, Salmon Cove, Mortier (Bousfield 1956b), Piccadilly (Palmén 1951; Bousfield 1956b).

This species was absent from Prince Rupert, British Columbia in 1927 (Walker 1927). In 1949 it was absent from the following localities in Newfoundland: Daniels Harbor, Port au Choix, and north of Eddie's Cove (Palmén 1951).

Unpublished Canadian distribution: BC: South of Prince Rupert, most records south of Kamloops (BugGuide 2023x; GBIF 2023c; iNaturalist 2023az); **AB:** Edmonton, Calgary (iNaturalist 2023ay; Cit. Sci.); **MB:** Winnipeg (iNaturalist 2023ba); **ON:** South of Thunder Bay, most records south of Sudbury (BugGuide 2023aa; GBIF 2023c; iNaturalist 2023be); **QC:** South of Sept-Iles, mostly along the St. Lawrence River (iNaturalist 2023bg); **NB**: Most records south of Fredericton except Edmundston, Kouchibouguac, and Petite-Aldouane (BugGuide 2023y; GBIF 2023c; iNaturalist 2023bb); **NS:** Widely distributed (GBIF 2023c; iNaturalist 2023bd); **PEI:** Widely distributed (GBIF 2023c; iNaturalist 2023bf); **NL:** Limited to the east coast, except Norris Point and Rocky Harbour (BugGuide 2023z; GBIF 2023c; iNaturalist 2023bc).

Canadian Habitat: Found in a wide variety of urban and natural habitats. This species has been recorded from greenhouses (Spencer 1942; Hatch 1947; Judd 1965); in gardens and yards (Judd 1965; Rafi and Thurston 1982); associated with buildings (Spencer 1942; Palmén 1951; Judd 1965; Taylor and Carefoot 1993); in garbage dumps (Judd 1965); in compost heaps (Bhella *et al*. 2006); under boards (Judd 1965; Wright 1989; Taylor and

Carefoot 1993); on shorelines (Richardson 1905); under driftwood (Wallace 1919; Walker 1927), stones, and dried seaweed (Bousfield 1956b); in decayed wood and under logs (Johansen 1924; Wright 1995); under stones (Packard 1867; Johansen 1924; Wright 1995); in decayed leaves (Fee 1926; Rafi and Thurston 1982; Taylor and Carefoot 1993); by marshes (Walker 1927); by lakes (Wright 1995); in woods (Palmén 1951; Wright 1995); beside streams (Palmén 1951); in fields of wheat and soy (Belaoussoff *et al*. 1998).

New collections: BC: Prince George, Vancouver, Sechelt, Parksville, Qualicum Beach, Bamfield; Port Clements, Masset (Strickland; this study); **AB:** Edmonton; **NL:** Channel-Port aux Basques, Blomidon Nature Trail, Notre Dame Provincial Park, Traytown, Lockston Path Provincial Park, Trinity, Fortune, Burgeo, St John's, Corner Brook, Lumsden.

New collections - Habitat: BC: In urban areas in yards and under rotting logs, planters, and pots; under a wooden board on mulch in a small backyard greenhouse; **AB:** In urban areas under rocks, plastic containers, bricks, cinderblocks, wood debris and concrete rubble, and in mulch; under cinderblocks in the vicinity of greenhouses; inside greenhouses under rocks on soil and pots on gravel, and on moss by an artificial waterfall; in a bathroom sink inside a building; **NL:** Under rocks in a disturbed open area; by roadsides; along trails; in fields; beside forests; in conifer and mixed forests, under detritus on sandy coastal beach.

Origin: Usually considered to be of European origin and introduced to North America (Van Name 1936; Hatch 1947; Lindroth 1957; Vandel 1962; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004). *Porcellio*

scaber has been introduced to new localities via shipments of building supplies (Slabber and Chown 2002). This species and others are thought to have been introduced to Kejimkujik National Park, Nova Scotia through farming activity (Wright 1995).

Some have argued that a subspecies of *Porcellio scaber* is native to North America. After noting morphological differences between European and North American west coast populations, Arcangeli (1932) named the North American population *P. scaber americanus* and suggested it was native to North America because the specimens had been collected far from human habitation. Hatch (1947) agreed with this assessment, noted that the name *P. scaber niger* Say had priority over *P. scaber americanus*, and added additional records that extended its distribution to the east coast of North America. Hatch did not disagree with the designation of a separate North American subspecies, but noted that drawings of *P. scaber niger* from California (Miller 1936) differed from Arcangeli (1932) and that there was substantial variation in the characteristics used to differentiate North American and European populations. Palmén (1951) came to a different conclusion: after examining *P. scaber* from Newfoundland and Europe and noting the variability in the characteristics separating *P. scaber niger* from European populations, he suggested that the differences between the two had been exaggerated and recommended further study. Vandel (1962) stated that *P. scaber niger* (= *P. scaber americanus*) was not a valid subspecies because the characters used to differentiate it represented normal variation within *P. scaber*, and believed that the North American populations of *P. scaber* were non-native. Most recently, Song (2020) noted that morphological differences between six subspecies of *P. scaber,* including *P. scaber americanus*, represent differences in age rather than subspecific differences. Song

concluded that all subspecies of *P. scaber* are synonymous after failing to find COI differences among South Korean populations of *P. scaber* (including individuals with differing morphology similar to that seen in *P. scaber* subspecies) and noting that COI sequences from *P. scaber* collected worldwide did not form geographically distinct clades. Comparison of genomic data between North American and European populations of *P. scaber* would provide additional insight into the question of whether there is a cryptic native species or subspecies of *P. scaber* in North America.

Note: *Porcellio scaber* typically exhibits dark grey, reddish, or light brown pigmentation, but three bright orange individuals (2 males, 1 female) were present in a population in British Columbia in collections made for this study (Appendix A Fig. A7). Orange individuals of *P. scaber* have been documented previously (George 1986; Bhella *et al*. 2006) and are also kept as pets (Smug Bug 2021).

(20) Porcellionidae: *Porcellio*: *Porcellio spinicornis* Say, 1818

= *Porcellio pictus* Brandt, 1833

(Stuxberg 1876; Underwood 1886)

First Canadian Record: 1876, Niagara, ON (Stuxberg 1876).

Published Canadian distribution: AB: Edmonton (Stormer and Proctor 2022); **ON:** Niagara (Stuxberg 1876; Underwood 1886; Richardson 1905), Ottawa (Johansen 1926; Rafi and Thurston 1982), Toronto (Walker 1927; Mcqueen 1976), Belleville, Humber Valley (Walker 1927), London (Judd 1965), Lake Erie (Dexter *et al.* 1988), Copper Cliff,

Little Current (Alikhan 1995); **QC:** Hemmingford (Walker 1927), Montreal (Orstan *et al.* 2008); **NS:** Kejimkujik National Park (Wright 1995).

Unpublished Canadian distribution: BC: Fairmont Hot Springs, Invermere, Salmon Arm, Kamloops, Fort St. John (iNaturalist 2023bi); **AB:** Fort McMurray, High Level, McLennan and Fort Vermillion, and scattered distribution south of Grande Prairie (BugGuide 2023ab; GBIF 2023c; iNaturalist 2023bh; Cit. Sci.); **SK:** Scattered distribution south of Spiritwood (BugGuide 2023ag; iNaturalist 2023bp); **MB:** Thompson and south of Riding Mountain National Park (BugGuide 2023ac; iNaturalist 2023bj); **ON:** Broadly distributed south of Sudbury, with scattered records as far north as Sioux Lookout (BugGuide 2023ae; GBIF 2023c; iNaturalist 2023bm); **QC:** South of Rivière-du-Loup mostly along the St. Lawrence River, but with records from Ville-Marie, Rouyn-Noranda, and Grand-Remous (BugGuide 2023af; GBIF 2023c; iNaturalist 2023bo); **NB:** Miramichi, Fredericton, Sussex, Hampton, Chamcook, Oak Bay, Saint Stephen (iNaturalist 2023bk); **NS:** Antigonish, Halifax, Windsor (iNaturalist 2023bl); **PEI:** Charlottetown (iNaturalist 2023bn); **NT:** Hay River (BugGuide 2023ad).

Canadian Habitat: Associated with buildings, yards, and lawns (Walker 1927; Judd 1965; Mcqueen 1976; Rafi and Thurston 1982; Orstan *et al.* 2008); in city gardens and in greenhouses (Rafi and Thurston 1982); in woods near urban areas (Alikhan 1995); under rocks and bricks (Walker 1927; Rafi and Thurston 1982); under boards (Mcqueen 1976); under leaves (Rafi and Thurston 1982); in garbage dumps and on golfing greens; by marshes (Judd 1965); in wooded areas and river banks (Judd 1965); under rocks on lake shores (Wright 1995); in dry areas (Dexter *et al.* 1988).

New collections: AB: Edmonton, Sherwood Park, St. Albert, Drumheller, Taber, Calgary, Pigeon Lake, Canmore, Claresholm, Crowsnest, Lethbridge, Coaldale (Strickland; this study); **SK:** Regina; **ON:** Port Hope.

New collections - Habitat: AB: In urban areas in mulch, gravel, compost piles, leaf piles, and soil piles; in urban areas under boards, pots, rocks, paving stones, concrete steps, metal parking signs, logs, bricks, and concrete rubble; by ponds in urban areas; under rocks on soil and on coniferous needles in urban gardens; in urban yards; crawling on sidewalks, brick walkways and wooden fences in urban areas; on floors inside buildings (including upper floors of condominiums and public buildings); in sinks; in damp places in basements; in heated garages, by walls outside buildings; under pots on an upper-floor apartment deck; in greenhouses under pots sitting on damp gravel concrete and landscape fabric, in gravel, and under concrete on mulch; in gravel in the vicinity of greenhouses; under large rocks in landscaping around cottage; **SK:** On floor inside building in urban area; **ON**: Under bricks bordering urban garden bed; under logs and bark by disturbed creek-side trail.

Origin: Native to Europe, introduced to North America (Van Name 1936; Hatch 1947; Lindroth 1957; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004). One population in Toronto, Ontario is assumed to have arrived in a shipment of gravel (Mcqueen 1976). This species and others are thought to have been introduced to Kejimkujik National Park, Nova Scotia through farming activity (Wright 1995).

(21) Porcellionidae: *Porcellionides*: *Porcellionides pruinosus* (Brandt, 1833)

= *Metoponorthus pruinosus* (Brandt, 1833)

(Walker 1927; Alikhan 1995; Belaoussoff *et al*. 1998)

Porcellionides 'pruinosus' represents a complex of several morphologically indistinguishable species (Lefebvre and Marcadé 2005; Delhoumi *et al*. 2019). Another species of *Porcellionides* occurs in North America: *Porcellionides floria* Garthwaite and Sassaman 1985. It is found in southern North America, including the southern United States and Mexico (Garthwaite and Sassaman 1985) and is highly morphologically similar to *P. pruinosus.* Characteristics that may differentiate it from *P. pruinosus* without use of an electron microscope include a smoother dorsal surface, flagellar articles that are more equal in length (although the ratio changes with age), and less distinct white bands on the antennae, but 10% of *Porcellionides* specimens examined were unidentifiable with these characteristics (Garthwaite and Sassaman 1985). As the northernmost published distribution of *P. floria* is southern California (Garthwaite and Sassaman 1985), all records of *Porcellionides* from Canada are likely to be a species other than *P. floria.* Therefore, iNaturalist records of sowbugs from Saskatchewan identified as *Porcellionides* sp. (iNaturalist 2023bq) are included here as *Porcellionides pruinosus*, s. lat.

First Canadian Record: 1924, De Grassi Point, ON (Walker 1927).

Published Canadian distribution: BC: Coastal (Austin 1985), Lytton (Hatch 1947); **ON:** De Grassi Point (Walker 1927), London (Judd 1965), Ottawa (Rafi and Thurston

1982), Lake Erie (Dexter *et al.* 1988), Ayr, Drumbo (Belaoussoff *et al*. 1998), Copper Cliff, Little Current (Alikhan 1995).

Unpublished Canadian distribution: BC: Coldstream, Kamloops (general area) (BugGuide 2023ah; iNaturalist 2023bs); **AB:** Edmonton, Calgary (iNaturalist 2023br); **SK:** Saskatoon (iNaturalist 2023bx); **MB:** Winnipeg (iNaturalist 2023bt); **ON:** South of Ottawa (iNaturalist 2023bv); **NS:** Wallace Bay (iNaturalist 2023bu); **QC:** Montreal (iNaturalist 2023bw).

Canadian Habitat: In manure (Walker 1927); in garbage dumps; in greenhouses; in fields; on river banks; in woods (Judd 1965); associated with buildings; under leaves; under stones; in gardens (Rafi and Thurston 1982); on shorelines (Austin 1985); in fields of corn, soy, and wheat (Belaoussoff *et al*. 1998); in woods near urban areas (Alikhan 1995).

New collections: AB: Drumheller.

New collections - Habitat: AB: In a residential area.

Origin: Native to the Mediterranean region, introduced to North America (Van Name 1936; Hatch 1947; Lindroth 1957; Vandel 1962; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004), but see note above.

(22) Trachelipodidae: *Nagurus*: *Nagurus cristatus* (Dollfus, 1889)

First Canadian Record: 2022, Edmonton, AB (Stormer and Proctor 2022).

Published Canadian Distribution: AB: Edmonton (Stormer and Proctor 2022).

Unpublished Canadian Distribution: No records.

Canadian Habitat: In a greenhouse under pots sitting on damp gravel.

Origin: Native to southeast Asia (Leistikow and Wägele 1999) but found worldwide, including the southern United States (Johnson 1986; Jass and Klausmeier 2000; iNaturalist 2023by). There are multiple records of this species from greenhouses in Europe (Shaw 1948; Holthuis 1949; Soesbergen 2003; Gregory 2014; De Smedt *et al*. 2017; Gregory and Lugg 2018). Its presence in a greenhouse in Edmonton can probably be attributed to introduction via potted plants or other gardening supplies.

(23) Trachelipodidae: *Trachelipus*: *Trachelipus rathkii* (Brandt, 1833)

= *Porcellio trilineatus* Koch, 1841

(Stuxberg 1876; Underwood 1886)

= *Porcellio rathkei* [sic]

(Pearse 1913; Johansen 1926, 1929; Walker 1927; Spencer 1942; Judd 1961)

= *Tracheoniscus rathkii* (Brandt, 1833)

(Judd 1963, 1965; Bousfield 1970)

= *Trachelipus rathkei* [sic]

(Hatch 1947; Palmén 1951; Bousfield 1956a; Rafi and Thurston 1982; Dexter *et al.* 1988; Rapp 1988; Wright 1989)

First Canadian Record: 1876, Niagara, ON (Stuxberg 1876).

Published Canadian distribution: BC: Vancouver (Spencer 1942; Hatch 1947), Salmon Arm, Shuswap Lake (Hatch 1947); **AB:** Edmonton (Li 2022); **ON:** Southern ON (Rapp 1988), London (Judd 1963, 1965), Niagara (Stuxberg 1876), Tondern Island (Pearse

1913), Ottawa (Johansen 1926; Rafi and Thurston 1982), St. Joseph Island (Johansen 1926), Credit River, Barrie, Belleville, Brockville, Camperdown, Galt, Long Point, Ottawa, Sparrow Lake, De Grassi Point (Walker 1927), Toronto (Walker 1927; Carnio 1974), Fanshawe Lake (Judd 1961) Lake Erie (Dexter *et al.* 1988), Ayr, Drumbo (Belaoussoff *et al*. 1998); **QC:** Québec City (Johansen 1926), Covey Hill, Montreal, Eastman, Hemmingford (Walker 1927); **NB:** St. Andrews (Wallace 1919; Walker 1927), Fredericton (Wallace 1919), Campobello Island (Walker 1927), Chatham, Shediac (Johansen 1929), Hunts Point Beach (Bousfield 1956a); **NS:** Sydney (Walker 1927), Halifax (Johansen 1929; Hatch 1947), Truro, Little Lake, Pictou, Pugwash, Scott Bay, Avonport (Johansen 1929), Sable Island (Bousfield 1970; Wright 1989), West Light (Bousfield 1970), Kejimkujik National Park (Wright 1995); **PEI:** Tyne Valley (Johansen 1929); **NL:** Holyrood, St. John's, Whitbourne (Palmén 1951).

In 1927 this species was absent from Lake Nipigon in Ontario, Lake Abitibi (province not specified, but would be either Ontario or Quebec) and Godbout, Québec (Walker 1927).

Unpublished Canadian distribution: BC: Cooper Creek, Kelowna, Lee Creek, Marble Canyon Provincial Park, Ten Mile Lake (iNaturalist 2023ca); **AB:** Edmonton, Calgary, Lethbridge, Medicine Hat (BugGuide 2023ai; iNaturalist 2023bz; Cit. Sci.); **MB:** Winnipeg, Selkirk, Falcon Lake (iNaturalist 2023cb); **ON:** Most records south of Sudbury, with scattered records extending as far north as Dryden (BugGuide 2023aj; GBIF 2023a; iNaturalist 2023ce); **QC:** South of Mont-Joli along the St. Lawrence River, but also with records from Ville-Marie, Notre-Dame-du-Nord, Rouyn-Noranda, and Chibougamau (BugGuide 2023ak; GBIF 2023a; iNaturalist 2023cg); **NB:** Bathurst, Caraquet, Betrand, Fredericton, Stewarton, New Bandon, Sackville, Etsey's Bridge,

Meadow Brook, Tracy, Oromocto, Mactaquac (iNaturalist 2023cc); **NS:** Halifax, Baddeck Bay, Chelsea, Bedford, Cole Harbour, Wolfville, Stellarton, Cape Breton Island, Truro, Forbes Point, McKay Section (iNaturalist 2023cd); **PEI:** Coleman, Springton, Corraville (iNaturalist 2023cf).

Canadian Habitat: In city gardens (Johansen 1929); in greenhouses; on lawns; on golfing greens (Judd 1965); associated with buildings (Palmén 1951) and inside buildings (Spencer 1942); in garbage dumps (Palmén 1951; Judd 1965; Rafi and Thurston 1982); in water reservoirs (Johansen 1929); under boards (Palmén 1951; Bousfield 1970; Wright 1989); under stones (Palmén 1951; Rafi and Thurston 1982; Wright 1995); under logs (Rafi and Thurston 1982; Wright 1989, 1995; Li 2022;); in leaf litter (Rafi and Thurston 1982; Wright 1995); in moss and lichens (Wright 1995); in fields (Palmén 1951; Judd 1965; Bousfield 1970; Rafi and Thurston 1982); in sand (Wallace 1919); on beaches (Bousfield 1956a); in woods (Wallace 1919; Judd 1963, 1965; Rafi and Thurston 1982; Rapp 1988; Wright 1995); in skunk cabbage (Judd 1961); on lake shores (Walker 1927; Judd 1965; Wright 1995); on river banks; in marshes (Judd 1965); in bogs (Judd 1963, 1965); in corn, soy, and wheat fields (Belaoussoff *et al*. 1998).

Rapp (1988) noted that this species was present in oak woodlands in southern Ontario but absent from coniferous woods.

New collections: BC: Prince George; **AB:** Edmonton, Westerose, Pigeon Lake, Calgary, Taber, Lethbridge, Coaldale, intersection of Highways 5 and 6; **ON:** Port Hope; **NL:** Pasadena.

New collections - Habitat: BC: Under damp rotting logs; **AB:** In urban areas under mulch, concrete debris, rocks, pots, logs, bags of soil, and boards sitting on damp grass and soil; in urban yards; under logs in mixed forest trails associated with urban areas; on riverbanks and on paths next to lake shores; in piles of dirt and sand; under logs on wet leaves; in gravel and mulch next to buildings; by dried pond on prairie; in *Salix* and *Populus* groves on prairie; in the vicinity of greenhouses under pots and wooden debris sitting on grass and in leaf litter; in greenhouses under plastic flower pot holders; in a roadside ditch under fibreglass detritus; **ON:** Under logs and bark by disturbed creek-side trail; **NL:** In gravel and sand on river bank.

Origin: Native to Europe, introduced to North America (Van Name 1936; Hatch 1947; Lindroth 1957; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2000; Schmalfuss 2004). This species and others are thought to have been introduced to Kejimkujik National Park, Nova Scotia through farming activity (Wright 1995).

Note: This species typically exhibits a dark grey or orange-brown pigmentation with dark eyes, but a single depigmented individual with red eyes was present in a population in Edmonton, Alberta in collections made for this study (Appendix A Fig. A7). Albinism in typically pigmented species has been documented in the terrestrial isopod families Agnaridae, Armadillidae, Armadillidiidae, Philosciidae, and Porcellionidae (Johnson 1980; Roder and Linsenmair 1998; Bhella *et al*. 2006; Achouri and Charfi-Cheikhrouha 2009). There appear to be no published records of albinism in Trachelipodidae.

(24) Trichoniscidae: *Androniscus*: *Androniscus dentiger* Verhoeff, 1908

First Canadian Record: 1935, London, ON (Medcof 1939).

Published Canadian distribution: ON: London, Toronto (Medcof 1939); **QC:** Montreal (Medcof 1939); **NL:** St. John's (Palmén 1951).

Unpublished Canadian distribution: ON: Toronto (BugGuide 2023al; iNaturalist 2023ch); **NS:** Halifax (iNaturalist 2023ci).

Canadian Habitat: In greenhouses (Medcof 1939; Palmén 1951), in basements (Medcof 1939).

Origin: Native to Europe and North Africa, introduced to North America (Lindroth 1957; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004)**.** Medcof (1939) proposed that this species arrived in North America via transport of greenhouse plants from Europe.

(25) Trichoniscidae: *Haplophthalmus*: *Haplophthalmus danicus* Budde-Lund, 1880

= *Haplopthalmus* [sic] *danicus*
(Walker 1928)

The presence of this species in British Columbia is supported by a single iNaturalist record (iNaturalist 76388720), which appears to be *Haplophthalmus* based on its 'spear-shaped' uropods, tapered antennae flagella, flattened body shape, lack of a stepped outline between the pereion and pleon, and pale coloration (Hopkin 1991). Besides *Haplophthalmus danicus*, another *Haplophthalmus* also occurs in Canada:

Haplophthalmus mengii (Zaddach) (see below). The two can be distinguished by presence or absence of a pair of large tubercles on the third pleon segment, which are present in *H. mengii* (Hopkin 1991; McAlpine and Fairweather 2016). It appears these tubercles are absent in the individual photographed in British Columbia, and so this record likely represents *Haplophthalmus danicus*.

First Canadian Record: 1927, Humber Valley, ON (Walker 1928).

Published Canadian distribution: ON: Humber Valley (Walker 1928), London (Judd 1965), Toronto (Van Name 1936), Pelee Island (Dexter *et al.* 1988); **NL:** Cape Broyle, Holyrood, St. John's (Palmén 1951).

Unpublished Canadian distribution: BC: Delta (iNaturalist 2023cj); **ON:** Toronto, Kitchener, Port Franks, Mallorytown, Windsor (BugGuide 2023am; GBIF 2023m; iNaturalist 2023cm); **QC:** Montreal, Québec City (BugGuide 2023an; GBIF 2023m; iNaturalist 2023cn); **NB:** Bathurst (iNaturalist 2023ck); **NS:** Halifax (iNaturalist 2023cl).

Canadian Habitat: In greenhouses (Van Name 1936); associated with urban areas and gardens (Palmén 1951); near watercourses (Walker 1928; Palmén 1951); under stones in ravines (Walker 1928); in wet leaf litter (Palmén 1951; Judd 1965); in rotting wood (Dexter *et al.* 1988).

Origin: Native to Europe, introduced to North America (Van Name 1936; Lindroth 1957; Vandel 1960; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004). Lohmander (1927) records this species being

transported to North America via soil associated with the “roots of asparagus from Germany”.

(26) Trichoniscidae: *Haplophthalmus*: *Haplophthalmus mengii* (Zaddach, 1844)

An iNaturalist record from southern British Columbia (Chiliwack River Provincial Park) shows a species of *Haplophthalmus* that clearly has large tubercles on the third pleon segment (iNaturalist 92717693). This feature rules out *Haplophthalmus danicus*, which lacks these tubercles, but would be consistent with *Haplophthalmus mengii* (Hopkin 1991). However, *H. montivagus* Verhoeff also has large tubercles, and is indistinguishable from *H. danicus* without close examination of the pereiopods (Hopkin 1991). Collection of specimens from this site would make it possible to determine which species of *Haplophthalmus* occurs in this area.

First Canadian Record: 2012, Miramichi, NB (McAlpine and Fairweather 2016).

Published Canadian distribution: NB: Miramichi (McAlpine and Fairweather 2016).

Unpublished Canadian distribution: No records.

Canadian Habitat: On decayed wood buried in soil (McAlpine and Fairweather 2016).

Origin: Native to Europe (Vandel 1960; Harding and Sutton 1985; Schmalfuss 2004), introduced to North America. McAlpine and Fairweather (2016) hypothesized that this species was brought to the North America in the 1800s via ship ballast.

(27) Trichoniscidae: *Hyloniscus*: *Hyloniscus riparius* (Koch, 1838)

First Canadian Record: 1949, St. John’s, NL (Palmén 1951).

Published Canadian distribution: ON: Braeside (McApline and Oldham 2011), Lake Erie (Dexter *et al.* 1988); **NL:** St. John's (Palmén 1951).

Unpublished Canadian distribution: ON: Scattered records south of St. Joseph Island, with most records around Toronto (BugGuide 2023ao; GBIF 2023m; iNaturalist 2023cq); **QC:** Montreal, Québec City (BugGuide 2023ap; GBIF 2023m; iNaturalist 2023cr); **NB:** Fredericton (iNaturalist 2023co); **NS:** Kentville (general area) (iNaturalist 2023cp).

Canadian Habitat: On shoreline (Dexter *et al.* 1988); on rocky plain (McApline and Oldham 2011); in city gardens and in greenhouses (Palmén 1951).

New collections: ON: Port Hope.

New collections - Habitat: ON: Under logs and bark by disturbed creek-side trail.

Origin: Native to Europe, introduced to North America (Lindroth 1957; Vandel 1960; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004).

(28) Trichoniscidae: *Trichoniscoides*: *Trichoniscoides sarsi* Patience, 1908

First Canadian Record: 1949, St John's, NL (Palmén 1951).

Published Canadian distribution: NL: Locality not specified (Muchmore 1990), St. John's (Palmén 1951).

Unpublished Canadian distribution: No records.

Canadian Habitat: Under rocks associated with urban areas (Palmén 1951; Muchmore 1990).

Origin: Native to Europe, introduced to North America (Lindroth 1957; Vandel 1960; Schmalfuss 2004; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001).

(29) Trichoniscidae: *Trichoniscus*: *Trichoniscus provisorius* Racovitza, 1908

The taxonomic status of "*T. provisorius*" is unclear. In the original description of the species, Racovitza (1908) noted that *T. provisorius* might be identical to *T. pusillus* Brandt, but was unable to determine if this was the case due to the vague original description of *T. pusillus*. Populations of *T. pusillus* are parthenogenic and produce males very rarely, while *T. provisorius* populations contain roughly equal numbers of males and females (Frankel *et al*. 1981). Palmén (1951) noted similarity between males of the two species but was unsure whether *T. provisorius* should be considered a subspecies of *T. pusillus*. Upon discovering that *T. pusillus* was triploid and *T. provisorius* was diploid , *T. provisorius* was proposed to be a subspecies of *T. pusillus* (Legrand *et al*. 1950). However, some preferred to use the term "form" rather than "subspecies" (Frankel *et al*. 1981; Harding and Sutton 1985), and others continued to use the name "*T. provisorius*" without listing it as a form or subspecies (Leistikow and Wägele 1999; Mattern 2003). In a global list of sowbug species, Schmalfuss (2004) elevated *T. pusillus provisorius* and three other subspecies of *T. pusillus* to species level. The basis for this taxonomic change is not clear, but may have been influenced by the discovery of high genetic divergences between subspecies of *T. pusillus* (Cobolli Sbordoni *et al*. 1997). Regardless, the change appears to have been accepted, as "*T. provisorius*" is now typically used instead of "*T. pusillus provisorius*" (Vilisics *et al*. 2011; De Smedt *et al*. 2016; Vittori and Štrus 2023).

For the purposes of this list I am considering *T. provisorius* and *T. pusillus* to be separate species.

First Canadian Record: 1949, St. John's, NL (Palmén 1951).

Published Canadian distribution: NL: St. John's, Holyrood (Palmén 1951).

Unpublished Canadian distribution: No records.

Canadian Habitat: Associated with urban areas, including on wet soil, in leaf litter, and by streams (Palmén 1951).

Origin: Native to Europe, parts of the Middle East and Northern Africa, and introduced to North America (Lindroth 1957; Vandel 1960; Harding and Sutton 1985; Jass and Klausmeier 2001; Schmalfuss 2004).

(30) Trichoniscidae: *Trichoniscus*: *Trichoniscus pusillus* Brandt, 1833

= *Trichoniscus pusilus* [sic]

(Rafi and Thurston 1982)

= *Trichoniscus demivirgo* Blake, 1931

(Van Name 1936; Hatch 1949; Judd 1965)

Species in the genus *Trichoniscus* can be distinguished by male pleopod morphology. It was initially impossible to tell if North American populations of this genus were identical with European *T. pusillus* because no male specimens had been found, and so the name *Trichoniscus demivirgo* Blake was used for North American specimens (Lohmander 1927; Hatch 1947; Palmén 1951). Later, Palmén (1951) found male *Trichoniscus* in

Newfoundland. Upon morphological comparison with male *T. pusillus* from Europe he concluded the two were identical and that *T. demivirgo* was likely a synonym of *T. pusillus*. Since comparison to European *Trichoniscus* has only taken place for Newfoundland specimens, it is possible that "*T. demivirgo*" from other parts of North America may differ from *T. pusillus*. However, for the purposes of my list, all records of *T. demivirgo* from Canada are considered *T. pusillus* rather than *T. demivirgo*.

First Canadian Record: 1876, Niagara, ON (Stuxberg 1876).

Published Canadian distribution: BC: North Vancouver (Hatch 1949); **ON:** Niagara (Stuxberg 1876; Underwood 1886), Toronto, De Grassi Point (Walker 1927), London (Judd 1965), Ottawa (Rafi and Thurston 1982); **NB:** St. Andrews (Walker 1927); **NS:** Halifax (Van Name 1936), Fourchu, Black Rock Point, North Pond (Bousfield 1956b), Kejimkujik National Park (Wright 1995); **NL:** Biscay Bay, Burgeo, Cape Broyle, Cook's Brook, Corner Brook, Cow Head, Crabbs River, Deer Lake, Englee, Glenburnie, Hare Bay, Kitty's Brook, Lomond, Norris Arm, Picadilly, Port au Choix, Port aux Basques, Port Saunders, Recontre West, Rose Blanche, South Branch, Spruce Brook, St. Albans, St. John Island, St. John's, Stephenville, Waterford Bridge, Woody Point (Palmén 1951), Campell's Creek Cove (Bousfield 1956b).

Unpublished Canadian distribution: BC: China Beach, North Vancouver, Grice Bay, Pender Island (GBIF 2023m; iNaturalist 2023cs); **ON:** Scattered records south of Tobermory (GBIF 2023m; iNaturalist 2023cu); **QC:** Québec City, Sainte-Madeleine-de-la-Rivière-Madeleine, Saint-Raymond (GBIF 2023m; iNaturalist 2023cv); **NS:** Hermans Island, Lomond, Cape Breton Highlands National Park (GBIF 2023m); **NL**: Gros Morne National Park (GBIF 2023m; iNaturalist 2023ct).

Canadian Habitat: In greenhouses (Van Name 1936; Judd 1965; Rafi and Thurston 1982) and outside greenhouses (Hatch 1947); in gardens; associated with buildings and railway stations; in graveyards (Palmén 1951); in garbage dumps; on golfing greens (Judd 1965); under rocks (Walker 1927; Palmén 1951; Bousfield 1956b); in leaves (Walker 1927; Palmén 1951; Rafi and Thurston 1982; Wright 1995); in moss (Palmén 1951); under logs (Walker 1927; Palmén 1951); associated with streams (Walker 1927; Palmén 1951; Judd 1965), springs (Palmén 1951), creeks (Walker 1927; Judd 1965), ponds, rivers (Palmén 1951; Judd 1965), and lakes (Walker 1927; Judd 1965; Wright 1995); in woods (Walker 1927; Palmén 1951; Judd 1965; Rafi and Thurston 1982; Wright 1995); under boards (Bousfield 1956b); in marshes; on wet soil; in wet fields (Palmén 1951; Judd 1965); on shorelines (Palmén 1951; Bousfield 1956b).

New collections: ON: Port Hope; **NL:** J.T. Cheeseman Provincial Park, Lockston Path Provincial Park, Butter Pot Provincial Park, La Manche Provincial Park.

New collections - Habitat: ON: Under logs and bark by disturbed creek-side trail; **NL:** In mixed and conifer forests.

Origin: Native to Europe, introduced to North America (Lindroth 1957; Harding and Sutton 1985; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004). Lohmander (1927) mentions this species being transported to North America via a plant shipment.

(31) Trichoniscidae: *Trichoniscus*: *Trichoniscus pygmaeus* Sars, 1898

First Canadian Record: 1949, St. John's, NL (Palmén 1951).

Published Canadian distribution: NL: St. John's, Port Saunders (Palmén 1951).

Unpublished Canadian distribution: ON: Welland, Hamilton (iNaturalist 2023cw).

Canadian Habitat: Associated with urban areas, including in gardens, in wet soil, and under boards (Palmén 1951).

Origin: Native to Europe, introduced to North America (Van Name 1936; Lindroth 1957; Harding and Sutton 1985; Vandel 1960; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004). Lohmander (1927) mentions transport of this species to North America via "lily bulbs" from Scotland.

Other Records of Interest

The following records lack strong support for the existence of a stable population in Canada and/or are not identified to species level.

(32) Alloniscidae: *Alloniscus*: *Alloniscus mirabilis* (Stuxberg, 1875)

This species is native to North America and is found along the southern west coast (Schultz 1984a; Leistikow and Wägele 1999; Jass and Klausmeier 2001; Schmalfuss 2004). One GBIF record lists this species from Vancouver Island, British Columbia (GBIF 1898260585), but there are no other records of this species north of California. The GBIF record may represent *Alloniscus perconvexus*, which is found in British Columbia (see previous section).

(33) Armadillidae: *Armadillo*: *Armadillo* sp.

A single GBIF record lists an "*Armadillo*" species recorded from British Columbia in 1890 (GBIF 1056464109). No specific locality is listed. All true *Armadillo* are found in tropical regions (Schmalfuss 2004). One "*Armadillo"* species, *Armadillo affinis* (Dana),

has been recorded from California, but it does not actually belong to the genus *Armadillo*, and the status of the name is unclear (Schmalfuss 2004). The GBIF record may be an error: the species is identified as "Oniscidea" in the original source for this record, and the genus listed in GBIF is noted as being "inferred". Possibly the transcriber intended to record this record as *Armadillidium* rather than *Armadillo*, as two *Armadillidium* species occur in British Columbia (see section above).

(34) Armadillidiidae: *Armadillidium*: *Armadillidium maculatum* (Risso 1816)

A video from Edmonton, Alberta submitted via the citizen science initiative for this study depicts a dark-colored sowbug with a convex body shape, truncated uropods, a smooth dorsal surface, and a thin bright white stripe running along the dorsal posterior edges of the pereion and pleon segments. This appearance is consistent with *Armadillidium maculatum* (Vandel 1962), which is a popular pet species (Jungle Jewel Exotics 2023). According to the participant who submitted the video, the individual from Edmonton was discovered next to a building under a rock, and only a single individual was found. *Armadillidium maculatum* is found along the Mediterranean coast of France and Italy (Vandel 1962; Schmalfuss 2004) and the only evidence of a wild population of this species in North America is an iNaturalist observation from Texas that might depict an individual in an outdoor environment (iNaturalist 193460958). The record from Edmonton likely represents a captive individual that had escaped or was released. There is currently no evidence to suggest that an established wild population of *A. maculatum* is present in Edmonton.

(35) Platyarthridae: *Trichorhina*: *Trichorhina* sp.

There are two GBIF records of this genus from 1992 in Montreal, Québec (GBIF 3045953335; GBIF 3045953331). Most *Trichorhina* species are found close to the equator (Schmalfuss 2004), but four are found in North America: *T. donaldsoni* Schultz, *T. heterophthalma* Lemos de Castro, *T. triocis* Mulaik and Mulaik, and *T. tomentosa* (Budde-Lund) (Jass and Klausmeier 2001; Schmalfuss 2004). Of these four, all can be found in the southern United States, and all except *T. tomentosa* are thought to be native to North America (Jass and Klausmeier 2001; Schmalfuss 2004). The species represented by the GBIF record would most likely be *Trichorhina tomentosa*, since this species has been widely spread and can be found in greenhouses in many parts of the world (Schmalfuss 2004; Gregory 2014). As there are no images associated with the GBIF record, it is not possible to confirm this identification.

The following genus level records are included here because they represent unusual collection localities or include other information of interest. Both genera contain multiple species that have been recorded from Canada.

(n/a) Porcellionidae: *Porcellio* sp.

One unpublished GBIF record of three individuals collected from the “Beaufort Sea”, NT (GBIF 1898322558). If the locality is correct, this would the northernmost sowbug record in all of North America. It is not clear if this record represents an established population or a temporary introduction (e.g. a few individuals introduced in the summer and discovered the same season).

(n/a) Trichoniscidae: *Trichoniscus* sp.

One unpublished GBIF record lists a collection of this genus from 1926 in what is now Nunavut, on the border with Manitoba (GBIF 1318364664). The record refers to a single specimen found “in soil used for *Dahlia* tubes packing”, as a transfer associated with the “Fed. Hort. Bd” (presumably referring to the Federal Horticulture Board). The card also includes the note “Chicago #371”. Possibly this refers to specimens recovered from a shipment of plants between Chicago and Nunavut, but it is not clear whether which location represents the destination. If the locality is correct, this record would represent the only sowbug recorded from Nunavut.

2.4. Discussion

Based on new collections in this study, postings on BugGuide and iNaturalist, reports from the citizen science initiative for this study, and my literature survey, at least 31 species and 9 families of sowbugs occur in Canada. Some are limited to the west coast: these include all Detonidae, *Littorophiloscia richardsonae* (Halophilosciidae), and all Ligiidae except *Ligia oceanica* and *Ligidium elrodii*. Other species are limited to the east coast: *Littorophiloscia vittata, Platyarthrus hoffmannseggii* (Platyarthridae)*, Porcellio laevis* (Porcellionidae)*,* the ligiids *Ligia oceanica* and *Ligidium elrodii,* and all Trichoniscidae except *Trichoniscus pusillus*. The remainder are found on both coasts, with varying distributions in Ontario, Québec, and the Prairie Provinces. Of the latter group, only *Porcellio spinicornis* appears to be widespread across Alberta, Saskatchewan, and Manitoba. It is surprising that other species common on both the east and west coasts are seemingly absent or uncommon in the Prairie Provinces (e.g. *Oniscus asellus, Porcellio scaber, Armadillidium vulgare*, *Cylisticus convexus*). However, it is difficult to draw conclusions about the apparently limited distribution of sowbugs in the Prairie Provinces for the following reasons: (1) many records in this area are from citizen science observations, which may favor large, conspicuous species (Caley *et al*. 2020); (2) most Canadian sowbug distribution data is presence-only (i.e. researchers rarely report searching for a particular species and not finding it, and many records originate from data generated by citizen scientists (iNaturalist and BugGuide); (3) focused investigations of sowbugs in this part of Canada are sparse - to my knowledge, the Prairie Provinces have never been surveyed for sowbugs aside from the present study. Additional surveys of this area, particularly targeting Saskatchewan and Manitoba, would help confirm which species are truly absent.

Of the 31 sowbug species in Canada, only nine are native to North America. The Canadian distribution of these species is limited to either the east coast (*Littorophiloscia vittata* and *Ligidium elrodii*) or west coast. Of the 22 non-native species, approximately two thirds (N=13) are found on both coasts. This is consistent with the observation that native North American sowbugs tend to occur on a single coast, but non-native species are found on both (Jass and Klausmeier 2000). The other eight non-native species are found only on the east coast, apart from *Nagurus cristatus,* which has only been reported from Alberta (present study).

The greater sowbug diversity in eastern Canada may reflect the longer history of European settlements in that region. All but one of the 22 non-native sowbugs that occur in Canada have a native range that includes Europe. Lindroth (1957) hypothesized that the thousands of tons of soil ballast brought from Europe to North America in the 1600-1800s played a major role in introducing new soil-associated species, and noted that ballast consisted not only of soil, but also of stones and bricks from demolitions in urban areas and gravel and sand from beaches. Ballast sources therefore covered a wide range of sowbug habitats and could have been the source of introduction for a variety of European species. There also appears to be a correlation between the extent of the Canadian distribution of a sowbug species and the date it was first recorded in Canada (Fig. A9). Of the 11 introduced species with the widest Canadian distribution, 10 have Canadian records dating prior to 1930: *Haplophthalmus danicus, Oniscus asellus, Cylisticus convexus, Porcellio spinicornis, Porcellio scaber, Porcellionides pruinosus, Trachelipus rathkii, Trichoniscus pusillus, Armadillidium nasatum,* and *Armadillidium vulgare*. The exception is *Philoscia muscorum*, for which the first Canadian record is 1958. All but *T. pusillus* and *H. danicus* are also among the 10 most common species in North America (Jass and Klausmeier 2000). These patterns could be the result of species with the earliest introductions

having had more time to disperse, which made them more common and more likely to be noticed and recorded. Alternatively, this pattern could simply be due to common species being noticed sooner regardless of date of introduction. The exception to the European origin of non-native Canadian sowbugs is *Nagurus cristatus*, which is native to southeast Asia (Leistikow and Wägele 1999). It is also found worldwide, including the southern United States (Johnson 1986; Jass and Klausmeier 2000; iNaturalist 2023by). Introduction of this species to Canada could have occurred secondarily from a North American locality, or directly from a southeastern Asian location.

Direct introduction of sowbugs via ship ballast would not have been possible in the land-locked provinces of Alberta and Saskatchewan. As sowbugs are generally assumed to be poor dispersers (Hornung 2011; Szlavecz *et al*. 2018; Dimitriou *et al*. 2022) it is unlikely that sowbugs in this area arrived via active dispersal from coastal populations into the interior of Canada. Instead, these populations may be the result of human-mediated introduction from the eastern and western coasts, and/or primary introductions directly from Europe. Sowbug transport could have been accidental (e.g. via shipments of landscaping and gardening materials, as stowaways in household belongings) or deliberate if they were imported as pets or as live pet food. Canadian Food Inspection Agency import records from 2015-2022 list only a single sowbug shipment consisting of 60 *Armadillidium* sp. sent from the United States to British Columbia in 2022 (CFIA 2022). The actual frequency of imports is likely higher, as these records only list shipments that had CFIA import authorization. Evidence of non-listed imports includes the fact that Alberta residents have kept ‘fancy’ sowbugs as pets prior to 2022, including selectively-bred forms as well as species not found in Canada (pers. obs. HP, HS). Molecular comparisons of European, coastal Canadian, and Prairie Province populations could

resolve the question of the origin of sowbugs in the Prairie Provinces (see Chapter 3 for an initial exploration of available molecular data for *P. spinicornis*).

The presence of sowbugs of European origin at high latitudes in the Prairie Provinces (Fig. 2.5, *Porcellio spinicornis*) raises the question of how these species can survive the winter. According to Wright (1997), sowbugs can live in regions with winter temperatures up to 40°C colder than their lethal limit by burrowing deeply in substrate or remaining next to heated buildings. If sowbugs in Canada survive winters by overwintering next to heated buildings (or even inside buildings), their distribution should be limited to urban areas. A sowbug survey with more extensive coverage of natural areas would determine whether this is the case. It is also possible that non-native sowbugs in Canda have undergone climatic adaptation. Further research investigating the current cold tolerance of sowbugs in Canada and comparing this data to similar studies on European populations of the same species may provide evidence of climate-associated selection and adaptation.

Although most sowbug species examined in this study yielded COI barcodes that matched closely with those from the species to which they belonged morphologically, this was not the case for *Nagurus cristatus*. COI barcodes from this species were dissimilar from those of congeneric and confamilial relatives when compared both as nucleotide sequences and as amino acid sequences, and the nucleotide sequences contained a lot of noise. These characteristics are associated with sequences that are nuclear mitochondrial pseudogenes (NUMTs) (Moulton *et al*. 2010). If so, the COI sequences obtained in this study are not the "true" sequences for this species, and this would represent the first record of an isopod NUMT, as NUMTs have not been recorded from this group (Raupach *et al.* 2022). However, the unusual placement of *N. cristatus* relative to other sowbug families based on its partial 18S sequence suggests that this species is in

fact considerably diverged from other Trachelipodidae. This raises the question of whether the COI sequences obtained in this study may actually represent the "true" sequences for this species, despite their dissimilarity to other sowbugs. In any case, the divergent 18S sequences obtained for *Nagurus cristatus* suggest this species may not belong in Trachelipodidae. Determining whether it belongs in Scyphacidae (as suggested by the 18S phylogeny) or in a new family would require detailed morphological examination and further molecular investigation that is beyond the scope of this study. Several of the other unusual placements of taxa in the 18S phylogeny are consistent with prior studies. *Levantoniscus* was originally described as Trachelipodidae (Cardoso *et al*. 2015) but was placed in Porcellionidae in the phylogeny (Fig. 2.4). The same placement also occurred a study that included sequences from several genes in addition to 18S (Dimitriou *et al*. 2018) and the authors suggested that the genus might belong to a new family rather than to Trachelipodidae or Porcellionidae. Similarly, *Porcellium* was placed in Cylisticidae instead of Trachelipodidae, but this placement also occurred in another 18S-based phylogeny (Mattern 2003) in which it was suggested that *Porcellium* does not belong to Trachelipodidae. The three other "misplacements" observed in the phylogeny (Philosciidae spp. with Platyarthridae; *Spherillo* spp. with *Tylos* instead of Armadillidae; *Trichorhina tomentosa* outside Platyarthridae) are difficult to explain, as the sequences involved were not noticeably shorter, less well-aligned, or less resolved than the other sequences.

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2.6. Tables and Figures

Table 2.1: Summary of the species of sowbugs (Isopoda: Oniscidea) reported from Canada. P = published record; U = unpublished record (iNaturalist, BugGuide, unpublished GBIF record); T = record from this study; ? = record is uncertain, see details in the Results; N = species is native to North America; IN = species is introduced to North America; * = the species identity associated with these records is unclear – see the main text for details; BC = British Columbia; AB = Alberta; SK = Saskatchewan; MB = Manitoba; ON = Ontario; QC = Québec; NB = New Brunswick; NS = Nova Scotia; PEI = Prince Edward Island, NL = Newfoundland and Labrador; NT = Northwest Territories; NU = Nunavut; YT = Yukon.

		Province/Territory (P = published record, U = unpublished record)												
Taxon	**Origin**	**BC**	**AB**	**SK**	**MB**	**ON**	**QC**	**NB**	**NS**	**PEI**	**NL**	**NT**	**NU**	**YT**
Alloniscus perconvexus Dana, 1854	N	P/U												
Armadillidium nasatum Budde-Lund, 1885	IN	P/U	T/U			P/U	P/U	U?	U					
Armadillidium vulgare (Latreille, 1804)	IN	T/P/U	T/U	U		P/U	P/U	U	U	U				
Cylisticus convexus (De Geer, 1778)	IN	P/U	T/U		U	T/P/U	P/U	P/U	P/U	U	T/P/U			
Armadilloniscus holmesi Arcangeli, 1933	N	P/U												
Detonella papillicornis (Richardson, 1904)	N	P/U												
Littorophiloscia richardsonae (Holmes & Gay, 1909)	N	P/U												
Littorophiloscia vittata (Say, 1818)	N								P/U					
Ligia occidentalis (Dana, 1853)*	N	U												
Ligia oceanica (Linnaeus, 1767)	IN	U?						U	P/U					
Ligia pallasii Brandt, 1833	N	P/U												
Ligidium elrodii (Packard, 1873)	N					P/U								
Ligidium gracile (Dana, 1854)	N	T/P/U												
Oniscus asellus Linnaeus, 1758	IN	T/P/U				P/U	P/U	P/U	P/U	U	T/P/U			
Philoscia muscorum (Scopoli, 1763)	IN	T/U				T/P?/U	U	U	P/U	U	U			
Platyarthrus hoffmannseggii Brandt, 1833	IN					U	U							

Porcellio dilatatus Brandt, 1831	IN	P	T						P		P			
Porcellio laevis Latreille, 1804	IN					P		U?	U?					
Porcellio scaber Latreille, 1804	IN	T/P/U	T/U		U	P/U	P/U	P/U	P/U	P/U	T/P/U			
Porcellio spinicornis Say, 1818	IN	U	T/U	T/U	U	T/P/U	P/U	U	P/U	U		U		
Porcellionides pruinosus (Brandt, 1833)	IN	P/U	T/U	U	U	P/U	U		U					
Nagurus cristatus (Dollfus, 1889)	IN		T											
Trachelipus rathkii (Brandt, 1833)	IN	T/P/U	T/P/U		U	T/P/U	P/U	P/U	P/U	P/U	T/P			
Androniscus dentiger Verhoeff, 1908	IN					P/U	P		U		P			
Haplophthalmus danicus Budde-Lund, 1880	IN	U?				P/U	U	U	U		P			
Haplophthalmus mengii (Zaddach, 1844)	IN	U?						P						
Hyloniscus riparius (Koch, 1838)	IN					T/P/U	U	U	U		P			
Trichoniscoides sarsi Patience, 1908	IN										P			
Trichoniscus provisorius / *Trichoniscus pusillus provisorius** Racovitza, 1908	IN										P			
Trichoniscus pusillus Brandt, 1833	IN	P/U				T/P/U	U	P	P/U		T/P/U			
Trichoniscus pygmaeus Sars, 1898	IN					U					P			
Doubtful Records – See main text for details														
Alloniscus mirabilis (Stuxberg, 1875)		U?												
Armadillo sp.		U?												
Armadillidium maculatum (Risso 1816)			U?											
Trichorhina sp.							U?							
Porcellio sp.												U?		
Trichoniscus sp.					U?								U?	

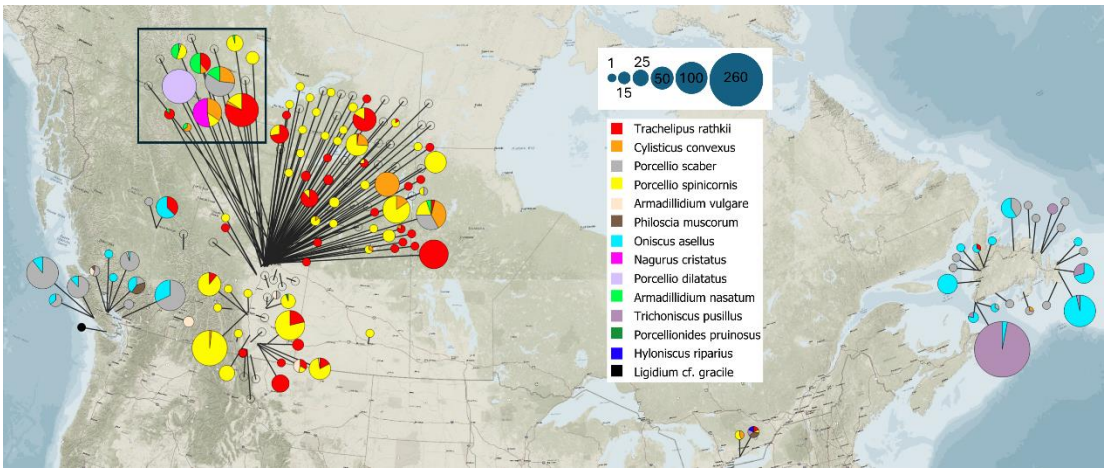


Figure 2.1: Sowbug species composition for sites in British Columbia, Alberta, Saskatchewan, Ontario, and Newfoundland where sowbugs were collected for this study. Each pie chart shows the species composition for a single collection event, with the size of the chart corresponding to the total number of sowbugs collected. Empty charts indicate localities where no sowbugs were found. The pie charts in the box show collections from greenhouses.

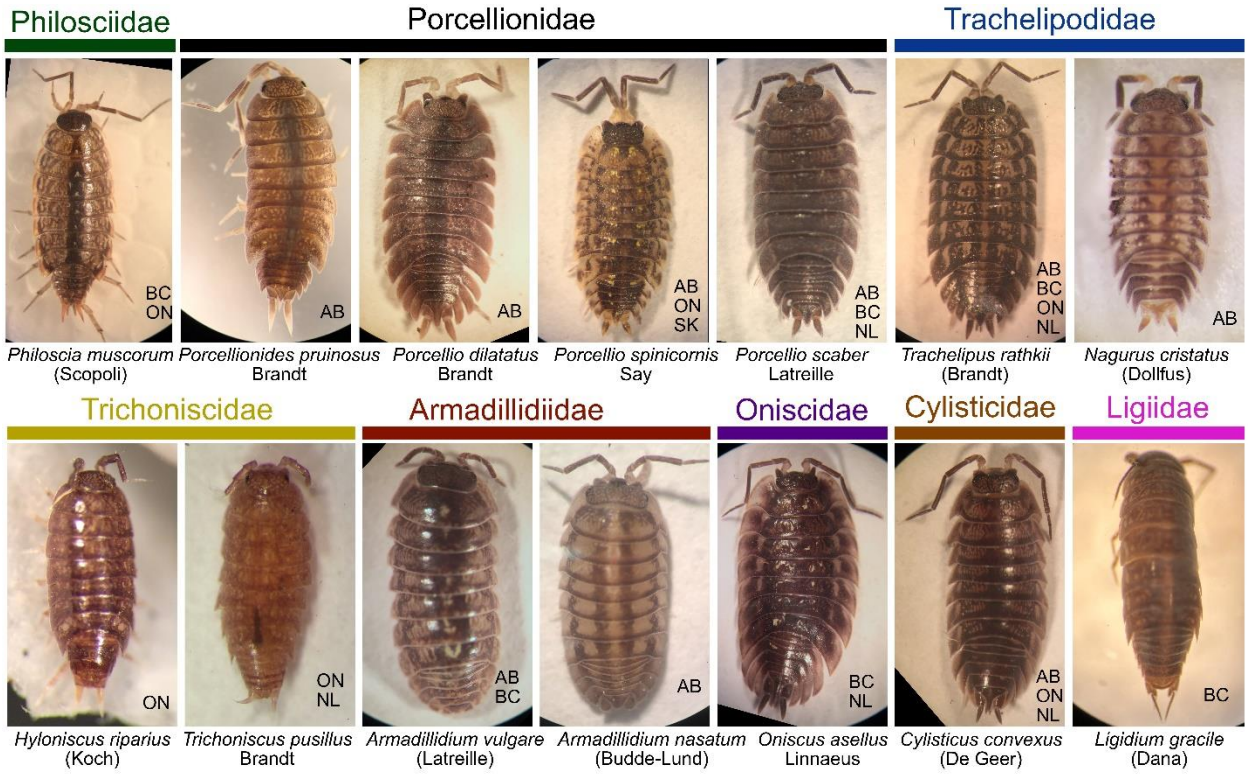
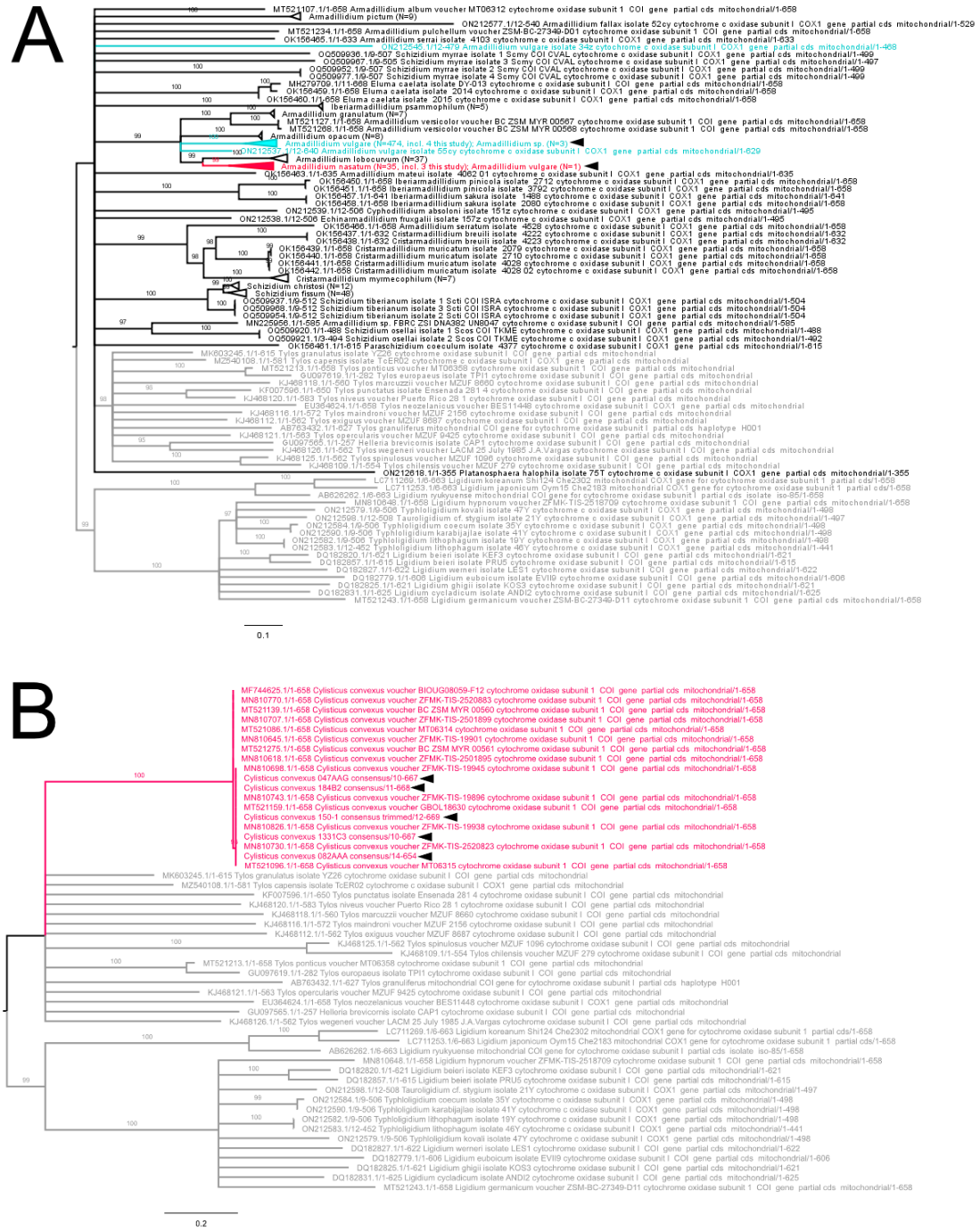
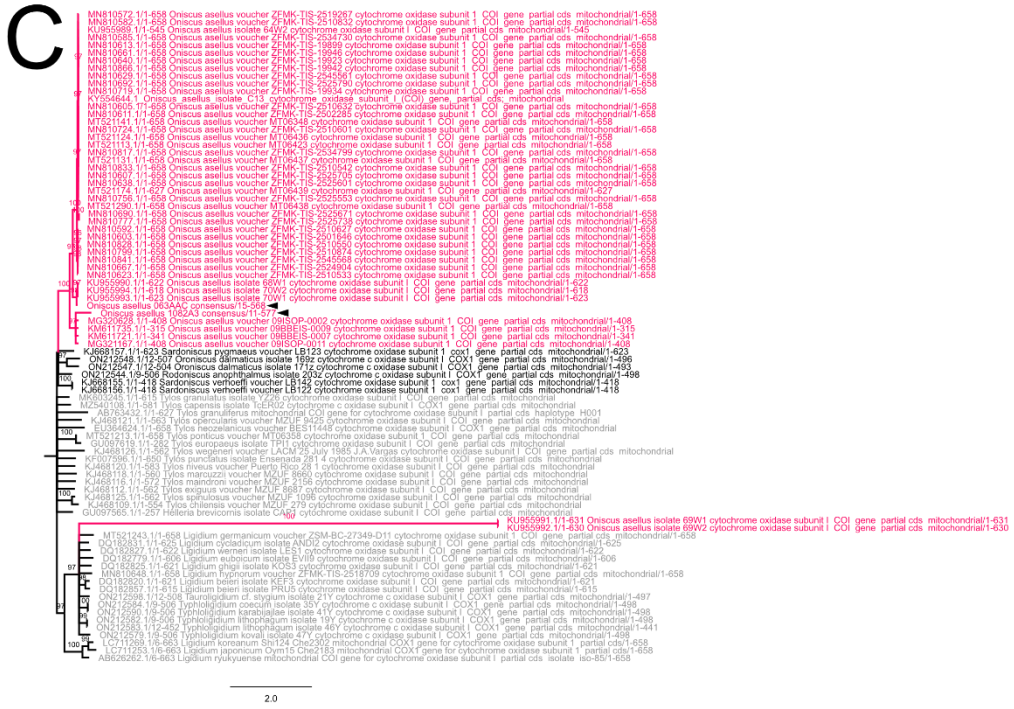


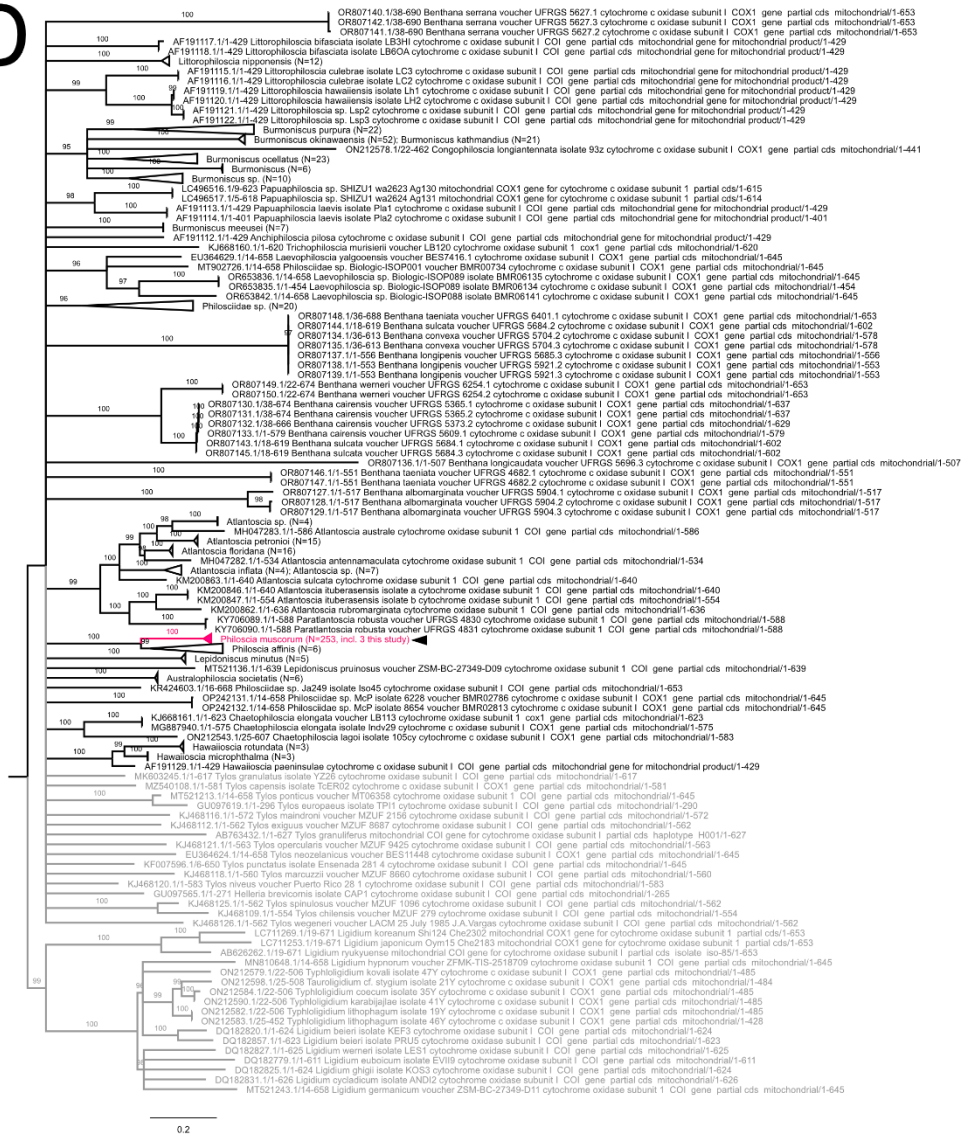
Figure 2.2: Sowbug species (Isopoda: Oniscidea) collected from Canada in this study. *Ligidium gracile* (Ligiidae) is missing both exopodites. Species are not shown to scale relative to each other. Provinces where each species was collected are listed in the lower right of each image. BC=British Columbia, AB=Alberta, SK=Saskatchewan, ON=Ontario, NL=Newfoundland and Labrador.

Figure 2.3 (next page)**:** Condensed maximum likelihood phylogenies for seven sowbug families built with COI barcode sequences. Zoom to see details. Large clades are collapsed and are indicated by triangles; for full trees, see Appendix A Fig. A8. Black arrows indicate sequences obtained in this study. Outgroup clades (Tylidae and Ligiidae, excluding *Ligia*) are colored grey; clades belonging to a species that had at least one COI barcode produced in this study are assigned a unique color for each species. Numbers above nodes show ultrafast bootstrap support. Nodes with <95% ultrafast bootstrap support are collapsed. In phylogeny F (Trachelipodidae), *Nagurus cristatus* forms a polytomy with Trachelipodidae and Tylidae. Please note that the inclusion of GenBank sequences in each family reflects the GenBank taxonomic classification of these genera, and may not be in accordance with currently-accepted taxonomy. A: Armadillidiidae; B: Cylisticidae; C: Oniscidae; D: Philosciidae; E: Porcellionidae; F: Trachelipodidae; G: Trichoniscidae.


A
MT521107.1/1-658 Armadillidium album voucher MT06312 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
Armadillidium pictum (N=9)
ON212577.1/12-540 Armadillidium fallax isolate 52cy cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-529
MT521234.1/1-658 Armadillidium pulchellum voucher ZSM-BC-27349-D01 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
OK156465.1/1-633 Armadillidium serrai isolate 4103 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-633
ON212545.1/12-479 Armadillidium vulgare isolate 34z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-468
OQ509936.1/9-507 Schizidium myrrae isolate 1 Scmy COI CVAL cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-499
OQ509967.1/9-506 Schizidium myrrae isolate 3 Scmy COI CVAL cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-497
OQ509952.1/9-507 Schizidium myrrae isolate 2 Scmy COI CVAL cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-499
OQ509977.1/9-507 Schizidium myrrae isolate 4 Scmy COI CVAL cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-499
MH279709.1/1-658 Eluma caelata isolate DY-013 cytochrome c oxidase subunit I COI gene partial cds mitochondrial/1-658
OK156459.1/1-658 Eluma caelata isolate 2014 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-658
OK156460.1/1-659 Eluma caelata isolate 2015 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-658
Iberiarmadillidium psammophilum (N=5)
Armadillidium granulatum (N=7)
MT521127.1/1-658 Armadillidium versicolor voucher BC ZSM MYR 00587 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521268.1/1-658 Armadillidium versicolor voucher BC ZSM MYR 00568 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
Armadillidium opacum (N=8)
Armadillidium vulgare (N=474, incl. 4 this study); Armadillidium sp. (N=3)
ON212533.1/12-640 Armadillidium vulgare isolate 55cy cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-629
Armadillidium lobocurvum (N=37)
Armadillidium nasatum (N=35, incl. 3 this study); Armadillidium vulgare (N=1)
OK156463.1/1-635 Armadillidium mateui isolate 4062 01 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-635
OK156450.1/1-658 Iberiarmadillidium pinicola isolate 2712 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-658
OK156451.1/1-658 Iberiarmadillidium pinicola isolate 3792 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-658
OK156457.1/1-641 Iberiarmadillidium sakura isolate 1488 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-641
OK156468.1/1-658 Iberiarmadillidium sakura isolate 2080 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-658
ON212539.1/12-506 Cyphodillidium absoloni isolate 151z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-495
ON212538.1/12-506 Echinarmadillidium fruxgalii isolate 157z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-495
OK156466.1/1-658 Armadillidium serratum isolate 4528 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-658
OK156437.1/1-632 Cristarmadillidium breuili isolate 4222 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-632
OK156439.1/1-632 Cristarmadillidium breuili isolate 4223 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-632
OK156439.1/1-658 Cristarmadillidium muricatum isolate 2079 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-658
OK156440.1/1-658 Cristarmadillidium muricatum isolate 2710 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-658
OK156441.1/1-658 Cristarmadillidium muricatum isolate 4028 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-658
OK156442.1/1-658 Cristarmadillidium muricatum isolate 4028 02 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-658
Cristarmadillidium myrmecophilum (N=7)
Schizidium christosi (N=12)
Schizidium fissum (N=48)
OQ509937.1/9-512 Schizidium tiberianum isolate 1 Scti COI ISRA cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-504
OQ509968.1/9-512 Schizidium tiberianum isolate 3 Scti COI ISRA cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-504
OQ509954.1/9-512 Schizidium tiberianum isolate 2 Scti COI ISRA cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-504
MN225956.1/1-595 Armadillidium sp. FBRC ZSI DNA382 UNB047 cytochrome c oxidase subunit I COI gene partial cds mitochondrial/1-595
OQ509920.1/1-488 Schizidium osellai isolate 1 Scos COI TKME cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-488
OQ509921.1/3-494 Schizidium osellai isolate 2 Scos COI TKME cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-492
OK156461.1/1-615 Paraschizidium caecilum isolate 4377 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-615
MK603245.1/1-615 Tylos granulatus isolate YZ26 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MZ540108.1/1-581 Tylos capensis isolate TcER02 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial
MT521213.1/1-658 Tylos ponticus voucher MT06358 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial
GU097619.1/1-282 Tylos europaeus isolate TPI1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468118.1/1-560 Tylos marcuzzii voucher MZUF 8660 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KF007596.1/1-650 Tylos punctatus isolate Ensenada 281 4 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468120.1/1-583 Tylos niveus voucher Puerto Rico 28 1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
EU364624.1/1-658 Tylos neozelanicus voucher BES11448 cytochrome oxidase subunit I COX1 gene partial cds mitochondrial
KJ468116.1/1-572 Tylos maindroni voucher MZUF 2156 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468112.1/1-562 Tylos exiguus voucher MZUF 8667 cytochrome oxidase subunit I COI gene partial cds mitochondrial
AB763432.1/1-627 Tylos granuliferus mitochondrial COI gene for cytochrome oxidase subunit I partial cds haplotype H001
KJ468121.1/1-563 Tylos opercularis voucher MZUF 9425 cytochrome oxidase subunit I COI gene partial cds mitochondrial
GU097565.1/1-257 Helleria brevicornis isolate CAP1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468126.1/1-562 Tylos wegeneri voucher LACM 25 July 1985 J.A.Vargas cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468125.1/1-562 Tylos spinulosus voucher MZUF 1096 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468109.1/1-554 Tylos chilensis voucher MZUF 279 cytochrome oxidase subunit I COI gene partial cds mitochondrial
ON212618.1/1-355 Platanosphaera halophila isolate 75T cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-355
LC711269.1/6-663 Ligidium koreanum Shi124 Che2302 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
LC711253.1/6-663 Ligidium japonicum Oym15 Che2183 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
AB626262.1/6-663 Ligidium yukyuense mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate iso-85/1-658
MN810648.1/1-658 Ligidium hypnorum voucher ZFMK-TIS-2518709 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
ON212579.1/9-506 Typhloligidium kovali isolate 47Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212598.1/12-508 Tauroligidium cf. stygium isolate 21Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-497
ON212584.1/9-506 Typhloligidium coecum isolate 35Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212590.1/9-506 Typhloligidium karabijajlae isolate 41Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212582.1/9-506 Typhloligidium lithophagum isolate 19Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212583.1/12-462 Typhloligidium lithophagum isolate 46Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-441
DQ182820.1/1-621 Ligidium beieri isolate KEF3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182857.1/1-615 Ligidium beieri isolate PRU5 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-615
DQ182827.1/1-622 Ligidium werneri isolate LES1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-622
DQ182779.1/1-606 Ligidium eubicum isolate EVII9 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-606
DQ182825.1/1-621 Ligidium ghigii isolate KOS3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182831.1/1-625 Ligidium cycladicum isolate ANDI2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-625
MT521243.1/1-658 Ligidium germanicum voucher ZSM-BC-27349-D11 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
0.1
B
MF744625.1/1-658 Cylisticus convexus voucher BIOUG08059-F12 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810770.1/1-658 Cylisticus convexus voucher ZFMK-TIS-2520883 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521139.1/1-658 Cylisticus convexus voucher BC ZSM MYR 00560 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810707.1/1-658 Cylisticus convexus voucher ZFMK-TIS-2501899 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521086.1/1-658 Cylisticus convexus voucher MT06314 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810645.1/1-658 Cylisticus convexus voucher ZFMK-TIS-19901 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521275.1/1-658 Cylisticus convexus voucher BC ZSM MYR 00561 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810618.1/1-658 Cylisticus convexus voucher ZFMK-TIS-2501895 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810698.1/1-658 Cylisticus convexus voucher ZFMK-TIS-19945 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
Cylisticus convexus 047AAG consensus/10-667
Cylisticus convexus 184B2 consensus/11-668
MN810743.1/1-658 Cylisticus convexus voucher ZFMK-TIS-19896 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521159.1/1-658 Cylisticus convexus voucher GBOL18630 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
Cylisticus convexus 150-1 consensus trimmed/12-669
MN810826.1/1-658 Cylisticus convexus voucher ZFMK-TIS-19938 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
Cylisticus convexus 1331C3 consensus/10-667
MN810730.1/1-658 Cylisticus convexus voucher ZFMK-TIS-2520823 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
Cylisticus convexus 082AAA consensus/14-654
MT521096.1/1-658 Cylisticus convexus voucher MT06315 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MK603245.1/1-615 Tylos granulatus isolate YZ26 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MZ540108.1/1-581 Tylos capensis isolate TcER02 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial
KF007596.1/1-650 Tylos punctatus isolate Ensenada 281 4 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468120.1/1-583 Tylos niveus voucher Puerto Rico 28 1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468118.1/1-560 Tylos marcuzzii voucher MZUF 8660 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468116.1/1-572 Tylos maindroni voucher MZUF 2156 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468112.1/1-562 Tylos exiguus voucher MZUF 8667 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468125.1/1-562 Tylos spinulosus voucher MZUF 1096 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468109.1/1-554 Tylos chilensis voucher MZUF 279 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MT521213.1/1-658 Tylos ponticus voucher MT06358 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial
GU097619.1/1-282 Tylos europaeus isolate TPI1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
AB763432.1/1-627 Tylos granuliferus mitochondrial COI gene for cytochrome oxidase subunit I partial cds haplotype H001
KJ468121.1/1-563 Tylos opercularis voucher MZUF 9425 cytochrome oxidase subunit I COI gene partial cds mitochondrial
GU097565.1/1-257 Helleria brevicornis isolate CAP1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468126.1/1-562 Tylos wegeneri voucher LACM 25 July 1985 J.A.Vargas cytochrome oxidase subunit I COI gene partial cds mitochondrial
LC711269.1/6-663 Ligidium koreanum Shi124 Che2302 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
LC711253.1/6-663 Ligidium japonicum Oym15 Che2183 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
AB626262.1/6-663 Ligidium yukyuense mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate iso-85/1-658
MN810648.1/1-658 Ligidium hypnorum voucher ZFMK-TIS-2518709 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
DQ182820.1/1-621 Ligidium beieri isolate KEF3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182857.1/1-615 Ligidium beieri isolate PRU5 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-615
ON212598.1/12-508 Tauroligidium cf. stygium isolate 21Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-497
ON212584.1/9-506 Typhloligidium coecum isolate 35Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212590.1/9-506 Typhloligidium karabijajlae isolate 41Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212582.1/9-506 Typhloligidium lithophagum isolate 19Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212583.1/12-462 Typhloligidium lithophagum isolate 46Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-441
ON212579.1/9-506 Typhloligidium kovali isolate 47Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
DQ182827.1/1-622 Ligidium werneri isolate LES1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-622
DQ182779.1/1-606 Ligidium eubicum isolate EVII9 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-606
DQ182825.1/1-621 Ligidium ghigii isolate KOS3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182831.1/1-625 Ligidium cycladicum isolate ANDI2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-625
MT521243.1/1-658 Ligidium germanicum voucher ZSM-BC-27349-D11 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
0.2


C
MN810572.1/1-658 Oniscus asellus voucher ZFMK-TIS-2519267 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810582.1/1-658 Oniscus asellus voucher ZFMK-TIS-2510832 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
KU855989.1/1-545 Oniscus asellus isolate 64W2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-545
MN810585.1/1-658 Oniscus asellus voucher ZFMK-TIS-2534730 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810613.1/1-658 Oniscus asellus voucher ZFMK-TIS-19899 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810661.1/1-658 Oniscus asellus voucher ZFMK-TIS-19946 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810640.1/1-658 Oniscus asellus voucher ZFMK-TIS-19923 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810666.1/1-658 Oniscus asellus voucher ZFMK-TIS-19942 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810629.1/1-658 Oniscus asellus voucher ZFMK-TIS-2542561 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810672.1/1-658 Oniscus asellus voucher ZFMK-TIS-2525790 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810719.1/1-658 Oniscus asellus voucher ZFMK-TIS-19934 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
KY554644.1 Oniscus asellus isolate C13 cytochrome oxidase subunit I (COI) gene partial cds mitochondrial
MN810605.1/1-658 Oniscus asellus voucher ZFMK-TIS-2510632 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810611.1/1-658 Oniscus asellus voucher ZFMK-TIS-2502285 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521141.1/1-658 Oniscus asellus voucher MT06348 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810724.1/1-658 Oniscus asellus voucher ZFMK-TIS-2510601 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521124.1/1-658 Oniscus asellus voucher MT06436 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521113.1/1-658 Oniscus asellus voucher MT06423 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810817.1/1-659 Oniscus asellus voucher ZFMK-TIS-2534799 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521131.1/1-658 Oniscus asellus voucher MT06437 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810633.1/1-658 Oniscus asellus voucher ZFMK-TIS-2510942 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810607.1/1-658 Oniscus asellus voucher ZFMK-TIS-2525705 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810638.1/1-658 Oniscus asellus voucher ZFMK-TIS-2525601 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521174.1/1-627 Oniscus asellus voucher MT06439 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-627
MN810756.1/1-658 Oniscus asellus voucher ZFMK-TIS-2525553 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521290.1/1-658 Oniscus asellus voucher MT06438 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810690.1/1-658 Oniscus asellus voucher ZFMK-TIS-2525671 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810777.1/1-658 Oniscus asellus voucher ZFMK-TIS-2525733 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810662.1/1-658 Oniscus asellus voucher ZFMK-TIS-2510627 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810603.1/1-658 Oniscus asellus voucher ZFMK-TIS-2501698 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810828.1/1-658 Oniscus asellus voucher ZFMK-TIS-2510650 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810799.1/1-658 Oniscus asellus voucher ZFMK-TIS-2510874 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810841.1/1-658 Oniscus asellus voucher ZFMK-TIS-2545568 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810667.1/1-658 Oniscus asellus voucher ZFMK-TIS-2524904 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810623.1/1-658 Oniscus asellus voucher ZFMK-TIS-2510533 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
KU855990.1/1-622 Oniscus asellus isolate 66W1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-622
KU855994.1/1-618 Oniscus asellus isolate 70W2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-618
KU855993.1/1-623 Oniscus asellus isolate 70W1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-623
Oniscus asellus 063AAC consensus/15-568
Oniscus asellus 1082A3 consensus/11-577
MG329628.1/1-408 Oniscus asellus voucher 09ISOP-0002 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-408
KM611735.1/1-315 Oniscus asellus voucher 09BBEIS-0009 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-315
KM611721.1/1-341 Oniscus asellus voucher 09BBEIS-0007 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-341
MG321187.1/1-408 Oniscus asellus voucher 09ISOP-0031 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-408
KJ668157.1/1-623 Sardoniscus pygmaeus voucher LB123 cytochrome oxidase subunit I cox1 gene partial cds mitochondrial/1-623
ON212548.1/12-507 Oroniscus dalmaticus isolate 169z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-496
ON212547.1/12-504 Oroniscus dalmaticus isolate 171z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-493
ON212544.1/9-506 Rodoniscus anophthalmus isolate 203z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
KJ668155.1/1-418 Sardoniscus verhoeffi voucher LB142 cytochrome oxidase subunit 1 cox1 gene partial cds mitochondrial/1-418
KJ668156.1/1-418 Sardoniscus verhoeffi voucher LB122 cytochrome oxidase subunit 1 cox1 gene partial cds mitochondrial/1-418
MK610248.1/1-615 Tylos granulatus isolate YZ26 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MZ540108.1/1-581 Tylos capensis isolate TcER02 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial
AB763432.1/1-627 Tylos granuliferus mitochondrial COI gene for cytochrome oxidase subunit I partial cds haplotype H001
KJ468121.1/1-563 Tylos opercularis voucher MZUF 8425 cytochrome oxidase subunit I COI gene partial cds mitochondrial
EU364624.1/1-658 Tylos heozelanicus voucher BES11448 cytochrome oxidase subunit I COX1 gene partial cds mitochondrial
MT521213.1/1-658 Tylos ponticus voucher MT06358 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial
GU067619.1/1-282 Tylos europaeus isolate TP1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468126.1/1-562 Tylos weigneri voucher LACM 23 July 1985 J.A.Vargas cytochrome oxidase subunit I COI gene partial cds mitochondrial
KF007596.1/1-650 Tylos punctatus isolate Ensenada 281 4 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468120.1/1-563 Tylos niveus voucher Puerto Rico 28.1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468118.1/1-560 Tylos marouzzi voucher MZUF 8662 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468116.1/1-572 Tylos maindroni voucher MZUF 8156 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468112.1/1-562 Tylos exiguus voucher MZUF 8687 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468125.1/1-562 Tylos spinulosus voucher MZUF 1096 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468109.1/1-554 Tylos chilensis voucher MZUF 279 cytochrome oxidase subunit I COI gene partial cds mitochondrial
GU097565.1/1-257 Helleria brevicornis isolate CA10 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KU855991.1/1-631 Oniscus asellus isolate 69W1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-631
KU855992.1/1-630 Oniscus asellus isolate 69W2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-630
MT521243.1/1-658 Ligidium germanicum voucher ZSM-BC-27349-D11 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
DQ182831.1/1-625 Ligidium cycladicum isolate ANDI2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-625
DQ182827.1/1-622 Ligidium werneri isolate LES1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-622
DQ182779.1/1-606 Ligidium subsicum isolate EVI6 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-606
DQ182825.1/1-621 Ligidium ghigii isolate KOS3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
MN810648.1/1-658 Ligidium hypnorum voucher ZFMK-TIS-2518709 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
DQ182820.1/1-621 Ligidium beieri isolate KEF3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182857.1/1-615 Ligidium beieri isolate PRU5 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-615
ON212598.1/12-508 Tauroligidium cf. stygium isolate 21Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-497
ON212584.1/9-506 Typhloligidium coecum isolate 35Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212590.1/9-506 Typhloligidium karabajalae isolate 41Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212582.1/9-506 Typhloligidium lithophagum isolate 19Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212583.1/12-452 Typhloligidium lithophagum isolate 46Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-441
ON212579.1/9-506 Typhloligidium kovali isolate 47Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
LC711259.1/6-663 Ligidium koreanum Shi124 Che2302 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
LC711253.1/6-663 Ligidium japonicum Oym15 Che2183 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
AB628262.1/6-663 Ligidium ryukyuense mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate iso-85/1-658
2.0

D


OR807140.1/38-690 Benthana serrana voucher UFRGS 5627.1 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-653
OR807142.1/38-690 Benthana serrana voucher UFRGS 5627.3 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-653
OR807141.1/38-690 Benthana serrana voucher UFRGS 5627.2 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-653
AF191117.1/1-429 Littorophiloscia bifasciata isolate LB3HI cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
AF191118.1/1-429 Littorophiloscia bifasciata isolate LB6OA cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
Littorophiloscia nipponensis (N=12)
AF191115.1/1-429 Littorophiloscia culebrae isolate LC3 cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
AF191116.1/1-429 Littorophiloscia culebrae isolate LC2 cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
AF191119.1/1-429 Littorophiloscia hawaiiensis isolate Lh1 cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
AF191120.1/1-429 Littorophiloscia hawaiiensis isolate LH2 cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
AF191121.1/1-429 Littorophiloscia sp. Lsp2 cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
AF191122.1/1-429 Littorophiloscia sp. Lsp3 cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
Burmoniscus purpura (N=22)
Burmoniscus okinawaensis (N=52); Burmoniscus kathmandius (N=21)
ON212578.1/22-462 Congophiloscia longiantennata isolate 93z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-441
Burmoniscus ocellatus (N=23)
Burmoniscus (N=6)
Burmoniscus sp. (N=10)
LC496516.1/9-623 Papuaphiloscia sp. SHIZU1 wa2623 Ag130 mitochondrial COX1 gene for cytochrome c oxidase subunit 1 partial cds/1-615
LC496517.1/5-618 Papuaphiloscia sp. SHIZU1 wa2624 Ag131 mitochondrial COX1 gene for cytochrome c oxidase subunit 1 partial cds/1-614
AF191113.1/1-429 Papuaphiloscia laevis isolate Pla1 cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
AF191114.1/1-401 Papuaphiloscia laevis isolate Pla2 cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-401
Burmoniscus meeusei (N=7)
AF191112.1/1-429 Anchiphiloscia pilosa cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
KJ668160.1/1-620 Trichophiloscia murisierii voucher LB120 cytochrome oxidase subunit 1 cox1 gene partial cds mitochondrial/1-620
EU364629.1/1-658 Laevophiloscia yalgoensis voucher BES7416.1 cytochrome oxidase subunit I COX1 gene partial cds mitochondrial/1-645
MT902726.1/14-658 Philosciidae sp. Biologic-ISOP001 voucher BMR00734 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-645
OR653836.1/14-658 Laevophiloscia sp. Biologic-ISOP089 isolate BMR06135 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-645
OR653835.1/1-454 Laevophiloscia sp. Biologic-ISOP089 isolate BMR06134 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-454
OR653842.1/14-658 Laevophiloscia sp. Biologic-ISOP088 isolate BMR06141 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-645
Philosciidae sp. (N=20)
OR807148.1/36-688 Benthana taeniata voucher UFRGS 6401.1 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-653
OR807144.1/18-619 Benthana sulcata voucher UFRGS 5684.2 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-602
OR807134.1/36-613 Benthana convexa voucher UFRGS 5704.2 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-578
OR807135.1/36-613 Benthana convexa voucher UFRGS 5704.3 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-578
OR807137.1/1-556 Benthana longipenis voucher UFRGS 5685.3 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-556
OR807138.1/1-553 Benthana longipenis voucher UFRGS 5921.2 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-553
OR807139.1/1-553 Benthana longipenis voucher UFRGS 5921.3 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-553
OR807149.1/22-674 Benthana werneri voucher UFRGS 6254.1 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-653
OR807150.1/22-674 Benthana werneri voucher UFRGS 6254.2 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-653
OR807130.1/38-674 Benthana cairensis voucher UFRGS 5365.1 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-637
OR807131.1/38-674 Benthana cairensis voucher UFRGS 5365.2 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-637
OR807132.1/38-666 Benthana cairensis voucher UFRGS 5373.2 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-629
OR807133.1/1-579 Benthana cairensis voucher UFRGS 5609.1 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-579
OR807143.1/18-619 Benthana sulcata voucher UFRGS 5684.1 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-602
OR807145.1/18-619 Benthana sulcata voucher UFRGS 5684.3 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-602
OR807136.1/1-507 Benthana longicaudata voucher UFRGS 5696.3 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-507
OR807146.1/1-551 Benthana taeniata voucher UFRGS 4682.1 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-551
OR807147.1/1-551 Benthana taeniata voucher UFRGS 4682.2 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-551
OR807127.1/1-517 Benthana albomarginata voucher UFRGS 5904.1 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-517
OR807128.1/1-517 Benthana albomarginata voucher UFRGS 5904.2 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-517
OR807129.1/1-517 Benthana albomarginata voucher UFRGS 5904.3 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-517
Atlantoscia sp. (N=4)
MH047283.1/1-586 Atlantoscia australe cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-586
Atlantoscia petronioi (N=15)
Atlantoscia floridana (N=16)
MH047282.1/1-534 Atlantoscia antennamaculata cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-534
Atlantoscia inflata (N=4); Atlantoscia sp. (N=7)
KM200863.1/1-640 Atlantoscia sulcata cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-640
KM200846.1/1-640 Atlantoscia ituberasensis isolate a cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-640
KM200847.1/1-554 Atlantoscia ituberasensis isolate b cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-554
KM200862.1/1-636 Atlantoscia rubromarginata cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-636
KY706089.1/1-588 Paratlantoscia robusta voucher UFRGS 4830 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-588
KY706090.1/1-588 Paratlantoscia robusta voucher UFRGS 4831 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-588
Philoscia muscorum (N=253, incl. 3 this study)
Philoscia affinis (N=6)
Lepidoniscus minutus (N=5)
MT521136.1/1-639 Lepidoniscus pruinosus voucher ZSM-BC-27349-D09 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-639
Australophiloscia societatis (N=6)
KR424603.1/16-668 Philosciidae sp. Ja249 isolate Iso45 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-653
OP242131.1/14-658 Philosciidae sp. McP isolate 6228 voucher BMR02786 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-645
OP242132.1/14-658 Philosciidae sp. McP isolate 8654 voucher BMR02813 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-645
KJ668161.1/1-623 Chaetophiloscia elongata voucher LB113 cytochrome oxidase subunit 1 cox1 gene partial cds mitochondrial/1-623
MG887940.1/1-575 Chaetophiloscia elongata isolate Indv29 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-575
ON212543.1/25-607 Chaetophiloscia lagoi isolate 105cy cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-583
Hawaiioscia rotundata (N=3)
Hawaioscia microphthalma (N=3)
AF191129.1/1-429 Hawaiioscia paeninsulae cytochrome c oxidase subunit I COI gene partial cds mitochondrial gene for mitochondrial product/1-429
MK603245.1/1-617 Tylos granulatus isolate YZ26 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-617
MZ540108.1/1-581 Tylos capensis isolate TcER02 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-581
MT521213.1/14-658 Tylos pontticus voucher MT06358 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-645
GU097619.1/1-296 Tylos europaeus isolate TPI1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-290
KJ468116.1/1-572 Tylos maindroni voucher MZUF 2156 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-572
KJ468112.1/1-562 Tylos exiguus voucher MZUF 8687 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-562
AB763432.1/1-627 Tylos granuliferus mitochondrial COI gene for cytochrome oxidase subunit I partial cds haplotype H001/1-627
KJ468121.1/1-563 Tylos opercularis voucher MZUF 9425 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-563
EU364624.1/14-658 Tylos neozelanicus voucher BES11448 cytochrome oxidase subunit I COX1 gene partial cds mitochondrial/1-645
KF007596.1/6-650 Tylos punctatus isolate Ensenada 281 4 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-645
KJ468118.1/1-560 Tylos marcuzzii voucher MZUF 8660 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-560
KJ468120.1/1-583 Tylos niveus voucher Puerto Rico 28.1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-583
GU097565.1/1-271 Helleia brevicorne isolate CAP1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-265
KJ468125.1/1-562 Tylos spinulosus voucher MZUF 1096 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-562
KJ468109.1/1-554 Tylos chilensis voucher MZUF 279 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-554
KJ468126.1/1-562 Tylos wegneri voucher LACM 25 July 1965 J.A.Vargas cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-562
LC711269.1/19-671 Ligidium koreanum Shi124 Che2302 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-653
LC711253.1/19-671 Ligidium japonicum Oym15 Che2183 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-653
AB626282.1/19-671 Ligidium ryukyuense mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate: iso-85/1-653
MN810648.1/14-658 Ligidium hypnorum voucher ZFMK-TIS-2518709 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-645
ON212579.1/22-506 Typhloligidium kovali isolate 47Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-485
ON212598.1/25-508 Taurioligidium cf. stygium isolate 21Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-484
ON212584.1/22-506 Typhloligidium coecum isolate 35Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-485
ON212590.1/22-506 Typhloligidium karabijajlae isolate 41Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-485
ON212582.1/22-506 Typhloligidium lithophagum isolate 19Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-485
ON212583.1/25-452 Typhloligidium lithophagum isolate 46Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-428
DQ182820.1/1-624 Ligidium beieri isolate KEF3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-624
DQ182857.1/1-623 Ligidium beieri isolate PRU5 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-623
DQ182827.1/1-625 Ligidium werneri isolate LES1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-625
DQ182779.1/1-611 Ligidium eubicum isolate EVII9 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-611
DQ182825.1/1-624 Ligidium ghigii isolate KOS3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-624
DQ182831.1/1-626 Ligidium cycladicum isolate AND2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-626
MT521243.1/14-658 Ligidium germanicum voucher ZSM-BC-27349-D11 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-645
0.2


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MG887945.1/24-450 Acaeroplastes melanurus melanurus isolate Indv18 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-427
MG887944.1/15-514 Porcellio nasutus isolate Indv10 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-500
MT521202.1/1-658 Porcellio monticola voucher ZSM-BC-27349-D06 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521255.1/1-658 Porcellio monticola voucher ZSM-BC-26830-G08 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
Porcellio spinicornis (N=24, incl. 6 this study); Porcellio sp. (N=1)
MG887932.1/24-436 Caeroplastes porphyrivagus isolate Indv13 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-413
Porcellio montanus (N=6)
MN689274.1/1-618 Agabiformius lentus voucher UJED-34 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-618
ON212535.1/12-513 Agabiformius lentus isolate 94cy cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-502
MG887931.1/24-450 Soleriscus laouensis isolate Indv19 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-427
ON212560.1/12-476 Porcellio sp. isolate 204z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-465
MG887946.1/12-527 Tura sp. ACD-2018 isolate Indv12 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-516
Porcellionides myrmecophilus (N=6)
Porcellionides pruinosus (N=6)
Porcellionides pruinosus (N=30)
Porcellionides pruinosus (N=6, incl. 1 this study)
MG887933.1/24-450 Proporcellio vulcanius isolate Indv1 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-427
Porcellio baidensis (N=5)
FN824127.1/1-632 Porcellio imbutus partial COI gene for cytochrome oxidase subunit 1 specimen voucher MIB Zpl 01433/1-632
FN824116.1/1-632 Porcellio siculoccidentalis partial COI gene for cytochrome oxidase subunit 1 specimen voucher MIB Zpl 01604/1-632
FN824125.1/1-632 Porcellio imbutus partial COI gene for cytochrome oxidase subunit 1 specimen voucher MIB Zpl 01422/1-632
FN824126.1/1-632 Porcellio imbutus partial COI gene for cytochrome oxidase subunit 1 specimen voucher MIB Zpl 01423/1-632
FN824115.1/1-632 Porcellio hylaeus partial COI gene for cytochrome oxidase subunit 1 specimen voucher MIB Zpl 01592/1-632
FN824117.1/1-632 Porcellio hylaeus partial COI gene for cytochrome oxidase subunit 1 specimen voucher MIB Zpl 01593/1-632
FN824118.1/1-632 Porcellio hylaeus partial COI gene for cytochrome oxidase subunit 1 specimen voucher MIB Zpl 01595/1-632
Porcellio laevis (N =58); Porcellio sp. (N=9); Porcellionidae sp. (N=1)
Porcellio dilatatus (N=7, incl. 1 this study); Porcellio sp. (N=11)
OK376217.1/1-629 Porcellionides virgatus voucher CIB-09B cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-629
OK376218.1/1-629 Porcellionides virgatus voucher CIB-49B cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-629
Porcellio scaber (N=437, incl. 7 this study)
MT521104.1/1-658 Porcellio scaber voucher MT06484 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521115.1/1-658 Porcellio scaber voucher MT06301 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521158.1/1-658 Porcellio scaber voucher MT06473 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
KF891466.1/1-461 Porcellionides pruinosus haplotype C29 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-461
MN810751.1/1-658 Porcellio scaber voucher ZFMK-TIS-2518812 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MH279713.1/12-606 Porcellio sp. DY-083 cytochrome c oxidase subunit I COI gene partial cds mitochondrial/1-595
MH279739.1/8-665 Porcellio sp. DY-234 cytochrome c oxidase subunit I COI gene partial cds mitochondrial/1-658
MH279740.1/8-663 Porcellio sp. DY-235 cytochrome c oxidase subunit I COI gene partial cds mitochondrial/1-658
Porcellionides sexfasciatus (N=4)
ON212536.1/12-509 Leptotrichus kosswigi isolate 1KR cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
MW325677.1/1-636 Porcellio laevis isolate Orange cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-636
MW449535.1/1-646 Porcellio laevis isolate Deshna cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-646
KF002745.1/1-657 Porcellio laevis haplotype Porlcox1 cytochrome oxidase subunit 1 cox1 gene partial cds mitochondrial/1-657
MK603245.1/1-615 Tylos granulatus isolate Y226 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MZ540108.1/1-581 Tylos capensis isolate TCER02 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial
KJ468118.1/1-560 Tylos marcuzzii voucher MZUF 8660 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MT521213.1/1-658 Tylos ponticus voucher MT06358 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial
GU097619.1/1-282 Tylos europaeus isolate TPI1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
GU097565.1/1-257 Helleria brevicornis isolate CAP1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468126.1/1-562 Tylos wegeneri voucher LACM 25 July 1985 J.A.Vargas cytochrome oxidase subunit I COI gene partial cds mitochondrial
KF007596.1/1-660 Tylos punctatus isolate Ensenada 281 4 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468120.1/1-583 Tylos niveus voucher Puerto Rico 28 1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
EU364624.1/1-658 Tylos neozelanicus voucher BES11448 cytochrome oxidase subunit I COX1 gene partial cds mitochondrial
AB763432.1/1-627 Tylos granuliferus mitochondrial COI gene for cytochrome oxidase subunit I partial cds haplotype H001
KJ468121.1/1-563 Tylos opercularis voucher MZUF 9425 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468116.1/1-572 Tylos maindroni voucher MZUF 2156 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468112.1/1-562 Tylos exiguus voucher MZUF 8687 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468125.1/1-562 Tylos spinulosus voucher MZUF 1096 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468109.1/1-554 Tylos chilensis voucher MZUF 279 cytochrome oxidase subunit I COI gene partial cds mitochondrial
LC711269.1/6-663 Ligidium koreanum Shi124 Che2302 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
LC711253.1/6-663 Ligidium japonicum Oym15 Che2183 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
AB626262.1/6-663 Ligidium ryukyuense mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate iso-85/1-658
MN810648.1/1-658 Ligidium hypnorum voucher ZFMK-TIS-2518709 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
ON212579.1/9-506 Typhloligidium kovali isolate 47Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212598.1/12-508 Taurioligidium cf. stygium isolate 21Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-497
ON212584.1/9-506 Typhloligidium coecum isolate 35Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212590.1/9-506 Typhloligidium karabajlaje isolate 41Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212582.1/9-506 Typhloligidium lithophagum isolate 19Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212583.1/12-452 Typhloligidium lithophagum isolate 46Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-441
DQ182820.1/1-621 Ligidium beieri isolate KEF3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182857.1/1-615 Ligidium beieri isolate PRU5 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-615
DQ182827.1/1-622 Ligidium werneri isolate LES1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-622
DQ182779.1/1-606 Ligidium eubolcum isolate EVI9 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-606
DQ182825.1/1-621 Ligidium ghigii isolate KOS3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182831.1/1-625 Ligidium cycladicum isolate ANDI2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-625
MT521243.1/1-658 Ligidium germanicum voucher ZSM-BC-27349-D11 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
0.1

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ON212546.1/79-407 Levantoniscus makrisi isolate 22z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-329
ON212541.1/82-517 Nagurus carinatus isolate 28cy cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-436
ON212542.1/82-640 Nagurus carinatus isolate 93cy cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-559
Trachelipus ratzeburgii (N=18)
Trachelipus aegaeus (N=10)
EF027412.1/88-533 Trachelipus kytherensis isolate KYT1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-446
EF027413.1/88-538 Trachelipus kytherensis isolate KYT2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-451
EF027414.1/88-541 Trachelipus kytherensis isolate KYT3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-454
EF027415.1/83-536 Trachelipus kytherensis isolate KYT4 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-454
KF891450.1/21-393 Trachelipus aegaeus haplotype C7 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-373
KF891451.1/15-387 Trachelipus aegaeus haplotype C8 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-373
Trachelipus aegaeus (N=7)
ON212614.1/1-437 Trachelipus cavaticus isolate 63T cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-437
EF027408.1/29-589 Trachelipus kytherensis isolate KRIT3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-561
EF027410.1/83-521 Trachelipus kytherensis isolate KRIT5 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-439
EF027409.1/83-536 Trachelipus kytherensis isolate KRIT4 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-454
EF027411.1/83-536 Trachelipus kytherensis isolate KRIT6 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-454
KF891448.1/79-464 Trachelipus aegaeus haplotype C4 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-386
Trachelipus kytherensis (N=18)
Trachelipus kytherensis (N=39); Trachelipus palustris (N=3)
KF891457.1/15-418 Trachelipus aegaeus haplotype C16 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-404
EF659956.1/85-518 Trachelipus sp. AP-2007 isolate AGA2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-434
EF659963.1/85-518 Trachelipus sp. AP-2007 isolate STN2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-434
EF659962.1/85-518 Trachelipus sp. AP-2007 isolate STN1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-434
EF659957.1/85-518 Trachelipus sp. AP-2007 isolate AGA3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-434
EF027452.1/48-479 Trachelipus kytherensis isolate VEL1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-432
EF027453.1/81-527 Trachelipus kytherensis isolate VEL2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-447
Trachelipus nodulosus (N=5)
Trachelipus rathkii (N=144, incl. 7 this study); Trachelipus sp. (N=205)
MN810814.1/71-658 Trachelipus rathkii voucher ZFMK-TIS-2557190 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-588
MT521239.1/71-658 Trachelipus rathkii voucher MT06485 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-588
MT521258.1/71-632 Trachelipus rathkii voucher MT06486 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-562
OM921003.1/80-628 Trachelipus rathkii isolate N94-3e cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-549
Nagurus cristatus 046005 consensus/84-671
Nagurus cristatus 046004 consensus/84-671
Nagurus cristatus 046008 consensus/87-651
Porcellium conspersum (N=7)
MT521102.1/71-658 Porcellium fiumanum salisburgense voucher BC ZSM MYR 00558 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-588
MT521289.1/71-658 Porcellium fiumanum salisburgense voucher BC ZSM MYR 00559 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-588
Protracheoniscus politus (N=8)
MH400724.1/71-622 Protracheoniscus nogaicus voucher Pnog B cytochrome oxidase subunit 1 COX1 gene partial cds mitochondrial/1-552
LC017825.1/66-652 Mongoloniscus koreanus mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate Ag-1 7-11 13-19 21-23/1-587
LC017826.1/66-652 Mongoloniscus koreanus mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate Ag-5/1-587
OR518588.1/1-374 Mongoloniscus sp. voucher CQT-024 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-374
Mongoloniscus sinensis (N=20)
Mongoloniscus sinensis (N=15); Mongoloniscus sp. (N=1)
LC017827.1/66-652 Mongoloniscus vannamei mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate Ag-20 24 28/1-587
LC496518.1/25-611 Mongoloniscus vannamei wa3435 Che560 mitochondrial COX1 gene for cytochrome c oxidase subunit 1 partial cds/1-587
LC496519.1/40-627 Mongoloniscus vannamei wa3436 Che561 mitochondrial COX1 gene for cytochrome c oxidase subunit 1 partial cds/1-588
Mongoloniscus sinensis (N=65)
KT424029.1/1-588 Mongoloniscus sinensis isolate X4 cytochrome c oxidase subunit I CoI gene partial cds mitochondrial/1-588
MH400723.1/71-622 Protracheoniscus pokarzhevskii voucher Psp A cytochrome oxidase subunit 1 COX1 gene partial cds mitochondrial/1-552
MG696253.1/73-624 Protracheoniscus sp. 1 IST-2017 isolate B cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-552
MH400727.1/71-622 Protracheoniscus kryszanovskii voucher Pkrz E cytochrome oxidase subunit 1 COX1 gene partial cds mitochondrial/1-552
MH400726.1/71-622 Protracheoniscus major voucher Pmjr D cytochrome oxidase subunit 1 COX1 gene partial cds mitochondrial/1-552
ON212530.1/82-506 Protracheoniscus major isolate 182z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-425
ON212531.1/82-506 Protracheoniscus major isolate 181z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-425
EF568937.1/1-418 Orthometopon dalmatinum haplotype Imvros Crete isl. cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-418
EF568938.1/1-418 Orthometopon dalmatinum haplotype Elos Crete isl. cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-418
EF568939.1/1-418 Orthometopon dalmatinum haplotype Idi Mnt Crete isl. cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-418
Orthometopon dalmatinum (N=4)
Orthometopon phaleronense (N=12); Orthometopon sp. (N=1)
EF568957.1/1-418 Orthometopon ferrarai haplotype Skala Lesvos isl. cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-418
EF568956.1/1-418 Orthometopon turcicum haplotype Agiasos Lesvos isl. cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-418
EF568958.1/1-418 Orthometopon sp. Ikaria cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-418
EF568959.1/1-418 Orthometopon sp. Patmos cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-418
EF568960.1/1-418 Orthometopon sp. Samos cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-418
EF568961.1/1-394 Orthometopon scheuerni haplotype Mugla Turkey cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-394
MK803245.1/28-615 Tylos granulatus isolate YZ26 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MZ540108.1/39-581 Tylos capensis isolate TcER02 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial
KJ468118.1/13-560 Tylos marcuzzii voucher MZUF 8660 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MT521213.1/71-658 Tylos ponticus voucher MT06358 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial
GU097619.1/1-282 Tylos europaeus isolate TP1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
GU097565.1/1-257 Helleria brevicornis isolate CAP1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468126.1/13-562 Tylos wegeneri voucher LACM 25 July 1985 J.A.Vargas cytochrome oxidase subunit I COI gene partial cds mitochondrial
KF007596.1/63-650 Tylos punctatus isolate Ensenada 281 4 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468120.1/13-583 Tylos niveus voucher Puerto Rico 28 1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
EU364624.1/71-658 Tylos neozelanicus voucher BES11448 cytochrome oxidase subunit I COX1 gene partial cds mitochondrial
AB763432.1/52-627 Tylos granuliferus mitochondrial COI gene for cytochrome oxidase subunit I partial cds haplotype H001
KJ468121.1/13-563 Tylos opercularis voucher MZUF 9425 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468116.1/13-572 Tylos maindroni voucher MZUF 2156 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468112.1/13-562 Tylos exiguus voucher MZUF 8687 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468125.1/13-562 Tylos spinulosus voucher MZUF 1096 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468109.1/13-554 Tylos chilensis voucher MZUF 279 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KT424028.1/1-588 Mongoloniscus sinensis isolate X6 cytochrome c oxidase subunit I CoI gene partial cds mitochondrial/1-588
LC711269.1/76-663 Ligidium koreanum Shi124 Che2302 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-588
LC711253.1/76-663 Ligidium japonicum Oym15 Che2183 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-588
AB626262.1/76-663 Ligidium ryukyuense mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate iso-BS/1-588
MN810648.1/71-658 Ligidium hypnorum voucher ZFMK-TIS-2518709 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-588
DQ182820.1/34-621 Ligidium beieri isolate KEF3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-588
DQ182857.1/28-615 Ligidium beieri isolate PRU5 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-588
ON212598.1/82-508 Tauroligidium cf. stygium isolate 21Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-427
ON212584.1/79-506 Typhloligidium coecum isolate 35Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-428
ON212590.1/79-506 Typhloligidium karabijajae isolate 41Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-428
ON212582.1/79-506 Typhloligidium lithophagum isolate 19Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-428
ON212583.1/82-452 Typhloligidium lithophagum isolate 46Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-371
ON212579.1/79-506 Typhloligidium kovali isolate 47Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-428
DQ182827.1/35-622 Ligidium wemeri isolate LES1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-588
DQ182779.1/19-606 Ligidium eubeicum isolate EVII9 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-588
DQ182825.1/34-621 Ligidium ghigii isolate KOS3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-588
DQ182831.1/38-625 Ligidium cycladicum isolate ANDI2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-588
MT521243.1/71-658 Ligidium germanicum voucher ZSM-BC-27349-D11 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-588
0.07

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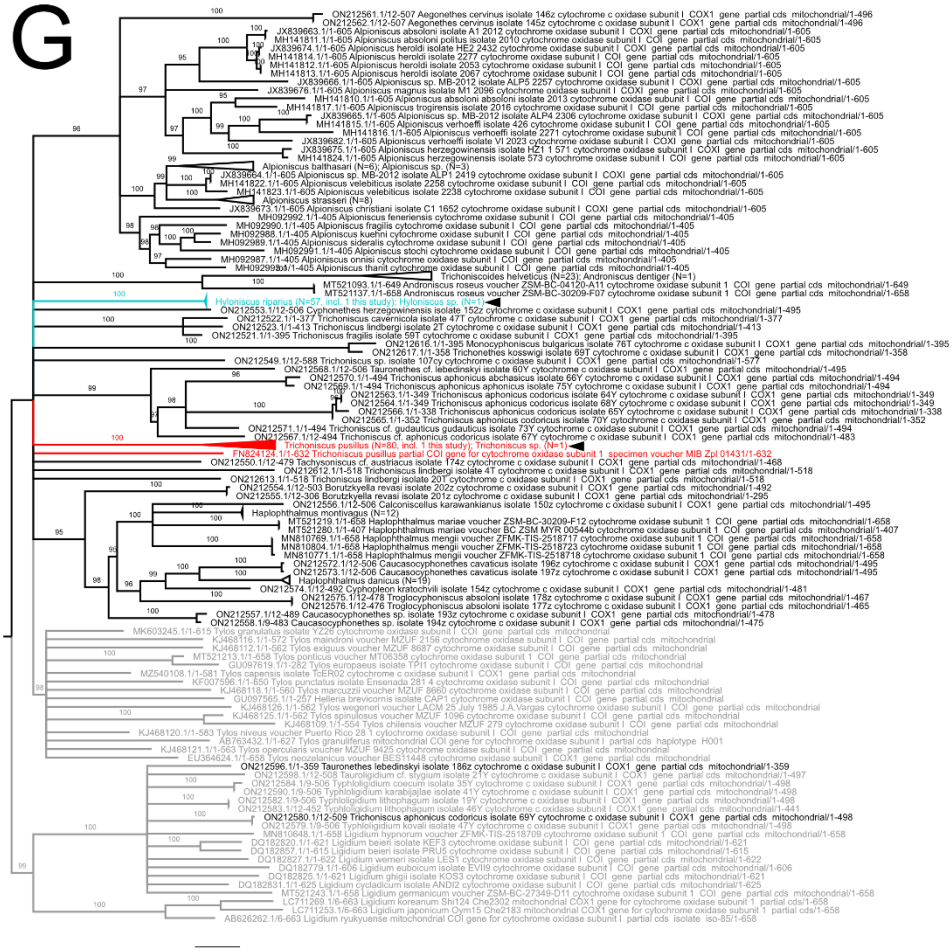

ON212561.1/12-507 Aegonethes cervinus isolate 146z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-496
ON212562.1/12-507 Aegonethes cervinus isolate 145z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-496
JX839663.1/1-605 Alpiniscus absoloni isolate A1 2012 cytochrome oxidase subunit I COXI gene partial cds mitochondrial/1-605
MH141811.1/1-605 Alpiniscus absoloni politus isolate 2010 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
JX839674.1/1-605 Alpiniscus heroldi isolate HE2 2432 cytochrome oxidase subunit I COXI gene partial cds mitochondrial/1-605
MH141814.1/1-605 Alpiniscus heroldi isolate 2277 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
MH141812.1/1-605 Alpiniscus heroldi isolate 2053 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
MH141813.1/1-605 Alpiniscus heroldi isolate 2067 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
JX839666.1/1-605 Alpiniscus sp. MB-2012 isolate ALP5 2257 cytochrome oxidase subunit I COXI gene partial cds mitochondrial/1-605
JX839678.1/1-605 Alpiniscus magnus isolate M1 2096 cytochrome oxidase subunit I COXI gene partial cds mitochondrial/1-605
MH141810.1/1-605 Alpiniscus absoloni absoloni isolate 2013 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
MH141817.1/1-605 Alpiniscus trogirensis isolate 2016 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
JX839665.1/1-605 Alpiniscus sp. MB-2012 isolate ALP4 2306 cytochrome oxidase subunit I COXI gene partial cds mitochondrial/1-605
MH141815.1/1-605 Alpiniscus verhoeffi isolate 426 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
MH141816.1/1-605 Alpiniscus verhoeffi isolate 2271 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
JX839682.1/1-605 Alpiniscus verhoeffi isolate VI 2023 cytochrome oxidase subunit I COXI gene partial cds mitochondrial/1-605
JX839675.1/1-605 Alpiniscus herzegowinensis isolate HZ1 1 571 cytochrome oxidase subunit I COXI gene partial cds mitochondrial/1-605
MH141824.1/1-605 Alpiniscus herzegowinensis isolate 573 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
Alpiniscus balthasari (N=6); Alpiniscus sp. (N=3)
JX839664.1/1-605 Alpiniscus sp. MB-2012 isolate ALP1 2419 cytochrome oxidase subunit I COXI gene partial cds mitochondrial/1-605
MH141822.1/1-605 Alpiniscus velebiticus isolate 2258 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
MH141823.1/1-605 Alpiniscus velebiticus isolate 2238 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-605
Alpiniscus strasseri (N=8)
JX839673.1/1-605 Alpiniscus christiani isolate C1 1652 cytochrome oxidase subunit I COXI gene partial cds mitochondrial/1-605
MH092992.1/1-405 Alpiniscus feneriensis cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-405
MH092990.1/1-405 Alpiniscus fragilis cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-405
MH092988.1/1-405 Alpiniscus kuehni cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-405
MH092989.1/1-405 Alpiniscus sideralis cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-405
MH092991.1/1-405 Alpiniscus stochi cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-405
MH092987.1/1-405 Alpiniscus onnisi cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-405
MH092993.1/1-405 Alpiniscus thanit cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-405
Trichoniscoides helveticus (N=23); Androniscus dentiger (N=1)
MT521093.1/1-649 Androniscus roseus voucher ZSM-BC-04120-A11 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-649
MT521137.1/1-658 Androniscus roseus voucher ZSM-BC-30209-F07 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-658
Hyloniscus riparius (N=57, incl. 1 this study); Hyloniscus sp. (N=1)
ON212553.1/12-506 Cyphonethes herzegowinensis isolate 152z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-495
ON212522.1/1-377 Trichoniscus cavernicola isolate 47T cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-377
ON212523.1/1-413 Trichoniscus lindbergi isolate 2T cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-413
ON212521.1/1-395 Trichoniscus fragilis isolate 59T cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-395
ON212616.1/1-395 Monocyphoniscus bulgaricus isolate 76T cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-395
ON212617.1/1-358 Trichonethes kosswigi isolate 69T cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-358
ON212549.1/12-588 Trichoniscus sp. isolate 107cy cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-577
ON212568.1/12-506 Tauronethes cf. lebedinskyi isolate 60Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-495
ON212570.1/1-494 Trichoniscus aphonicus abchasicus isolate 66Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-494
ON212569.1/1-494 Trichoniscus aphonicus aphonicus isolate 75Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-494
ON212563.1/1-349 Trichoniscus aphonicus codoricus isolate 64Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-349
ON212564.1/1-349 Trichoniscus aphonicus codoricus isolate 68Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-349
ON212566.1/1-338 Trichoniscus aphonicus codoricus isolate 65Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-338
ON212565.1/1-352 Trichoniscus aphonicus codoricus isolate 70Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-352
ON212571.1/1-494 Trichoniscus cf. gudauticus gudauticus isolate 73Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-494
ON212567.1/12-494 Trichoniscus cf. aphonicus codoricus isolate 67Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-483
Trichoniscus pusillus (N=80, incl. 1 this study); Trichoniscus sp. (N=1)
FN824124.1/1-632 Trichoniscus pusillus partial COI gene for cytochrome oxidase subunit 1, specimen voucher MIB Zpl 01431/1-632
ON212550.1/12-479 Tachysoniscus cf. austriacus isolate 174z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-468
ON212612.1/1-518 Trichoniscus lindbergi isolate 4T cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-518
ON212613.1/1-518 Trichoniscus lindbergi isolate 20T cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-518
ON212554.1/12-503 Borutzkyella revasi isolate 202z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-492
ON212555.1/12-306 Borutzkyella revasi isolate 201z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-295
ON212556.1/12-506 Calconiscellus karawankianus isolate 150z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-495
Haplophthalmus montivagus (N=12)
MT521219.1/1-658 Haplophthalmus mariae voucher ZSM-BC-30209-F12 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521280.1/1-407 Haplophthalmus mariae voucher BC ZSM MYR 00544b cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-407
MN810769.1/1-658 Haplophthalmus mengii voucher ZFMK-TIS-2518717 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810804.1/1-658 Haplophthalmus mengii voucher ZFMK-TIS-2518723 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810771.1/1-658 Haplophthalmus mengii voucher ZFMK-TIS-2518718 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
ON212572.1/12-506 Caucasocyphonethes cavaticus isolate 196z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-495
ON212573.1/12-506 Caucasocyphonethes cavaticus isolate 197z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-495
Haplophthalmus danicus (N=19)
ON212574.1/12-492 Cyphopleon kratochvili isolate 154z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-481
ON212575.1/12-478 Troglocyphoniscus absoloni isolate 178z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-467
ON212576.1/12-476 Troglocyphoniscus absoloni isolate 177z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-465
ON212557.1/12-489 Caucasocyphonethes sp. isolate 193z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-478
ON212558.1/9-483 Caucasocyphonethes sp. isolate 194z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-475
MK603245.1/1-615 Tylos granulatus isolate YZ29 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468116.1/1-572 Tylos maindroni voucher MZUF 2156 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468112.1/1-562 Tylos exiguus voucher MZUF 8687 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MT521213.1/1-658 Tylos ponticus voucher MT06358 cytochrome oxidase subunit I COI gene partial cds mitochondrial
GU097619.1/1-282 Tylos europaeus isolate TP11 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MZ540108.1/1-581 Tylos capensis isolate TcER02 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial
KF007596.1/1-650 Tylos punctatus isolate Ensenada 281 4 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468118.1/1-560 Tylos marcuzzii voucher MZUF 8660 cytochrome oxidase subunit I COI gene partial cds mitochondrial
GU097565.1/1-257 Helleia brevicornis isolate CAP1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468126.1/1-562 Tylos wegeneri voucher LACM 25 July 1985 J.A.Vargas cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468125.1/1-562 Tylos spinulosus voucher MZUF 1096 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468109.1/1-554 Tylos chilensis voucher MZUF 279 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468120.1/1-583 Tylos niveus voucher Puerto Rico 28 1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
AB763432.1/1-627 Tylos granuliferus mitochondrial COI gene for cytochrome oxidase subunit I partial cds haplotype H001
KJ468121.1/1-563 Tylos opercularis voucher MZUF 9425 cytochrome oxidase subunit I COI gene partial cds mitochondrial
EU364624.1/1-658 Tylos hexagonicus voucher BES11448 cytochrome oxidase subunit I COX1 gene partial cds mitochondrial
ON212596.1/1-359 Tauronethes lebedinskyi isolate 186z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-359
ON212598.1/12-508 Tauroligidium cf. stygium isolate 21Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-497
ON212594.1/9-506 Typhloligidium cavicolum isolate 35Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212590.1/9-506 Typhloligidium karabajalae isolate 41Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212582.1/9-506 Typhloligidium lithophagum isolate 19Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212583.1/12-452 Typhloligidium lithophagum isolate 46Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-441
ON212580.1/12-509 Trichoniscus aphonicus codoricus isolate 69Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212579.1/9-506 Typhloligidium kovali isolate 47Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
MN810648.1/1-658 Ligidium hypnorum voucher ZFMK-TIS-2518709 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
DQ182820.1/1-621 Ligidium beieri isolate KEF3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182857.1/1-615 Ligidium beieri isolate PRU5 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-615
DQ182827.1/1-622 Ligidium werneri isolate LES1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-622
DQ182779.1/1-606 Ligidium eubocum isolate EVI9 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-606
DQ182825.1/1-621 Ligidium ghigii isolate KOS3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182831.1/1-625 Ligidium cyclaticum isolate ANDI2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-625
MT521243.1/1-658 Ligidium germanicum voucher ZSM-BC-27349-D11 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
LC711269.1/6-663 Ligidium koreanum Sh124 Che2302 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
LC711253.1/6-663 Ligidium japonicum Oym15 Che2183 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
AB626262.1/6-663 Ligidium ryukyuense mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate iso-85/1-658
0.1



Figure 2.4: Maximum likelihood phylogeny of sowbug 18S sequences aligned with the E-INS-I algorithm. Sequences are colored by family. Families represented by a single sequence are colored black. *Nagurus cristatus* sequences (Trachelipodidae) are at the top of the phylogeny in a clade containing Scyphacidae, Porcellionidae, and *Levantoniscus*. Numbers above nodes show ultrafast bootstrap support. Nodes with <70% ultrafast bootstrap support are collapsed.



Figure 2.5: Compilation of distribution maps of terrestrial isopod species (Isopoda: Oniscidea) found in Canada, sorted by family. Zoom to see details or see Appendix A Fig. A6 for larger individual maps. Maps show only the Canadian distribution for each species. For distribution in other parts of North America, see Jass and Klausmeier (2000; 2001). Records with the locality listed at province-level are boxed; two records for *Ligia pallasii* appear to be located in Washington due to coordinate imprecision and are also boxed. Doubtful records are indicated with a question mark (see main text for details). Symbols indicate the source of a record: square = previous publication; 5-point star = collections from this study; 4-point star = citizen science initiative from this study; diamond = BugGuide; circle = iNaturalist; triangle = GBIF; heart = E.H. Strickland Entomological Museum.

Chapter 3.

Symbionts of sowbugs (Isopoda: Oniscidea) in Alberta and British Columbia with a review of the sowbug symbiome

3.1. Introduction

Introduced species can have enormous medical, economic, and ecological impact on areas to which they are introduced (Pyšek and Richardson 2010; Bradshaw *et al*. 2016). Ecological changes resulting from species introduction include trophic reorganization due to the presence of a new consumer or food source (Britton *et al*. 2018), changes in disease dynamics among native species resulting from the addition of a new host (Young *et al.* 2017), or a decline in native species via predation by or competition with the introduced species (Usio *et al*. 2001; Hautier *et al*. 2011). Indirect impact of an introduced species can result from co-introduction of species located internally or externally on the introduced species (Bojko *et al.* 2021; Foster *et al.* 2021), including commensals, mutualists, parasitoids and parasites (hereafter "symbionts"). The impact of co-introduced symbionts on an environment to which they are introduced may equal or even surpass the impact caused by their host (Bojko *et al*. 2021; Foster *et al*. 2021). Introduced symbionts may include parasites that are more virulent in native species than their introduced host, resulting in population declines in native species (Lymbery *et al*. 2014; Vilcinskas 2015) or may include species that negatively impact human health, such as helminth parasites carried by rats (*Rattus*) (Monte *et al*. 2012; Morand *et al*. 2015). It is important to determine what symbionts are associated with introduced species to fully assess the impact they can have on

areas to which they are introduced (Bojko *et al*. 2021; Foster *et al*. 2021). This is particularly important for species that are frequently introduced to new areas.

Terrestrial isopods, also known as sowbugs, are crustaceans belonging to the suborder Oniscidea (Schmidt 2008). With over 3700 species, sowbugs form the largest isopod suborder (Schmalfuss 2004; Sfenthourakis and Taiti 2015) and are one of the few groups of crustaceans with fully terrestrial members (Richardson and Araujo 2015). Sowbugs typically feed on plant detritus (Zimmer 2002) but may also consume seeds (Saska 2008), dead animal matter (Kensley 1974) and live plants (Johnson *et al*. 2012). Sowbugs are found worldwide and occupy a range of different habitats, including caves, deserts, shorelines, ant nests, and urban areas (Hornung 2011; Szlavecz *et al*. 2018), but the highest species diversity occurs in the Mediterranean region and other areas with temperate climates (Sfenthourakis and Hornung 2018). Sowbugs are readily transported to new areas via human activity, and some species have established populations in many different parts of the world (Jass and Klausmeier 2000; Schmalfuss 2004; Szlavecz *et al.* 2018). Human-mediated cross-continental sowbug introductions may have originally occurred through transport of soil ballast on ships (Lindroth 1957), and present-day introduction may take place through sale of sowbugs as pet food (Cochard *et al*. 2010), as pets themselves (e.g. Jungle Jewel Exotics 2023), through shipment of building materials (Slabber and Chown 2002) and gravel (McQueen 1976), or via shipment of soil, plants, and other gardening supplies to greenhouses and gardens (Hatch 1947; Jass and Klausmeier 2000; Vilisics and Hornung 2009; Cochard *et al.* 2010; De Smedt *et al*. 2017).

Sowbugs may directly impact areas to which they are introduced by altering soil microbe communities through feeding on detritus (Des Marteaux *et al*. 2020) and causing damage to crops in fields and greenhouses if their populations reach large numbers (Messelink and

Bloemhard 2007; Souty-Grosset and Faberi 2018). However, non-native sowbugs species in Europe have been said to present little threat to the economy or to native ecosystems due to their being found only in urban environments (Cochard *et al.* 2010), although in some cases non-native sowbugs in Europe have also been found in natural areas (Gongalsky *et al*. 2013; Gongalsky and Kuznetsova 2021). Indirect impact of sowbugs on areas to which they are introduced may occur through co-introduction of symbiotic species. Symbionts of sowbugs include several taxa with ecological, economic, or medical importance. These include the trematode *Platynosomum illiciens* (Braun) (= *P. fastosum* Kossak) which is distributed worldwide and causes platynosomiasis in domestic cats (Pinto *et al*. 2014; Pinto *et al*. 2018). Other trematodes for which sowbugs are intermediate hosts include species of *Lypersomum* and *Maritrema*, which infect birds (Hendow and James 1988; Hildebrand *et al*. 2019). Sowbugs are intermediate hosts for several genera of nematodes that infect wild and domesticated birds (Carreno 2008) and are also intermediate hosts for acanthocephalans (Marchand and Grita-Timoulali 1991; Vakarenko and Lisitsina 2001; Dimitrova 2009) that infect birds, mammals, reptiles and fishes (Smales 2007; Salgado-Maldonado and Novelo-Turcotte 2009; Nakao 2016; Muhammad *et al*. 2019; Steinauer *et al*. 2020).

Given the prevalence of introduced sowbugs in many parts of the world and the fact that sowbugs are readily introduced to new areas, it is important to catalogue the symbiomes of sowbugs in their non-native ranges to determine which symbionts have been co-introduced to these areas, and in their native ranges to determine what symbionts could potentially be co-introduced in the future. Prior studies of sowbug symbionts have typically focused on the relationship between a single species of symbiont and a limited number of sowbug species (Poinar 1981; Abd El-Aal and Holdich 1987; Baird 1999; Levri and Coppola 2004; Dimitrova

2009; Yoshino and Waki 2021). Rarely, relationships between many sowbug and symbiont taxa have been compiled (Vandel 1960, 1962; Siddikov 1987), but only for a limited geographic area that typically represents the native range for most of the sowbug species included in these lists. Surveys of symbiont diversity on introduced populations of sowbugs are lacking, even in areas where introduced sowbugs are extremely common. Sowbugs from Europe have been introduced extensively across North America (Hatch 1947; Jass and Klausmeier 2000) and at northern latitudes (e.g. Canada), native sowbugs are limited to the coasts, with sowbugs in non-coastal provinces consisting almost entirely of non-native species (see Chapter 2). Symbionts have been recorded from non-native European sowbugs in the United States, and include mites (Cordaux *et al.* 2001), acanthocephalans (Schmidt and Olsen 1964; Levri and Coppola 2004), flies (Jones 1948; Sassaman and Garthwaite 1984), and nematodes (Poinar 1981). Sowbugs in Canada have never been examined to assess symbiont diversity. The only published record of a non-bacterial sowbug symbiont from Canada is the nematode *Caenorhabditis remanei* Sudhaus, which was recovered from unidentified sowbugs in Ontario (Dey *et al*. 2012). Without a global list of sowbug-associated taxa and examination of symbiont diversity in non-native sowbug populations, is difficult to assess the indirect impact of introduced sowbugs via their co-introduced symbiotic species.

Introduced populations of a species often have lower levels of parasitism than native populations, even when accounting for infection by parasites native to their introduced range (Torchin *et al*. 2002, 2003). This is consistent with the enemy-release hypothesis, which relates the success of introduced species to their “escape” from many of the predators and parasites in their native range (Keane and Crawley 2002; Colautti *et al*. 2004; Vilcinskas 2015). The reasons why parasites and other symbionts may be lacking in introduced populations of a species have

been reviewed previously (Torchin *et al*. 2002; Colautti *et al*. 2004; Dunn 2009). These reasons include failure for parasites to be introduced in the first place due to low prevalence of the parasite in the native population, death of parasitized individuals due to increased stress during transport, and lack of required hosts in the introduced range. The latter may be due to low density of the introduced species, reducing transmission (Torchin *et al.* 2002), or to a lack of one or more additional host species for parasites with complex life cycles (Torchin *et al.* 2002, 2003; Lymbery *et al*. 2014). Introduced sowbugs in Canada and other areas may therefore lack many of the parasitic symbionts recorded from conspecific populations in their native range, and any parasites associated with introduced sowbugs from Canada and other areas would likely have direct (single host) life cycles. Climate may also play a role in further reducing the number of introduced symbiont species. Symbiont species may be more sensitive to extreme temperatures than their hosts (Olsen *et al*. 2015), or hosts infected with a parasitic taxon may experienced increased mortality in harsh conditions (Knapp *et al*. 2022) which may lead to the loss of parasites in the introduced population. Since non-native sowbugs in Canada originate primarily from Europe (see Chapter 2; Jass and Klausmeier 2000), sowbugs from climatically mild coastal areas of British Columbia may have a greater diversity of symbionts than sowbugs from the relatively drier and colder climate of central Alberta (Environment and Climate Change Canada, 2020a, 2020b).

This study is the first to survey symbionts associated with introduced sowbugs in Canada, with emphasis on Alberta and British Columbia. I also include a review of the sowbug symbiome, including all metazoans with a documented non-predatory association with at least one species of sowbug. A representative list of symbiotic non-metazoans (bacteria, viruses, protists, and fungi) is given rather than an exhaustive list because of the incredibly high diversity

of sowbug microbial communities, which is comparable to that found in termites (Dittmer *et al*. 2016). This review will facilitate identification of sowbug-associated symbionts in future studies and aid in determining what symbionts are present in introduced and native sowbug populations, allowing assessment of the potential impact of introduced sowbugs on native ecosystems through co-introduction of their symbionts.

3.2. Methods

3.2.1. Literature review

To determine what types of symbionts may be present in sowbugs and how to detect them in Canadian sowbug populations, I conducted a literature review of all symbionts associated with sowbugs. This review was exhaustive for all symbiont taxa except bacteria and fungi, as sowbugs have extremely diverse microbiota (Dittmer *et al*. 2016). I conducted the review by searching for articles in Google Scholar using combinations of the keywords "parasite", "symbiont", "terrestrial isopod", "sowbug", "woodlice", and "woodlouse", as well as keywords for specific parasites ("cestoda", "trematoda", "diptera", "nematoda", "acanthocephala", etc.). This is similar to the search strategy proposed by Foster *et al*. (2021) for cataloguing the symbiome of introduced aquatic taxa. I obtained additional records from the Natural History Museum parasite database (https://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/database/search.jsp) and from lists compiled by previous authors, including summaries of the associations between the fly family Rhinophoridae and sowbugs (Herting 2017; Wood *et al*. 2018), a review of species of sowbugs infected by iridovirus and mermithid nematodes (Hess and Poinar 1985), a list of the arthropod hosts of "Trichomycetes" (Lichtwardt 1986), reviews of the sowbug gut microbiome (Kostanjšek *et al*. 2006; Bouchon *et al*. 2016), a review of sowbug hosts of *Plagiorhynchus cylindraceus* (Dimitrova 2009), and records of numerous sowbug-associated symbionts compiled by Vandel (1960, 1962). The original source for all listed associations was consulted and cited whenever possible. I did not include associations supported only by experimental infection, as these associations may not actually occur outside of lab conditions. I included associations found "accidentally" occurring in lab populations of sowbugs (i.e. not induced via experimental

infection) since these associations may have originated in the wild populations of sowbugs used to start the lab colony. Whenever possible I recorded each association using the currently accepted name for the symbiont and the sowbug host. In addition to taxonomic literature, I obtained taxon names from the List of Prokaryotic names with Standing in Nomenclature (LPSN) database (https://lpsn.dsmz.de/), the MycoBank database (https://www.mycobank.org/), the Integrated Taxonomic Information System (ITIS) database (https://www.itis.gov/) and the World Register of Marine Species (WORMS) database (https://www.marinespecies.org/index.php).

Recent molecular evidence suggests the sowbug family Ligiidae is polyphyletic, with *Ligia* more closely related to marine isopods (Dimitriou *et al*. 2019). This would result in the exclusion of *Ligia* from Oniscidea, while *Ligidium* and other genera formerly in Ligiidae would be assigned to the new family 'Ligidiidae' (Dimitriou *et al*. 2019). These changes would mean *Ligia* is not a terrestrial isopod and so should not be included in this review, and that *Ligidium* should be listed under the family Ligidiidae instead of Ligiidae. Both these changes are debated on the grounds that they do not match morphological evidence that supports the monophyly of Oniscidea (Tabacaru and Giurginca 2021). The conflict between molecular and morphological evidence for the placement of Ligiidae has not yet been resolved. As *Ligia* has traditionally been considered part of Oniscidea, I have included *Ligia* in this list for continuity with older lists of sowbugs. For the same reason the name 'Ligiidae' is used in the old sense throughout this paper (i.e. including both *Ligia* and *Ligidium*).

3.2.2. Sowbug collections

My own collecting efforts focused on the greater Edmonton area (Alberta), with smaller opportunistic collections from British Columbia and Ontario (see Chapter 2 for details). I

collected sowbugs in the spring, summer, and fall from a variety of urban areas, disturbed natural areas (e.g. nature trails in residential areas), and relatively undisturbed natural areas (e.g. trails in rural areas). In addition to outdoor collections I also searched for sowbugs in greenhouses in the Edmonton area with permission from greenhouse managers. Collection methods were similar across all types of collection sites: I hand-collected sowbugs by turning over gravel and mulch and lifting items on the ground, and obtained smaller sowbugs from Tullgren funnel extractions from leaf piles and soil. All collected sowbugs were temporarily housed alive in containers with a damp paper towel until they were identified morphologically (see Chapter 2), checked for symbionts, and photographed, after which they were euthanized with carbon dioxide gas and either preserved in 95% ethanol for DNA extraction and molecular identification (see Chapter 2), preserved 70% ethanol as morphological vouchers, or dissected. My own collections were augmented with collections by colleagues from Newfoundland, British Columbia, Saskatchewan and Alberta. In most cases these were received after the sowbugs were preserved in ethanol, but several large collections of sowbugs from British Columbia were received live.

3.2.3. Symbiont survey

I examined live sowbugs with a dissecting microscope to look for external symbionts (mites) and internal symbionts visible through the transparent cuticle (e.g. mermithid nematodes, acanthocephalans, dipteran larva). I also checked for visual evidence of internal microbial infections, some of which turn the internal organs "milky" (Wijnhoven 2001a), and iridoviruses, which turn the sowbug an iridescent blue (Hess and Poinar 1985; Wijnhoven and Berg 1999). However, with the exception of checking one sowbug population for *Wolbachia* bacteria (see below), I did not use molecular methods to assess presence of bacteria, fungi, viruses, or protists; thus, I cannot state with certainty that lack of visual evidence of microbial infection reflected true

absence. Sowbugs from collections that were received after they had been preserved in ethanol were examined only for evidence of iridovirus infection; the blue coloration in the tissues is produced by the arrangement of viral particles and remains visible even after tissues have been prepared for electron microscopy (Lupetti *et al*. 2013). Live sowbugs were restrained with a piece of thin plastic wrap to enable detailed examination of the legs, cephalon, dorsal and ventral cuticle, and body cavity. With the exception of a few darkly pigmented *Porcellio scaber* Latreille individuals, all sowbugs examined in this study exhibited translucent sternites through which the internal organs (e.g., gut, hepatopancreas, testes) were clearly visible (Fig. 3.1). As sex ratios strongly biased towards females may indicate the presence of feminizing *Wolbachia* bacteria (Rigaud *et al*. 1999, Sumi *et al*. 2017), I recorded sex-ratios from each collection site and noted the presence of any intersex individuals. I dissected up to 10 sowbugs per collection site with equal numbers of males and females (when possible) to look for internal symbionts. Individuals that exhibited atypical coloration or behavior (e.g. lethargic movements, pale color, external deformities, presence of visible parasites in the body cavity) were specifically chosen for dissection to maximize the chance of obtaining parasites; individuals were chosen randomly if none exhibited these features. I euthanized sowbugs with carbon dioxide gas and sprayed them with water prior to dissection to dislodge external nematodes. Dissection was performed with the sowbug immersed in water and consisted of separating the cephalon and pleon from the rest of the body (which also removed the digestive glands, testes (if present), and gut), followed by removal of the ovaries (if present) and the dorsal nerve cord, separation of the sternites and tergites in the pleon and pereion to expose the body cavity, and splitting the cephalon in half. The tissues were visually inspected for symbionts using a dissecting microscope. For each collection site I placed half of the total number of dissected sowbugs in a Baermann funnel to

extract small nematodes (Weller *et al*. 2010), and squashed the tissues from the remaining dissected sowbugs between two glass slides to look for trematode metacercariae and other encysted symbionts with a compound microscope. On two occasions I placed dissected sowbugs on an agar plate seeded with *Escherichia coli* (Migula) as an alternative method for collecting nematodes. I checked the funnel extractions daily for extracted nematodes and checked the plates daily for nematode tracks (Padmanabhan *et al.* 2012), and preserved any nematodes in 95% ethanol for molecular identification. Acanthocephalan proboscises, mites, and residual nematodes were deposited in the E.H. Strickland Entomological Museum collections (University of Alberta) under accession numbers UASM407297 - UASM407326. Sowbug hosts for these symbionts are deposited under accession numbers UASM407042 - UASM407364 (see Table 3.4).

3.2.4. Acanthocephalan processing

I everted acanthocephalan cystacanths in tap water before photographing them under a dissecting microscope, after which I preserved the proboscis in 95% ethanol as a morphological voucher and preserved the remainder of the body in 95% ethanol for molecular identification. DNA extraction, amplification, and sequencing of the cytochrome c oxidase subunit I (COI) barcode region was performed by the University of Alberta Molecular Biology Service Unit (MBSU). DNA was extracted with a DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol, but with one final elution of 50 µl. PCR was performed using the primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HC02198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al*. 1994), with a reaction volume of 25 µl (5 µl DNA template, 2.5 µl of each primer (5 µM concentration), 2.5 µl of dNTPs (ThermoScientific R0241), 2.5 µl 10x Taq buffer, 0.25 µl of Taq (ThermoScientific EP0402),

0.25 µl BSA (New England Biolabs B9000S), 2.5 µl $MgCl_2$, 7 µl water). Amplification conditions consistent of initial denaturation at 95°C, followed by 5 cycles of 95°C for 30 seconds, 45°C for 40 seconds, and 72°C for 60 seconds, then 30 cycles with the annealing temperature elevated to 50°C, and a final extension at 72°C for 10 minutes. PCR products were purified with Cytiva Sera-Mag Select beads (Fisher Scientific 09928107) following the manufacturer's instructions and using a ratio of 0.85x beads to 1x PCR product.

3.2.5. Mite processing

I photographed mites *in situ* on their hosts, after which I removed the mites with a jet of water and slide-mounted 1-2 individuals for morphological identification. If mites were abundant I also preserved additional individuals in 95% ethanol for molecular identification. Slide-mounted mites were identified morphologically with keys (Lindquist and Evans 1965; Christian and Karg 2006; Lindquist *et al*. 2009; Moraza and Lindquist 2011; De Moraes *et al.* 2016; Moraza and Lindquist 2018) and by comparison to original species descriptions (Colloff and Hopkin 1987). Identifications were also confirmed by Drs. Alexandr Khaustov, Frederic Beaulieu and Dave Walter. Only one mite species was sufficiently abundant to undergo molecular identification via sequencing of the cytochrome c oxidase subunit I (COI) barcode region. I extracted DNA from two *Bakerdania elliptica* (Krczal) (Neopygmephoridae) with a DNeasy Blood and Tissue Kit (Qiagen) following a non-destructive extraction protocol (Dabert *et al*. 2008) but with a 48-hour incubation time after the addition of proteinase K, a final elution volume of 40 µl, and the addition of 4 µl of RNase A after incubation with proteinase K. I extracted DNA separately from each mite and slide-mounted the exoskeletons after DNA extraction as morphological vouchers. I used primers bcdF01 (5'-CATTTTCHACTAAYCATAARGATATTGG-3') (Dabert *et al*. 2010) and bcdR04 (5'-TATAAACYTCDGGATGNCCAAAAAA-3') (Dabert *et al*. 2008) to amplify

the COI barcode region. I followed the amplification protocol from Dabert *et al*. (2008) but with a denaturation temperature of 85°C and a 10 µl reaction volume consisting of 4 µl of DNA template, 0.5 µl of each primer (10 µM) and 5 µl of AccuStart II GelTrack® PCR SuperMix (Quantabio). I assessed amplification success with gel electrophoresis, cleaned amplified DNA with a column-based PCR cleanup kit (Truin Science) and submitted the samples to the Molecular Biology Service Unit (MBSU) for bidirectional Sanger sequencing.

3.2.6. Nematode processing

I photographed nematodes with a compound microscope prior to preserving them in 95% ethanol for molecular identification. Several specimens were preserved in DESS (dimethyl sulphoxide, disodium EDTA and NaCl) instead of ethanol; these were washed thoroughly in water prior to DNA extraction. I extracted DNA from nematodes using Method C described by Orlando *et al*. (2020) and amplified ~1000 bp of the 18S gene with primers Nem_18S_F (5'-CGCGAATRGCTCATTACAACAGC-3') and Nem_18S_R (5'- GGGCGGTATCTGATCGCC-3') (Floyd *et al*. 2005), which are designed to amplify 18S from a wide variety of nematodes. I followed the PCR amplification protocol designed for these primers (Floyd *et al*. 2005). In most cases I extracted DNA from single nematodes. At one collection site nematodes were numerous but extremely small, so I extracted DNA from multiple (3-10) nematodes combined in one sample. I assessed amplification success with gel electrophoresis, cleaned amplified DNA with a column-based PCR cleanup kit (Truin Science), and submitted the samples to the Molecular Biology Service Unit (MBSU) for bidirectional Sanger sequencing. For nematode samples where 18S amplification was unsuccessful, I attempted to amplify the cytochrome c oxidase I (COI) barcode region using nematode-specific COI primers NEM_COI_F (5'-GGWSMAMMAAATCATAAAGATATTGG-3') and NEM_COI_R (5'-

GTAATAGCMMCHGCYAAHACMG -3') (Malysheva *et al.* 2016). Amplification conditions followed those specified by Malysheva *et al.* (2016). The reaction volume was 25 µl and contained 1 µl of template DNA, 0.5 µl of each primer (10 µM), 11.5 µl of water, and 11.5 µl of AccuStart II GelTrack® PCR SuperMix (Quantabio). I assessed amplification success with gel electrophoresis.

3.2.7. Molecular identification of symbionts

To identify sowbug symbionts molecularly, I manually trimmed and aligned forward and reverse reads using JalView (Waterhouse *et al*. 2009) to create consensus COI sequences for mites and acanthocephalans and consensus 18S sequences for nematodes. I searched for similar COI and 18S sequences in NCBI BLAST (Altschul *et al*. 1990) using default settings, and also searched for similar COI sequences in BOLD (Ratnasingham and Hebert 2007). Probable species identity for acanthocephalans and nematodes was assigned based on high percent identity (>98%) to an existing sequence. The identity of *Bakerdania elliptica* could not be assessed molecularly, as no COI sequences of Neopygmephoridae were available for comparison from either GenBank or BOLD. Nematode 18S sequences obtained in this study are deposited in GenBank under accession numbers PQ001363 - PQ001369, acanthocephalan COI sequences are deposited under accession numbers PQ002160 and PQ002161, and the *Bakerdania elliptica* COI sequence is deposited under accession number PQ008649.

I also assessed nematode identities by constructing phylogenies to determine whether each sequence was included in a well-supported (>95%) single-species clade. I constructed a maximum likelihood phylogeny for each genus of nematode obtained in this study to assess the feasibility of identifying the nematodes to species level based on their partial 18S sequences. Each phylogeny contained all partial 18S sequences from every species level representative of

the genus available from GenBank (https://www.ncbi.nlm.nih.gov/nucleotide/) as well as the sequence(s) from each genus that were obtained in this study. I constructed a separate phylogeny for *Panagrolaimus*, *Pristionchus* and *Aphelenchoides*, but combined *Oscheius* and *Rhabditis* in a single phylogeny because of the close affinity of these taxa (Abolafia and Peña-Santiago 2019) and because the same species were sometimes placed in both *Oscheius* and *Rhabditis* in GenBank. There were no partial 18S sequences of *Rhabditophanes* available on GenBank that had been identified to species level, and so it was not possible to construct a phylogeny to assess the possibility of using partial 18S to identify members of this genus. Outgroup taxa for each phylogeny were chosen based on the relationships between genera indicated in previous studies (Fang *et al*. 2014; Susoy *et al*. 2015; Fanelli *et al*. 2017; Abolafia and Peña-Santiago 2019; Schurkman *et al*. 2022). I aligned each set of sequences separately for each genus using MAFFT (Nakamura *et al*. 2018) with the E-INS-I alignment algorithm, which is recommended for RNA polymerase sequences (https://mafft.cbrc.jp/alignment/software/algorithms/algorithms.html). After inspecting and manually trimming the alignments using JalView (Waterhouse *et al*. 2009), I constructed each phylogeny with IQ-TREE version 2.2.2.7 (Nguyen *et al*. 2015). I used ModelFinder (Kalyaanamoorthy *et al*. 2017) to test substitution models and choose the model with the lowest Bayesian information criterion (BIC) score for each phylogeny (-m MFP). Phylogenies were assessed with ultrafast bootstrap (Hoang *et al*. 2018) using 5000 replicates (-B 5000) and allowing up to 5000 bootstrap iterations (-nm 5000). Finally, I used FigTree (Rambaut 2009) and TreeGraph2 (Stöver and Müller 2010) to format the phylogenies for easier interpretation.

3.2.8. *Wolbachia* screening

PCR-based detection of *Wolbachia* in arthropods is common and effective, and many primers are available for this purpose (Simões *et al*. 2011). I chose the primers 553F_W (5'-CTTCATRYACTCGAGTTGCWGAGT-3') and 1334R_W (5'-GAKTTAAAYCGYGCAGGBGTT-3') (Simões *et al*. 2011) for detecting *Wolbachia* in sowbugs. These primers target 781 bp of the *Wolbachia* 16S gene and exhibit both high specificity and sensitivity to a variety of *Wolbachia* supergroups, including supergroup B (Simões *et al*. 2011), which is the most common group in sowbugs (Zimmermann *et al*. 2015). I screened one intersex *Porcellio spinicornis* Say individual and ten others from the same population for *Wolbachia* infection; DNA was extracted separately from the body and ovaries of the intersex individual to assess presence of *Wolbachia* in these tissues. I extracted sowbug DNA with a DNeasy Blood and Tissue Kit (Qiagen) according to the manufacturer's instructions with the following modifications: (1) tissue was ground with a pestle after adding buffer ATL; (2) incubation time was 3 hours after adding proteinase K; (3) 4 µl of RNAse A was added after incubation. As a positive control, I used the same protocol to extract DNA from four *Drosophila melanogaster* Meigen strain wMel3 (Bloomington Drosophila Stock Center #65281) which are known to contain *Wolbachia.* Flies were euthanized by freezing and were preserved in 95% ethanol. Since insect eye pigments can sometimes act as PCR inhibitors (Boncristiani *et al*. 2011), I removed the head from two of these flies prior to DNA extraction. Amplification conditions for *Wolbachia* 16S followed the protocol designed for these primers (Simões *et al*. 2011). I performed gel electrophoresis to assess *Wolbachia* presence based on the presence of amplified DNA of the correct size. To assess DNA extraction success, I also amplified the cytochrome c oxidase subunit I (COI) barcode region all of the *P. spinicornis* and *D.*

melanogaster that were assessed for *Wolbachia* presence. Residual ovarian tissues and other tissues from the intersex individual are deposited in the E.H. Strickland Entomological Museum collections (University of Alberta) under accession numbers UASM407378 - UASM407379, and conspecifics from the same collection site are deposited under accession numbers UASM407022 - UASM407025 and UASM407338 - UASM407340.

3.3. Results

3.3.1. Literature review

I found records of sowbug-associated symbionts in 202 publications. Metazoan and non-metazoan symbionts are summarized separately and are sorted by symbiont taxonomy (Table 3.1, Table C1) and by sowbug host taxonomy (Table 3.2, Table C2). Symbiont associations from sowbugs in Canada that were observed in this study (see details below) are included in these tables and are also summarized separately (Table 3.4). See the Discussion for an overview of the biology of the major groups of sowbug symbionts.

3.3.2. Sowbug collection and symbiont survey

My colleagues and I searched for sowbugs in 118 sites in Alberta, 14 sites in British Columbia, 22 in Newfoundland, 2 in Ontario, and 1 in Saskatchewan. The collection sites in Alberta included 15 greenhouses. Of the 2382 sowbugs collected, I examined 1292 live individuals for external parasites and signs of internal symbionts and examined 2246 live, ethanol-preserved or dead individuals for signs of iridovirus infection (i.e. blue coloration). All 498 sowbugs from Newfoundland had been preserved in ethanol and so were only examined for iridovirus. Of the 1292 live individuals examined for internal and external symbionts, most were *Porcellio spinicornis*, *P. scaber*, *Trachelipus rathkii* (Brandt) or *Cylisticus convexus* (De Geer) (Table 3.3). I dissected 241 sowbugs to look for internal symbionts, of which 236 were examined further to look for encysted symbionts (N=116 sowbugs) or for nematodes (N=120 sowbugs). I did not find evidence of iridovirus, trematodes, cestodes, mermithid nematodes or dipteran larva in any of the sowbugs I examined.

3.3.3. Acanthocephalans

There were no acanthocephalans in sowbugs from Alberta, but acanthocephalans were present in 1/29 *Porcellio scaber* from Parksville, British Columbia, and 1/9 and 1/76 *P. scaber* from two collections from Bamfield, British Columbia (Table 3.4). Each infected sowbug contained a single cystacanth occupying approximately 25-50% of the body cavity (Fig. 3.1). Cytochrome c oxidase subunit I (COI) barcodes from the acanthocephalans from Bamfield were 96% identical to each other, and both matched with >98% identity to *Plagiorhynchus cylindraceus* (Goeze) (=*P. transversus* (Rudolphi)) (GenBank NC_029767.1). It was not possible to compare the sequences with other Plagiorhynchidae, as the only plagiorhynchid COI sequences available on BOLD and GenBank were from *Plagiorhynchus cylindraceus* (=*P. transversus*).

3.3.4. Mites

I recovered several mite taxa from sowbugs from British Columbia and Alberta (Fig. 3.2). Mites were present on *Trachelipus rathkii* at two non-greenhouse sites in Edmonton, Alberta, with a prevalence of 1/60 (one unkeyable astigmatan nymph, cf. Acaridae, on the ventral surface) and 1/71 (one mite, Stigmaeidae, on the leg) (Table 3.4). Two *Cylisticus convexus* from a greenhouse in Edmonton each had a single mesostigmatan mite on the cephalon between the antennae. One was identified as *Lasioseius* cf. (*Crinidens*) sp. (Blattisociidae), and the other as *Proctolaelaps* sp. (Melicharidae). The only sowbug-associated mite found in British Columbia was *Bakerdania elliptica* (Prostigmata: Neopygmephoridae), which was not found on sowbugs from Alberta. These mites were always located on the posterior sternites of the host pereion, typically near the basis of the pleopods (Table 3.4). *Bakerdania elliptica* were present on 10/53 *Porcellio scaber* from Stanley Park, British Columbia, averaging 1.3 mites per individual (maximum 2), and on 7/25 *Oniscus asellus* Linnaeus from the same locality, averaging 2.6 mites per individual

(maximum 7). *Porcellio scaber* from Bamfield, British Columbia had 1-2 *B. elliptica* on 3/36 individuals. COI sequencing was successful from one of two *B. elliptica* specimens from Stanley Park, and yielded a sequence that most closely matched an unidentified species of Pygmephoridae with 80.24% identity (GenBank MF749028.1) and 81.01% identity (BOLD CNGIH195-13). There were no COI sequences from Neopygmephoridae on BOLD or GenBank.

3.3.5. Nematodes

I obtained several genera of nematodes from sowbugs in this study (Fig. 3.3; Table 3.4). Amplification of both partial 18S and COI was unsuccessful for all nematode samples that had been preserved in DESS, but partial 18S was successfully amplified for 7/9 nematode samples that had been preserved in 95% ethanol. COI amplification was unsuccessful for the two samples for which partial 18S failed to amplify. All partial 18S sequences matched with >97% identity to an existing sequence in GenBank (Table 3.4).

In Alberta, I recovered nematodes from several different sowbug species at a variety of sites. Nematodes were associated with 2/4, 1/5, 3/4, and 1/11 *Trachelipus rathkii* at four non-greenhouse sites in Edmonton, with 1-6 nematodes per sowbug. Amplification of partial 18S was successful for a single nematode each from two of these sites. One was a close match (99.76%) to *Rhabditophanes* sp. (GenBank LK995728.1). The other sequence was similar (97.4%) to *Panagrolaimus rigidus* (GenBank KC522706.1) and fell within a moderately-supported clade containing only *P. rigidus* (Schneider) and *P. superbus* (Fuchs) (Fig. 3.4). Sowbug-associated nematodes were also found in greenhouses. Three nematodes were obtained from a Baermann funnel extraction of five *Cylisticus convexus* from a greenhouse in Edmonton, and partial 18S sequences from two of these nematodes both matched closely (99.77%) to *Oscheius* sp. and *Oscheius myriophilus* (Poinar) (=*Rhabditis myriophila* Poinar) (GenBank AF082994.1,

U81588.1). The sequences fell within a moderately-supported clade containing only *Oscheius myriophilus* (=*Rhabditis myriophila*) when placed in a phylogeny with other *Oscheius* and *Rhabditis* partial 18S sequences (Fig. 3.5). At another Edmonton greenhouse, 1/7 *Porcellio spinicornis* had a single external nematode. Partial 18S from this nematode matched with 97.92% identity to *Aphelenchoides* sp. (GenBank JQ957884.1) and with 97.8% identity to *A. blastophthorus* Franklin (GenBank JQ957879.1). When this sequence was included in a phylogeny with other *Aphelenchoides* 18S sequences (including unidentified *Aphelenchoides* environmental samples), the sequence fell within a clade containing only *A. blastophthorus* and an *Aphelenchoides* environmental sample (Fig. 3.6). However, when the unidentified *Aphelenchoides* environmental DNA (eDNA) samples were removed prior to alignment, the clade collapsed into a polytomy that included *A. fragariae* (Ritzema Bos)*, A. centralis* Thorne & Malek*, A. limberi* Steiner*,* and *A. saprophilus* Franklin (Fig. C1).

In British Columbia, I found nematodes only on *Porcellio scaber*. One nematode was obtained from Baermann funnel extraction of five *P. scaber* from a site near Bamfield, but amplification of partial 18S from this sample was unsuccessful. At a second Bamfield collection site, 5/8 *P. scaber* had external nematodes, with 2 to >100 nematodes per individual. An additional seven nematodes were obtained from a Baermann funnel extraction of five other *P. scaber* from the same site. Amplification of partial 18S from two samples of the external nematodes was successful, and both yielded sequences that matched closely (99.55% and 99.88%) to *Pristionchus entomophagus* (Steiner) (GenBank KT188843.1). In a phylogeny with other *Pristionchus* partial 18S sequences, these sequences were placed in a well-supported clade containing both *P. lheritieri* (Maupas) and *P entomophagus* (Fig. 3.7).

3.3.6. Wolbachia

Most populations of *Porcellio spinicornis* in Alberta exhibited sex ratios with an excess of females, whereas populations of *Trachelipus rathkii,* another common species, did not appear to be consistently biased towards one particular sex (Fig. C2). One *Porcellio spinicornis* from a population in central Edmonton had reduced modified endopodites (i.e. male gonopods) (Fig. C3) but also had enlarged ovaries. Oostegites were present on the posterior sternites of the pereion, which would occur in a female sowbug undergoing a parturial molt to form a marsupium (Hornung 2011). The combination of ovaries and reduced male gonopods can be found in female-like intersex individuals resulting from partial *Wolbachia*-induced feminization (Herran *et al*. 2021). The sex ratio in the sowbug population containing the intersex individual was 24:25 (F:M) rather than the female-biased sex-ratios often reported for *Wolbachia*-infected sowbug populations (Bouchon *et al*. 1998; Rigaud *et al*. 1999; Ben Nasr *et al*. 2010; Sumi *et al*. 2017). My attempts to amplify *Wolbachia* 16S from the body and ovaries of the intersex individual did not yield any amplified DNA, as was also the case for ten other *P. spinicornis* from the same population. *Wolbachia* 16S also failed to amplify from all four *Wolbachia*-containing *Drosophila melanogaster* positive controls. However, COI amplification was successful from 12/12 *P. spinicornis* samples (including body and ovaries of the intersex individual) and 4/4 *D. melanogaster* that had also been assessed for *Wolbachia*, indicating that the lack of amplification success for *Wolbachia* 16S was not due to unsuccessful DNA extraction.

3.3.7. Other symbionts

A female *Porcellio scaber* from a greenhouse in Edmonton had a small growth resembling hepatopancreatic tissue that was associated with one of the ovaries. This tissue contained numerous spherical and ellipsoid objects that each contained a pair of circular structures (Fig. C4). The objects somewhat resemble yeast asci (Ascomycota) (see Fig. 3C in Zhou *et al*. 2019).

3.4. Discussion

3.4.1. General conclusions

I observed eleven taxa in association with introduced sowbugs in Canada. These include five nematode genera, one species of acanthocephalan and five species of mites. Four of the five nematode genera and all mites except *Bakerdania elliptica* have never been recorded from sowbugs. Nine of the eleven taxa associated with sowbugs in Canada likely have a phoretic or necromenic relationship with sowbugs and are not known to be obligate parasites of sowbugs or of other taxa. Dipteran parasitoids of sowbugs (Rhinophoridae), trematodes, mermithid nematodes, obligate parasitic nematodes and iridovirus were not observed in any of the sowbugs examined, despite these taxa having been recovered from conspecific sowbugs in Europe. For example, Canadian populations of the sowbug *Porcellio scaber* examined in this study were associated with one mite (*Bakerdania elliptica*), one acanthocephalan (*Plagiorhynchus* cf. *cylindraceus*), and one nematode (*Pristionchus* cf. *lheritieri* / *entomophagus*), but European populations of this species contain a much wider variety of symbionts, including seven species of parasitoid flies (Rhinophoridae), one acanthocephalan (Echinorhychidae sp.), one species of parasitic nematode (*Dispharynx nasuta* (Rudolphi)), two species of necromenic nematodes (*Caenorhabditis remanei* and *C. elegans* (Maupas)), one mermithid nematode (*Thaumamermis cosgrovei* Poinar), two species of trematode (*Corrigia corrigia* Braun and *Lyperosomum petiolatum* (Railliet), and iridovirus (Table 3.2; Table C2). The relative lack of obligate parasitic taxa associated with introduced sowbugs in Canada when compared to European populations is consistent with prior observations of lower levels of parasitism in introduced populations of a species when compared to native populations (Torchin *et al*. 2002, 2003). Oddly, none of the three taxa associated with Canadian populations of *P. scaber* have been recorded in native

European populations of this species, despite the fact that two of the taxa, *Plagiorhynchus cylindraceus* and *Bakerdania elliptica*, are apparently native to Europe (Krczal 1959; Schmidt 1981; Skuballa *et al*. 2010). This may be because native populations of *P. scaber* have never been examined specifically for these taxa, which suggests there may be many taxa associated with native populations of sowbugs that have not yet been recorded.

The only definitely parasitic taxon I recovered from sowbugs in Canada was an acanthocephalan (Plagiorhynchidae: *Plagiorhynchus* cf. *cylindraceus*). This acanthocephalan has a complex life cycle in which sowbugs serve as intermediate hosts (Dimitrova 2009). *Plagiorhynchus cylindraceus* is thought to be native to Europe but has been introduced worldwide, possibly via introduction of sowbugs (Schmidt 1981; Skuballa *et al*. 2010). The presence of a non-native parasite with a complex lifecycle in sowbugs from Canada was unexpected, as parasites with complex lifecycles would theoretically be unlikely to persist in introduced populations due to low numbers of introduced hosts and the potential absence of one or more required hosts in a new area (Torchin *et al*. 2002, 2003; Lymbery *et al*. 2014). The survival of *P. cylindraceus* after its introduction in Canada may have been due to its ability to use a very wide variety of avian and mammalian taxa as final hosts (Llanos-Soto *et al.* 2019) and may have been further assisted by the presence of introduced European species such as European Starlings (*Sturnus vulgaris* Linnaeus) (Kessel 1953) which serve as a final host for *P. cylindraceus* in its native range (Connors and Nickol 1991).

Several species of nematodes in the genus *Aphelenchoides* are facultative plant parasites and are important pests of crop plants and ornamental plants (Nicol *et al*. 2011; Sanchez-Monge *et al*. 2015; An *et al*. 2017). It was not possible to determine whether the *Aphelenchoides* species associated with a sowbug in this study was a major plant parasite (*A. fragariae*), a minor plant

parasite (*A. blastophthorus* or *A. saprophilus*) or a fungivorous species (*A. centralis* or *A. limberi*) (Sanchez-Monge *et al*. 2015). If *Aphelenchoides* nematodes have a phoretic relationship with sowbugs, this suggests sowbugs could facilitate the spread of these nematodes among host plants, which is concerning given the tendency of introduced sowbugs to be associated with gardens and greenhouses (Hatch 1947; Rapp 2001; Korsós *et al*. 2002; Gregory 2014; De Smedt *et al.* 2017). Introduction of sowbugs may therefore indirectly result in economic impact if plant-parasitic nematodes are co-introduced, or if sowbugs facilitate transport of native plant-parasitic nematode species among host plants. However, only one *Aphelenchoides* individual was recovered from all sowbugs examined in this study, so the association may have been incidental rather than representing a common phoretic relationship.

Of the 39 extant sowbug families (Ahyong *et al*. 2011; Javidkar *et al*. 2015; Sfenthourakis and Taiti 2015), symbionts have been recorded from only 15, and of approximately 3710 described species of sowbugs (Schmalfuss 2004; Sfenthourakis and Taiti 2015), only 86 species have at least one recorded symbiont (Table 3.2). While it is possible that very few sowbug species have symbiotic relationships with other species, the lack of records is likely due to a lack of research. This study was the first to attempt to survey the entire eukaryotic diversity of symbiotic species associated with sowbugs in a particular area, and yielded eight taxa that had never been recorded in association with sowbugs, even though these sowbugs represented introduced populations and so had likely lost many associated taxa. Known sowbug associations therefore likely represent only a fraction of the total diversity of organisms associated with sowbugs. Prior to this study there were 62 species of non-fungal eukaryotic taxa that have been previously recorded in association with sowbugs. These taxa cover a wide taxonomic range and include multiple species with known economic, ecological, or medical

importance, including trematodes, cestodes, and parasitic nematodes. Introduced sowbugs therefore have the potential to have an indirect negative impact on areas to which they are introduced via their co-introduced symbiotic species. However, based on my observations, non-native European sowbugs in the Canadian Prairie Provinces carry very few symbionts, most of which are not obligate parasites, which suggests sowbug-associated parasitic symbionts may fail to establish if co-introduced. Additional sowbug symbiome surveys and studies of the biology of these interactions, particularly in sowbug native ranges, may yield a more complete picture of sowbug symbionts and aid in further evaluating the indirect effects of sowbugs on areas to which they are introduced.

Below is a summary of the major taxa that have been found symbiotically associated with sowbugs. Each section includes a discussion of the nature of the relationship between each taxon and their sowbug hosts, the life history of the symbiont, associations of the symbiont with other taxa (if applicable), and records of sowbug associations with the taxon that were obtained from this study (if applicable).

3.4.2. Viruses

Sowbugs can be infected by iridovirus IIV-31, which also infects beetles and nematodes (Hess and Poinar 1985; Karasawa *et al*. 2012). Infected sowbugs are easy to spot in the field, as infection and subsequent viral multiplication results in the host turning a bright iridescent blue or purple (Hess and Poinar 1985; Wijnhoven and Berg 1999). Iridovirus infection in sowbugs is both geographically and taxonomically widespread: sowbugs with abnormal blue or purple coloration have been found in North America, Europe, and Asia, and include 17 sowbug genera (Table C1). Infection prevalence is highly variable (Williams 2008): a population of *Armadillidium vulgare* Latreille in the United States had an infection prevalence of 5%, while

Porcellio dilatatus Brandt and *P. scaber* from the same area had infection prevalences of 45% and 15-20% respectively (Federici 1980; Cole and Morris 1980). Sowbugs may become infected through consumption of dead infected conspecifics or through puncture with an object contaminated with the virus (Cole and Morris 1980; Federici 1980). Dead individuals cease to be infectious after 5 days in laboratory conditions (Grosholz 1993). Viral particles multiply in the cytoplasm of multiple types of tissue in infected individuals (Federici 1980; Karasawa *et al.* 2012) and result in an increase in color intensity until death, which typically occurs within a month after infection (Federici 1980; Wijnhoven and Berg 1999; Lupetti *et al.* 2013). Sowbug behavior appears mostly normal throughout the course of the infection (Federici 1980) aside from decreased food consumption and response time (Wijnhoven and Berg 1999; Lupetti *et al.* 2013). Infected females are still able to brood and give birth to young (Lupetti *et al.* 2013). I did not find any evidence of iridovirus (i.e. blue coloration) in any of the sowbugs I examined for this study.

3.4.3. Bacteria

Sowbugs contain an extremely wide variety of bacteria (Table C1), comparable in diversity to the bacterial communities found in termites (Dittmer *et al*. 2016). Bacteria can be found within the hepatopancreas (Eberl 2010) where they are thought to aid digestion by producing enzymes that break down cellulose (Zimmer and Topp 1998). Other bacteria appear to be sowbug pathogens: *Porcellio scaber* infected with intracellular *Candidatus* Rhabdochlamydia porcellionis Kostanjšek *et al*. (=*Chlamydia isopodii* Shay *et al*.) (Chlamydiales) experience cellular damage and develop white spots on the hepatopancreas (Kostanjsek *et al.* 2004). The most studied bacterial symbiont occurring in sowbugs is *Wolbachia*, a genus of intracellular bacteria found in a wide variety of arthropods, including many crustaceans (Bouchon *et al.* 1998;

Cordaux *et al*. 2012). *Wolbachia* is widespread among sowbugs and occurs in at least 50 different species (Zimmermann *et al*. 2015). It is typically transmitted vertically (Rigaud *et al*. 1999) but horizontal transmission between termites and sowbugs may also occur (Zimmermann *et al*. 2021). The effects of *Wolbachia* on sowbugs include total or partial conversion of genetic males to functional females, which can sometimes result in an intersex phenotype (Ben Nasr *et al*. 2010; Herran *et al*. 2021), and cytoplasmic incompatibility, where mating between individuals harboring different strains of *Wolbachia* results in reduced reproductive success (Sicard *et al*. 2014). DNA can also be transferred from *Wolbachia* to its sowbug hosts: large portions of the *Wolbachia* genome have been incorporated into the genome of *Armadillidium vulgare*, where it functions as a sex chromosome due to its feminizing effect (Leclercq *et al*. 2016). *Wolbachia* infections are thought to influence the evolution of sowbug sex chromosomes (Leclercq *et al*. 2016; Chebbi *et al.* 2019).

One *Porcellio spinicornis* obtained in this study exhibited an intersex phenotype, which suggests *Wolbachia* may have been present in this individual and in others from the same population. It was not possible to determine whether this was the case, as amplification of *Wolbachia* from this individual and from the positive controls (*Drosophila melanogaster*) was unsuccessful. It is not clear why *Wolbachia* failed to amplify in the positive controls. The flies were from a stock that carries *Wolbachia* strain wmel3, which belongs to *Wolbachia* supergroup A (Wu *et al*. 2004; Riegler *et al*. 2005), and the primers that were used in this study are able to amplify this supergroup (Simões *et al*. 2011). *Wolbachia* may have failed to amplify from the sowbugs if the strain belonged to supergroup F, as the primers used in this study do not always amplify this supergroup (Simões *et al*. 2011). However, supergroup F occurs only rarely in sowbugs, with supergroup B being far more common (Zimmermann *et al*. 2021) and the primers

used in this study are capable of amplifying supergroup B (Simões *et al*. 2011). Populations of sowbugs infected with *Wolbachia* typically exhibit female-biased sex ratios due to feminization of genetic males (Bouchon *et al*. 1998; Rigaud *et al*. 1999; Ben Nasr *et al*. 2010; Sumi *et al*. 2017), but the population from which the intersex individual originated had an even sex ratio. It is therefore possible that the intersex phenotype observed in this study may have resulted from a mechanism other than *Wolbachia* infection. When *Wolbachia* failed to amplify in an intersex *Porcellio scaber* (Zarka *et al*. 2022), the authors hypothesized that viral infection or exposure to pollution may have been the cause of the intersex phenotype. The authors also noted that their COI control failed to amplify and suggested that degradation of the sample may have affected *Wolbachia* amplification success (Zarka *et al*. 2022). That was not the case in this study, as COI was amplified successfully from both the *Drosophila* controls and from the sowbug samples.

3.4.4. Protists

A variety of protists can be found in the liquid (water and excretory products) associated with the pleopods of sowbugs. These include the amoeboid protist *Discella ligidii* Němec (Němec 1895), at least three ciliate species (Němec 1895; Dogel and Fursenko 1920; Bonnefoy and Marchal 1942; Matthes 1949), and seven species of Oligohymenophorea (Cuénot 1891; Dogel and Fursenko 1920; Remy 1928; Bonnefoy and Marchal 1942; Matthes 1949; Vandel 1960; Paliyenko and Boshko 2002). These associations have only been recorded in sowbugs from Europe (Table C1). Pleopod-associated protist communities have been observed on sowbug genera that are closely associated with water, including *Ligia* and *Ligidium* (Němec 1895; Bonnefoy and Marchal 1942; Matthes 1949) but also on species with terrestrial lifestyles, including *Porcellio scaber* (Remy 1928; Paliyenko and Boshko 2002) and *Oniscus asellus* (Bonnefoy and Marchal 1942; Matthes 1949). The colonies formed by these protists vary in size:

up to 70 *Ballodora dimorpha* Dogiel & Furssenko have been recorded from a single sowbug (Dogel and Fursenko 1920) whereas *Chilodonella porcellionis* Dogiel & Furssenko has only been found with a maximum of 12 individuals per host (Dogel and Fursenko 1920). Prevalence also varies: in France, *Ballodora marceli* Remy prevalence on *Trichoniscus provisorius* Racovitza varied from 8 - 75% depending on the collection locality (Remy 1928). Pleopod-associated protists have been described as having a commensal relationship with their hosts (Cuénot 1891) and are thought to feed on bacteria found in the liquid surrounding the pleopods (Remy 1928). Some species are able to maintain their association with a sowbug host even when the sowbug molts: mobile *Ballodora dimorpha* move off the old cuticle and onto the new one, while sessile individuals remain attached by having previously passed the base of their body through the old cuticle and attached to the new one (Dogel and Fursenko 1920).

Two groups of former "Trichomycetes" contain species that are obligate symbionts of marine isopods and sowbugs. These include the Asellariales, which are now classified as fungi in the Kickxellomycota subphylum Kickxellomycotina (Tretter *et al*. 2014; Tedersoo *et al*. 2018), and the Eccrinales, which are mesomycetozoans (Cafaro 2005). Since the Asellariales share a very similar relationship to their sowbug hosts as the Eccrinales, the two groups are discussed together in this section. Both colonize the hindgut of their host and share similar life cycles: propagules exit via host feces and enter a new host via ingestion (Lichtwardt 1986). They are thought to be commensals (Lichtwardt 1986). Prevalence of Asellariales in populations of sowbugs varies from 1.4% (Chien and Hsieh 2001) to 30% (Suyama *et al*. 2021), and Eccrinales vary from 10% (Langlois 2017) to 20% (Tuzet and Manier 1947). Sowbug-associated Eccrinales and Asellariales are both extremely widespread and are associated with a diverse range of sowbug hosts (Table C1, C2). It is difficult to tell whether there is evidence of host specificity in

either of these groups, since both have very few records, although some species appear to be associated with particular sowbug genera (e.g. *Asellaria ligiae* Manier and *Ligia*) (Table C2).

Two groups of Conoidasida (Apicomplexa) have been reported from sowbugs: gregarines (Gregarinasina) and coccidia (Coccidiasina). Gregarines (Gregarinasina) are all symbionts of non-vertebrates and are hosted by both crustaceans and insects (Perkins *et al*. 2000; Clopton 2002). They are often located in the host gut (Perkins *et al*. 2000; Clopton 2002) where their effect can range from mutualistic to parasitic (Rueckert *et al*. 2019). Reports of gregarines from sowbugs are rare and consist of only two published records: gregarines were recovered from the seminal vesicle of a single *Chaetophiloscia elongata* (Dollfus) originating from a captive culture (Vandel 1962) and from a single *Armadillidium vulgare* (Criado-Fernelio *et al*. 2013). The scarcity of these records may be due to the structure of the sowbug gut, which could make them resistant to gregarine establishment (Crawley 1903). The majority of coccidia (Coccidiasina) are vertebrate parasites that are typically bloodborne and have invertebrate intermediate hosts (Perkins *et al*. 2000). The only record of coccidia in sowbugs comes from Europe, where "a coccidian" was present in three sowbug species (Thompson 1934). This association is mentioned in passing and is not supported by any morphological or molecular evidence, so it is possible that this record may represent a gregarine.

I did not find evidence of protists on or inside any of the sowbugs I examined for this study. However, aside from looking for sowbugs with an atypical appearance, I did not search specifically for protist symbionts via detailed pleopod and gut examination and molecular detection methods. It is therefore not possible to confirm that symbiotic protists were absent from the sowbugs examined in this study.

3.4.5. Fungi

An extremely wide variety of fungi are associated with sowbugs (a partial list is presented in Table C1), most of which occur in the gut and hepatopancreas (Kayang and Sharma 1999; Thanh *et al*. 2002; Marden 2019). Fungi associated with sowbugs can have a variety of relationships with their hosts. Some of the fungi found in sowbug guts can produce enzymes that degrade lignin and so may aid digestion, but there is no evidence of a consistent mycobiome across different sowbug individuals within the same species (Marden 2019). Other fungi are pathogenic: two fungal species, *Lecanicillium psalliotae* (Treschew) (=*Lecanicillium saksenae* Kushwaha) and *Clonostachys rosea* f. *catenulata* (Gilman & Abbot) caused mass mortality in lab cultures of sowbugs (pers. comm, N. Jones, 2023). Another possible fungal pathogen is an unknown "yeast-like organism" found in the hemolymph of wild populations of *Oniscus asellus*, *Haplophthalmus danicus* Budde-Lund, and *Porcellio scaber* from the Netherlands (Wijnhoven 2001a). Infected individuals were pale and swollen and died within a few weeks when kept in a lab culture, and as none of the infected females carried eggs, the fungi presumably inhibit reproduction. Lab cultures could become infected through contact with an individual that died from the disease, possibly via ingestion of infected material. Ectoparasitic fungi are potentially also associated with sowbugs: there is a record of "Laboulbeniaceen" [sic] (Laboulbeniales) on the legs, antennae, and setae of *Trachelipus arcuatus* (Budde-Lund) and *Trichoniscoides albidus* (Budde-Lund) from Germany (Graeve 1914). Laboulbeniales are obligate ectoparasites on a variety of arthropods (Haelewaters *et al*. 2021) but Graeve (1914) is the only record from sowbugs. Vandel (1962) suggested that the observation recorded by Graeve (1914) actually represents nematode eggs. Finally, some of the fungi associated with sowbugs are commensals. As the Asellariales

share a very similar relationship to their sowbug hosts as the Eccrinales, the two groups have been discussed together in the “Protists” section.

One *Porcellio scaber* I collected from a greenhouse in Edmonton contained structures resembling yeast asci (Ascomycota) (see Fig. 3C in Zhou *et al*. 2019). These were embedded in an abnormal tissue growth attached to one of the ovaries. The structures appear very similar to the unknown “yeast-like organisms” found in the hemolymph of sowbugs in the Netherlands (see Fig. 31 in Wijnhoven 2001a). However, the structures observed in this study were found embedded in tissue rather than floating in the hemolymph and were cylindrical rather than strongly ellipsoid, and the sowbug in this study did not exhibit the pale coloration exhibited by infected sowbugs in the Netherlands (Wijnhoven 2001a). These structures could be a different form of the same pathogen, a different type of fungal pathogen, a non-fungal organism, or possibly a cellular structure associated with abnormal growth of the tissue. Isolation of these structures from infected sowbugs followed by amplification of fungal barcode regions may help determine the identity of these structures.

3.4.6. Nematoda

Nematodes are hyperdiverse and hyperabundant, numbering in the billions of billions globally (van den Hoogen *et al*. 2019), so it is not surprising that some species are associated with sowbugs. Very little is known about many sowbug-associated nematodes outside of their association with a sowbug host, but others are well-studied. For example, the model species *Caenorhabditis elegans* (Rhabditidae) has been recorded from four sowbug species in Europe (Table 3.1) with which it may have a phoretic relationship (Petersen *et al*. 2015). It is not possible to determine whether *C. elegans* is associated externally or internally with the host because they are typically recovered by placing a sowbug on an agar plate and waiting for the

nematodes to leave the host (Barrière and Félix 2005; Cutter 2006; Petersen *et al*. 2015). A related species, *Caenorhabditis remanei*, can also be found associated with sowbugs. Hosts with *C. remanei* are indistinguishable from those without nematodes in terms of activity and reproductive output (Baird *et al*. 1994) so the association is thought to be necromenic: the nematodes remain as dauers (developmentally arrested juveniles) until their host dies, at which point they resume development, feed on bacterial growth, and reproduce (Baird *et al*. 1994). Several sowbug-associated nematodes are important parasites of birds: these include *Dispharynx nasuta*, *Acuaria* sp. and *Tetrameres mohtedai* (Bhalerao & Rao). The nematode *Dispharynx nasuta* (Acuariidae) is found worldwide and infects a wide variety of birds, including game birds and domestic chickens and turkeys (Cram 1931; Goble and Kutz 1945; Carreno 2008; Hernandez-Urraca *et al*. 2022). Sowbugs are the intermediate host for *D. nasuta*: larvae live inside the sowbug and enter an avian final host when the sowbug is consumed (Cram 1931; Carreno 2008). An unidentified species of *Acuaria* (Acuariidae) has been recorded from several species of *Hemilepistus* sowbugs. Like *D. nasuta,* members of the genus *Acuaria* are parasites of birds (Mutafchiev *et al*. 2017). As *D. nasuta* was formerly placed in the genus *Acuaria* (Rickard 1985), it is possible that the records of *Acuaria* from sowbugs actually represent *D. nasuta*. Sowbugs are also intermediate hosts of *Tetrameres mohtedai* (Chowdhury 1994), which is a parasite of domestic chickens in India and Singapore (Lim 1975; Pallabi *et al*. 2017). In addition to sowbugs, *Tetrameres* species can use grasshoppers, cockroaches, and lepidopteran larvae as intermediate hosts (Cram 1931; Lim 1975). Other nematodes associated with sowbugs include *Rhabditis*, which is a bacterivorous genus found in organic substrates (Andrássy 1983; Yeates 1999). Three genera of nematodes belonging to the family Mermithidae have also been recorded in association with sowbugs (Table 3.1). Larval mermithid nematodes infect a variety of

arthropods and typically act as parasitoids by killing their host when they emerge as adults (Petersen 1985). One species of sowbug-associated mermithid, *Thaumamermis cosgrovei*, can be infected with the same iridovirus that infects its sowbug hosts (Poinar 1981).

Sowbug-associated nematodes recorded in this study belong to the genera *Rhabditophanes, Aphelenchoides*, *Panagrolaimus*, *Pristionchus*, or *Oscheius* / *Rhabditis*. All these genera include free-living members that have been found associated with slugs (Sudhaus 2018; Brophy *et al*. 2020) and all have been recorded in association with arthropods in a phoretic or necromenic relationship, so it is reasonable that they would be associated with sowbugs. *Rhabditophanes* belongs to the superfamily Strongyloidoidea, but unlike the other members of this group, it is free-living and saprophagous (Andrássy 1983; Dorris *et al*. 2002; Dulovic *et al*. 2020). *Rhabditophanes* is phoretic on arthropods: hosts of *Rhabditophanes* have been reviewed by Ćurčić *et al.* (2008) and include mites (Mesostigmata, Oribatida), spiders (Araneae), pseudoscorpions (Pseudoscorpiones), beetles (Coleoptera), and springtails (Collembola). *Pristionchus* has been found both internally and externally on a variety of insect families (Mahboob and Tahseen 2021) and has also been found in snails (d'Ovidio *et al.* 2019) and slugs (Withanage *et al*. 2023). Members of the genus feed on bacteria and other nematodes and have a phoretic or necromenic association with insects (Félix *et al*. 2018). *Panagrolaimus* spp. feed on bacteria and have been found in soil and moss (Sohlenius and Boström 2009) and are also associated with slugs (Withanage *et al.* 2023). Both *Panagrolaimus* and *Aphelenchoides* have been found under the elytra of bark beetles (Curculionidae) (Cardoza *et al*. 2008). The genus *Aphelenchoides* contains several species that are important parasites of agricultural plants, including *A. fragariae* (Kohl 2011; Sanchez-Monge *et al*. 2015) although most species in the genus are free-living fungivores (Franklin 1978; Yeates 1999). The sequence from a sowbug-

associated nematode recovered in this study was similar to *Aphelenchoides blastophthorus*, which is a minor parasite of a variety of plants (Sanchez-Monge *et al*. 2015; Consoli *et al*. 2019); however, due to the relatively low percent identity (97.8-97.9%) to existing *A. blastophthorus* sequences and the fact that the monophyly of *A. blastophthorus* was inconsistent, the identity of the *Aphelenchoides* recovered in this study is uncertain. *Rhabditis* is a bacterivorous genus (Andrássy 1983; Yeates 1999) and includes species that are necromenic associates of arthropods (Stock *et al.* 2005; Mahboob and Tahseen 2021), snail-associated species (d'Ovidio *et al*. 2019), and species associated with earthworms or found in terrestrial detritus (Andrássy 1983). Occasionally *Rhabditis* has been implicated in symptomatic infections in vertebrates, including humans; these associations have been reviewed by d'Ovidio *et al.* (2019). *Oscheius* is a close relative of *Rhabditis* and includes species associated internally and externally with a wide variety of insects (Mahboob and Tahseen 2021), as well as species found in decaying wood (Abolafia and Peña-Santiago 2019) and in dung (Andrássy 1983). Many *Oscheius* species are insect pathogens, and some have been proposed as biocontrol agents (Onwong *et al*. 2023). An *Oscheius* species (cf. *myriophilus*) was recovered in this study from live sowbug hosts four days after the sowbugs were initially collected, so the sowbugs had survived at least 96 hours in association with the nematodes. If *Oscheius* are pathogens of sowbugs, they are evidently less virulent than when associated with insects, where death of the host typically occurs within 96 hours of infection (Onwong *et al*. 2023). Alternatively, the relationship of *Oscheius* with sowbugs may be phoretic. Other entomopathogenic nematode taxa are capable of being transported by sowbugs and do not appear to cause harm to the sowbug host (Eng *et al*. 2005).

3.4.7. Cestoda

There are only two records of tapeworms associated with sowbugs, of which only one, *Oochoristica tuberculata* (Rudolphi), has been identified more finely than the level of order (Cordero-del-Campillo *et al*. 1994). *Oochoristica tuberculata* infects reptiles (Hughes 1940; Dugarov *et al*. 2012) and is found throughout the Palearctic, where its typical intermediate hosts are beetles (Dermestidae, Tenebrionidae), moths (Pyralidae) and grasshoppers (Acrididae) (Dugarov *et al*. 2012). *Oochoristica tuberculata* has been recorded once from *Oniscus asellus* (Cordero-del-Campillo *et al*. 1994) but there are no other published records of this species from *O. asellus* or other sowbugs. The other record of a sowbug-associated cestode consists of an unidentified cysticercoid from *Armadillidium vulgare* in the United States (Webster 1949). I did not find tapeworms in any of the sowbugs I examined.

3.4.8. Trematoda

Sowbugs are intermediate hosts of three trematode genera from the family Dicrocoeliidae: *Lypersomum*, *Platynosomum,* and *Corrigia*. *Lypersomum petiolatum* has a wide variety of birds as final hosts, and its larvae inhabit terrestrial snails as first intermediate hosts and sowbugs as second intermediate hosts (Hildebrand *et al*. 2019). Similarly, sowbugs are second intermediate hosts of *Platynosomum illiciens*, which infects terrestrial snails as first intermediate hosts, and mammals (including domestic cats) as final hosts (Pinto *et al.* 2018). *Platynosomum illiciens* is distributed worldwide and causes platynosomiasis in domestic cats (Pinto *et al*. 2014, 2018). Finally, sowbugs are also hosts of *Corrigia* spp., which inhabit the pancreatic canal of the final hosts, including mice (Harvey and Channon 1956) as well as galliform, anseriform, and charadriiform birds (Daniels and Freeman 1976; Dronen and Bradley 1979; Köroğlu and Taşan 1996). Sowbugs of the marine littoral genus *Ligia* are intermediate hosts for three genera of

trematodes in the family Microphallidae that infect marine birds as final hosts: *Maritrema, Megalophallus,* and *Levinsiella*. The life cycle of *Maritrema linguilla* Jägerskiöld has been reviewed by Hendow and James (1988) and consists of a marine snail as first intermediate host, and a sowbug as second intermediate host, and a marine bird as the final host. Similarly, *Megalophallus reamesi* Overstreet & Heard uses snails as first intermediate hosts, sowbugs as second intermediate hosts, and gruiform and charadriiform birds as final hosts (Overstreet and Heard 1995). *Levinsiella* also uses marine birds as its final host, but inhabits crabs, marine isopods and sowbugs as intermediate hosts (Rankin 1939; Lester and Sewell 1989). I did not find trematodes in any of the sowbugs examined in this study.

3.4.9. Diptera

Flies of the family Rhinophoridae are parasitoids of sowbugs (Cerretti *et al*. 2020). Rhinophorid larvae develop in the body cavity of an infected sowbug, where they consume the organs, grow to fill the body, and eventually kill the host (Wood *et al.* 2018). Rhinophorids are found in a wide variety of sowbug species (Table 3.1). Associations between sowbugs and rhinophorids have been reviewed previously (Wood *et al*. 2018) and include 18 sowbug species, with the distribution of associations ranging from the Palearctic to the Nearctic and Neotropics. The only other dipteran reported in association with sowbugs is “muscides” (=Muscidae?) from *Philoscia affinis* Verhoeff (Verhoeff 1931; Vandel 1962). This record may be an error: two genera of Muscidae (*Eginia* and *Syngamoptera*) have larva that are endoparasites of Diplopoda (Skidmore 1985) but neither of these genera have been recorded from sowbugs. I did not find any dipterans associated with the sowbugs examined in this study.

3.4.10. Acanthocephala

Acanthocephalans are typically rare in sowbug populations, although prevalence can range from 0.07% (Schmidt and Olsen 1964) to 27% (Seidenberg 1973) depending on the locality, sowbug host species, and species of acanthocephalan. Sowbugs are intermediate hosts for three families of acanthocephalans. Two genera belonging to the family Echinorhynchidae have been recorded from sowbugs: *Pseudoacanthocephalus*, which has amphibians as final hosts (Nakao 2016), and *Acanthocephalus*, which infects fish, frogs and reptiles as final hosts (Smales 2007; Salgado-Maldonado and Novelo-Turcotte 2009). Genera from the acanthocephalan family Centrorhynchidae that have been found in sowbugs include *Centrorhynchus*, which uses mammals and birds as final hosts (Steinauer *et al.* 2020), and *Sphaerirostris*, which is found in birds (Muhammad *et al*. 2019). By far the most common acanthocephalan family reported from sowbugs is Plagiorhynchidae, of which only *Plagiorhynchus cylindraceus* has been recorded from sowbugs. *Plagiorhynchus cylindraceus* has been found in seven species of sowbugs across Europe, Asia, and North America (Table 3.1). All members of Plagiorhynchidae use birds and/or mammals as final hosts (Smales 2002). Adult *P. cylindraceus* have been found in an extremely wide variety of birds and mammals. These have been reviewed previously (Llanos-Soto *et al.* 2019) and include 18 families of birds and 10 families of mammals. The life cycle of *Plagiorhynchus cylindraceus* has been experimentally demonstrated in European Starlings (*Sturnus vulgaris*) (Schmidt and Olsen 1964). In brief, embryonated eggs in bird feces are eaten by sowbugs, where they enter the midgut, hatch, penetrate the gut wall, and grow in the body cavity. When the sowbug is eaten by the final avian host, the acanthella attaches to the gut wall and develops into an adult worm. Sowbugs infected with *P. cylindraceus* show altered behavior compared to uninfected sowbugs. This includes increased movement and a preference for less

humid areas with light colored substrate, which results in European Starlings feeding preferentially on infected sowbugs (Moore 1983).

Prior to this study acanthocephalans had never been reported from sowbugs in Canada. The acanthocephalans I obtained from *Porcellio scaber* in British Columbia yielded COI sequences very similar to *P. cylindraceus*. Since this was the only species of Plagiorhynchidae for which COI sequences were available, it was not possible to determine whether species level identification of *Plagiorhynchus* is possible using COI alone. However, *P. cylindraceus* is the only species of Plagiorhynchidae that has been reported from sowbugs, is the most commonly-reported sowbug-associated acanthocephalan (Table 3.1), and has been found in sowbugs from the United States (Schmidt and Olsen 1964; Levri and Coppola 2004). Therefore, the acanthocephalans found in this study likely represent *P. cylindraceus*. The prevalence reported here for *P. cylindraceus* in populations of *P. scaber* in British Columbia (1.3 - 11.1%) is consistent with previous reports of 2.3% for *Porcellio scaber* (Levri and Coppola 2004) and 4 - 9.3% for *Trachelipus squamuliger* Verhoeff (Dimitrova 2009). Mature *P. cylindraceus* have been reported from Canada in raccoons (*Procyon lotor* (Linnaeus)) from British Columbia (Ching *et al*. 2000) and in Spotted Sandpipers (*Actitis macularius* Linnaeus) from New Brunswick (Didyk *et al.* 2007), but until this study there were no Canadian records of *P. cylindraceus* in an intermediate host.

3.4.11. Mites ("Acari")

Bakerdania elliptica is the only sowbug-associated mite that has been identified to species level (Table 3.1). It has been recorded previously from *Oniscus asellus* from England and the Netherlands (Colloff and Hopkin 1986; Wijnhoven 2001a) and has also been found free-living in Germany (Krczal 1959). Only female *B. elliptica* are associated with sowbugs, and can be found

externally on the underside of the host, particularly on the lateral parts of the posterior body segments (Colloff and Hopkin 1986). The mites do not feed on the sowbugs, and the relationship appears to be phoretic (Colloff and Hopkin 1986). This study represents the first record of *Bakerdania elliptica* from North America and is also the first time this mite has been reported in association with *Porcellio scaber*. I observed *Bakerdania elliptica* individuals on the posterior sternites of *P. scaber* from British Columbia, which is consistent with prior observations of this mite in England (Colloff and Hopkin 1986).

In this study I found associations between sowbugs and several mite taxa for which association with sowbugs has not been previously reported. These include nymphal Astigmata tentatively identified to Acaridae, Stigmaeidae (Prostigmata), and mesostigmatan mites of the genera *Lasioseius* and *Proctolaelaps*. Many Acaridae are found in aquatic habitats (Walter and Proctor 2013). Some are pests of food products or crop plants, but others feed on fungi and nematodes (OConnor 2009) or decaying plant and animal tissue (Walter and Proctor 2013). Several genera of Acaridae are associated with hermit crabs (McDermott *et al*. 2010) while others are phoretic on fleas or beetles, or live in association with bees, ants, or termites (OConnor 2009), and so a phoretic association with sowbugs is plausible. The phoretic stage in Astigmata is the deutonymph (Walter and Proctor 2013), but the astigmatans I found were not in this life stage, so the association could be accidental. The family Stigmaeidae contains almost 600 described species, including species that feed on moss, and predators of invertebrates that include crop pests (Walter *et al*. 2009; Walter and Proctor 2013; Fan *et al*. 2016). Aside from the parasitic association of some stigmaeids with sandflies (Diptera: Psychodidae), non-predatory associations with other arthropods are uncommon (Walter *et al*. 2009; Fan *et al*. 2016). The association between a sowbug and a stigmaeid observed in this study may have been accidental

(i.e., the mite happened to be observed while crawling over a sowbug). *Lasioseius* and *Proctolaelaps* spp. have also never been recorded in association with sowbugs. Both genera occupy a wide range of habitats, feed on fungi and small invertebrates, and have phoretic associations with beetles, moths, and flower-feeding birds (Lindquist *et al*. 2009; Walter and Proctor 2013). Both genera are found between the palps when associated with moths, as this region is relatively sheltered and difficult for the host to groom (Treat 1975). Similarly, I observed both *Lasioseius* and *Proctolaelaps* between the antennae of sowbugs in this study, which may also represent a relatively sheltered site. The relationship of these mites with sowbugs may be phoretic.

3.5. References

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3.6. Tables and Figures

Table 3.1 (following pages): Metazoan symbionts associated with terrestrial isopods, sorted by symbiont species. See Table C1 for a representative list of protists, bacteria, fungi, and viruses associated with terrestrial isopods. Associations that are supported only by experimental infection are not included, but associations found "accidentally" occurring in lab populations of isopods are included. Taxon names are listed in their most recent form, with alternative name(s) given in the original source(s) listed below the most recent name. Most often these are synonymies, but occasionally are due to misidentifications that were noted and corrected in later literature or to misspellings. Note that the localities listed for the associations are supported by a minimum of one of the listed references, but not necessarily by all of them. References for this table are included at the bottom of the table.

Taxonomy (Symbiont)	Host Species	Localities	References
Syndermata			
Bdelloidea			
Philodinidae			
***Mniobia branchicola* (Nemec, 1895)** = *Macrotrachela branchicola* Harring, 1913 = *Callidina branchicola* Nemec, 1895	***Ligidium hypnorum* (Cuvier, 1792)**	France, Czech Republic and/or Slovakia, Europe	161, 164, 165
	***Ligidium* sp.**	?	178
"Acanthocephala"			
	***Philoscia muscorum* (Scopoli, 1763)**	France	27
Palaeacanthocephala			
Echinorhynchida			
Echinorhynchidae			
	***Philoscia muscorum* (Scopoli, 1763)**	Europe	38
	***Porcellio scaber* Latreille, 1804**	Europe	38
	***Armadillidium vulgare* (Latreille, 1804)**	Europe	38
***Acanthocephalus falcatus* (Frölich, 1789) Lühe, 1911**	***Ligidium hypnorum* (Cuvier, 1792)**	Ukraine	90
***Pseudoacanthocephalus bufonis* (Shipley, 1903) Petrochenko, 1956**	***Armadillidium vulgare* (Latreille, 1804)**	Republic of Uzbekistan	97
	***Hemilepistus fedtschenkoi* (Uljanin, 1875)** = *Porcellio fedtschencoi* Uljanin, 1875	Republic of Uzbekistan	97
	***Lucasioides latus* (Uljanin, 1875)** = *Porcellio latus* Uljanin, 1875	Republic of Uzbekistan	97
***Pseudoacanthocephalus toshimai* Nakao, 2016**	***Ligidium japonicum* Verhoeff, 1918**	Japan	85
Polymorphida			
Plagiorhynchidae			
***Plagiorhynchus cylindraceus* (Goeze, 1782)** = *Plagiorhynchus formosus* Van Cleave, 1918 = *Prosthorhynchus formosus* (Van Cleave, 1918) = *Prosthorhynchus cylindraceus* (Goeze, 1782) = *Prosthorhynchus transversus* (Rudolphi, 1819) = *Plagiorhynchus transversus* (Rudolphi, 1819)	***Armadillidium versicolor* Stein, 1859** ***Armadillidium vulgare* (Latreille, 1804)**	Ukraine Republic of Bulgaria, Ukraine, France, United States, Republic of Poland	8 4, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 19, 103, 104, 105
	***Hemilepistus fedtschenkoi* (Uljanin, 1875)** = *Porcellio fedtschencoi* Uljanin, 1875	Republic of Uzbekistan, Eastern Europe*	6, 7, 18, 93, 95
	***Hemilepistus reductus* Borutzkii, 1945** = *Porcellio reductus* Borutzkii	Republic of Uzbekistan, Eastern Europe*	6, 95
	***Porcellio scaber* Latreille, 1804**	United States, Canada	5, 11, this study
	***Trachelipus squamuliger* (Verhoeff, 1907)**	Republic of Bulgaria	4
Centrorhynchidae			
***Centrorhynchus milvus* Ward, 1956**	***Porcellionides pruinosus* (Brandt, 1833)**	Republic of Senegal	96
***Centrorhynchus* sp.**	***Atlantoscia floridana* (Van Name, 1940)**	Federative Republic of Brazil	1
***Sphaerirostris scanensis* (Lundström, 1942)**	***Lucasioides latus* (Uljanin, 1875)** = *Porcellio latus* Uljanin, 1875	Republic of Uzbekistan	97
***Sphaerirostris teres* (Rudolphi, 1819)**	***Armadillidium versicolor* Stein, 1859**	Ukraine, Romania and/or Republic of Moldova	8, 102
***Sphaerirostris lancea* (Westrumb, 1821)** = *Centrorhynchus lanceoides* Petrochenko, 1949	***Hemilepistus crenulatus* (Pallas, 1771)** = *Porcellio pectinatus*	Republic of Uzbekistan, Eastern Europe*	6, 95
	***Hemilepistus fedtschenkoi* (Uljanin, 1875)** = *Porcellio fedtschencoi* Uljanin, 1875	Republic of Uzbekistan, Eastern Europe*	6, 93, 95
	***Hemilepistus reductus* Borutzkii, 1945**	Republic of Uzbekistan, Eastern Europe*	6, 93, 95
Arthropoda			
Arachnida			
"Acari" (unidentified "mite")			
	***Armadillidium vulgare* (Latreille, 1804)**	England	181
	***Armadillo* sp.**	State of Libya	183
	***Ligia cinerascens* Budde-Lund, 1885**	Japan	94

Mesostigmata			
"Gamasides" (=Gamasida?)	***Armadillidium vulgare* (Latreille, 1804)**	Republic of Lebanon	182
Blattisociidae			
***Lasioseius* cf. *(Crinidens)* sp.**	***Cylisticus convexus* (De Geer, 1778)**	Canada	This study
Eviphididae			
***Thinoseius setifer* Takaku, 2000**	***Ligia cinerascens* Budde-Lund, 1885**	Japan	198
Melicharidae			
***Proctolaelaps* sp.**	***Cylisticus convexus* (De Geer, 1778)**	Canada	This study
Oribatida			
	***Armadillidium vulgare* (Latreille, 1804)**	United States	27
Sarcoptiformes			
cf. Acaridae (unkeyable nymph)	***Trachelipus rathkii* (Brandt, 1833)**	Canada	This study
Saproglyphidae			
	***Armadillidium vulgare* (Latreille, 1804)**	France	27
Trombidiformes			
Neopygmephoridae			
***Bakerdania elliptica* (Krczal, 1959)**	***Oniscus asellus* Linnaeus, 1758**	England, the Netherlands, Canada	57, 58, this study
	***Porcellio scaber* Latreille, 1804**	Canada	This study
Stigmaeidae			
	***Trachelipus rathkii* (Brandt, 1833)**	Canada	This study
Insecta			
Diptera			
"muscides" (=Muscidae?) This may be a misidentification of Rhinophoridae; see the main text for details.	***Philoscia affinis* Verhoeff, 1908**	France	69, 193
Rhinophoridae			
	***Armadillidium nasatum* Budde-Lund, 1885**	France	27
	***Balloniscus glaber* Araujo & Zaido, 1996**	Federative Republic of Brazil	24
***Melanophora roralis* (Linnaeus, 1758)**	***Armadillidium* sp.**	Federative Republic of Brazil	36
	***Oniscus asellus* Linnaeus, 1758**	United States	33
	***Porcellio scaber* Latreille, 1804**	Great Britain, United States, England	28, 33, 37, 38
	***Porcellio spinicornis* Say, 1818**	England	32
	***Porcellio* sp.**	United States	40
	***Porcellionides pruinosus* (Brandt, 1833)**	United States	37
***Paykullia maculata* (Fallén, 1815)** = *Chaetostevenia maculata* (Fallén, 1820) = *Plesina maculata* Fallén	***Trachelipus rathkii* (Brandt, 1833)**	The Netherlands	39
	***Protracheoniscus politus* (Koch, 1841)** = *Protracheoniscus amoneus* Koch, 1841	Europe	26
	***Trachelipus ratzeburgii* (Brandt, 1833)** **=** *Tracheoniscus ratzeburgii*	Federal Republic of Germany	26
	***Oniscus asellus* Linnaeus, 1758**	Great Britain, England	28, 38
	***Porcellio scaber* Latreille, 1804**	Great Britain, England, France	28, 38
***Phyto angustifrons* (Rondani, 1856)** = *Cyrillia angustifrons* Rondani, 1856	***Porcellionides pruinosus* (Brandt, 1833)**	France	38
***Phyto armadillonis* Kugler, 1978**	***Armadillo officinalis* Duméril, 1816**	State of Israel	34
***Phyto discrepans* (Pandellé, 1896)** = *Styloneuria discrepans* Pandelle, 1896	***Oniscus asellus* Linnaeus, 1758**	Great Britain	28
	***Porcellio scaber* Latreille, 1804**	Great Britain, England, France	28, 38
	***Porcellionides pruinosus* (Brandt, 1833)**	France	38
***Phyto luteisquama* Kugler, 1978**	***Porcellio laevis* Latreille, 1804**	State of Israel	34
***Phyto melanocephala* (Meigen, 1824)**	***Armadillidium nasatum* Budde-Lund, 1885**	France	26, 174
	***Armadillidium silvestrii* Verhoeff, 1931**	Europe	26

		***Armadillidium versicolor* Stein, 1859**	Europe	26
		***Armadillidium vulgare* (Latreille, 1804)**	England, France	28, 38, 174
		***Oniscus asellus* Linnaeus, 1758**	England	38, 168
		***Porcellio scaber* Latreille, 1804**	Great Britain, England, France	28, 38, 168, 174
		***Porcellio spinicornis* Say, 1818** = *Porcellio pictus* Brandt	France	26, 174
	***Rhinomorinia sarcophagina* (Schiner, 1861)**	***Cylisticus convexus* (De Geer, 1778)** = *Cilisticus* [sic] *convexus*	Republic of Poland	31
	***Rhinophora lepida* (Meigen, 1824)**	***Porcellio scaber* Latreille, 1804**	Great Britain, England, France, the Netherlands	28, 38, 39
	***Stevenia atramentaria* (Meigen, 1824)** = *Tachina atramentaria* Meigen, 1824 = *Rhinophora atramentaria*	***Oniscus asellus* Linnaeus, 1758**	Europe	109, 167
		***Philoscia affinis* Verhoeff, 1908**	Europe	26
		***Porcellio scaber* Latreille, 1804**	Swiss Confederation	38
		***Trachelipus rathkii* (Brandt, 1833)** = *Tracheoniscus rathkii* Brandt	Great Britain, Republic of Poland	28, 31
	The record of *S. atramentaria* in association with *Oniscus asellus* may be incorrect (Wood *et al*. 2018)	***Trachelipus arcuatus* (Budde-Lund, 1885)**	Europe	26
	***Stevenia deceptoria* (Loew, 1847)**	***Porcellio* sp.**	Italy	30
	***Stevenia signata* (Mik, 1866)**	***Armadillidium pallasii* Brandt, 1833** = *Armadillidium frontirostre* Budde-Lund, 1885	Republic of Croatia	25, 29
		***Armadillidium vulgare* (Latreille, 1804)**	Republic of Croatia	25, 29
	***Stevenia umbratica* (Fallén, 1820)** = *Rhinophora umbratica* Fallén	***Oniscus asellus* Linnaeus, 1758**	?	109
	***Stevenia* sp.**	***Porcellio scaber* Latreille, 1804**	France	27
	***Tricogena rubricosa* (Meigen, 1824)** = *Frauenfeldia rubricosa* (Meigen, 1824) = *Frauenfeldia trilineata* Meigen, 1824 = *Tricogena ribricosa* [sic]	***Oniscus asellus* Linnaeus, 1758**	?	69
		***Porcellio scaber* Latreille, 1804**	Republic of Poland, Ireland, Great Britain, England, France	28, 31, 35, 38
		***Trachelipus rathkii* (Brandt, 1833)**	Republic of Poland	31
Nematoda				
		***Armadillidium vulgare* (Latreille, 1804)**	France	27
		***Ligia oceanica* (Linnaeus, 1767)**	France	189
		***Oniscus asellus* Linnaeus, 1758**	The Netherlands, France	27, 58
		***Porcellio scaber* Latreille, 1804**	United States	203
		***Tylos latreillei* Audouin, 1826** nom. dub.	France	161
	***Agamonematodum armadillonis pillularis* Leidy, 1853** incertae sedis	***Armadillidium vulgare* (Latreille, 1804)** = *Armadillidium pillularis*	North America	176
	***Agamonematodum hospes* von Linstow, 1882** incertae sedis	***Armadillidium vulgare* (Latreille, 1804)**	Europe	177, 178
Chromadorea				
Ascaridida				
Oxyuridae				
	***Oniscicula oniscicula* Schwenk, 1927**	**Philosciidae sp.** Host resembled *Littorophiloscia vittata* (Say, 1818) (=*Philoscia vittata* Say 1818) but was thought to be a new species.	United States	46
Rhabditida				
Acuariidae				
	***Acuaria* sp.**	***Hemilepistus crenulatus* (Pallas, 1771)** = *Porcellio pectinatus*	Eastern Europe*	6
		***Hemilepistus fedtschenkoi* (Uljanin, 1875)** = *Porcellio fedtschencoi* Uljanin, 1875	Republic of Uzbekistan, Eastern Europe*	6, 93
		***Hemilepistus reductus* Borutzkii, 1945** = *Porcellio reductus* Borutzkii	Republic of Uzbekistan	93

***Dispharynx nasuta* (Rudolphi, 1819)** = *Acuaria nasuta* (Rudolphi, 1819) = *Acuaria spiralis* Molin, 1858 = *Dispharynx spiralis* (Molin, 1858) = *Dispharagus nasutus* (Rudolphi, 1819)	***Armadillidium vulgare* (Latreille, 1804)** = *Armadillidium pillularis* ***Hemilepistus crenulatus* (Pallas, 1771)** = *Porcellio pectinatus* ***Hemilepistus fedtschenkoi* (Uljanin, 1875)** = *Porcellio fedtschencoi* Uljanin, 1875 ***Hemilepistus reductus* Borutzkii, 1945** = *Porcellio reductus* Borutzkii ***Porcellio laevis* Latreille, 1804** ***Porcellio scaber* Latreille, 1804** ***Porcellionides pruinosus* (Brandt, 1833)** ?	Spain, Andalusia Eastern Europe* Republic of Uzbekistan, Eastern Europe* Republic of Uzbekistan, Eastern Europe* Spain, Andalusia Spain, Andalusia Federative Republic of Brazil Ukraine	98, 171 6 6, 93 6, 93 98, 170, 171, 172, 173, 178 98, 171 89 20
Alloionematidae			
***Rhabditophanes* sp.**	***Trachelipus rathkii* (Brandt, 1833)**	Canada	This study
Aphelenchoididae			
***Aphelenchoides* cf. *blastophthorus* Franklin 1952**	***Porcellio spinicornis* Say, 1818**	Canada	This study
Diplogastridae			
Pristionchus* cf. *lheritieri / entomophagus	***Porcellio scaber* Latreille, 1804**	Canada	This study
Panagrolaimidae			
***Panagrolaimus* cf. *rigidus* (Schneider 1866)**	***Trachelipus rathkii* (Brandt, 1833)**	Canada	This study
Rhabditidae			
	***Alpioniscus feneriensis* (Parona, 1880)** = *Trichoniscus dispersus* Racovitza, 1907 ***Ligia oceanica* (Linnaeus, 1767)**	France France	187 185
***Caenorhabditis elegans* (Maupas, 1899) Dougherty, 1953**	***Armadillidium vulgare* (Latreille, 1804)** ***Oniscus asellus* Linnaeus, 1758** ***Porcellio scaber* Latreille, 1804** ***Porcellio spinicornis* Say, 1818** = *Porcellio pictus* Brandt, 1833 ?	Federal Republic of Germany France, Federal Republic of Germany Federal Republic of Germany, Scotland Scotland France, Scotland	84 82, 84 81, 84 81 81, 83
***Caenorhabditis remanei* (Sudhaus, 1974) Andrássy, 1983** = *Caenorhabditis vulgaris* Baird *et al.*, 1994	***Armadillidium nasatum* Budde-Lund, 1885** ***Armadillidium vulgare* (Latreille, 1804)** ***Cylisticus convexus* (De Geer, 1778)** = *Cilisticus* [sic] *convexus* ***Oniscus asellus* Linnaeus, 1758** ***Porcellio scaber* Latreille, 1804** ***Trachelipus rathkii* (Brandt, 1833)** ?	United States Federal Republic of Germany United States Federal Republic of Germany United States, Federal Republic of Germany United States, Canada, Federal Republic of Germany, United States, People's Republic of China	44, 45 45, 84 44 84 44, 84 44 92
***Matthesonema tylosa* Osche, 1955** **cf. *Oscheius myriophilus* (Poinar, 1986)** = *Rhabditis myriophila* Poinar 1986	***Tylos latreillei* Audouin, 1826** nom. dub. ***Cylisticus convexus* (De Geer, 1778)**	? Canada	41 This study
***Rhabditis* sp.**	***Ligia oceanica* (Linnaeus, 1767)**	?	178
Spirurida			
Tetrameridae			
***Tetrameres mohtedai* (Bhalerao & Rao, 1944)**	***Porcellio laevis* Latreille, 1804**	Republic of India	99
Dorylaimea			
Mermithida			
Mermithidae			
	? ***Ligidium* sp.** ***Platyarthrus caudatus* Aubert & Dollfus, 1890**	Italy Japan Italy	144 21 159

***Agamermis* sp.**	***Armadillidium vulgare* (Latreille, 1804)**	Oriental Republic of Uruguay, Argentine Republic	43, 202
***Mermis* sp.**	***Armadillidium assimile* Budde-Lund, 1885**	France	69
	***Armadillidium vulgare* (Latreille, 1804)**	France	69
	***Porcellio* sp.**	Italy	100
	***Porcellionides sexfasciatus* (Budde-Lund, 1885)** = *Metoponorthus sexfasciatus* Budde-Lund, 1885	?	69
	***Platyarthrus hoffmannseggii* Brandt, 1833**	?	69
	***Trichoniscus provisorius* Racovitza, 1908** = *Trichoniscus pusillus provisorius* Racovitza, 1908	?	166
	***Trichoniscus pusillus* Brandt, 1833**	?	166
***Thaumamermis cosgrovei* Poinar, 1981**	***Armadillidium vulgare* (Latreille, 1804)**	United States	42, 63, 190, 200
	***Porcellio laevis* Latreille, 1804**	United States	63
	***Porcellio scaber* Latreille, 1804**	United States	42, 190
Platyhelminthes			
Cestoda			
	***Armadillidium vulgare* (Latreille, 1804)**	United States	180
Cyclophyllidea			
Anoplocephalidae			
***Oochoristica tuberculata* (Rudolphi, 1819)**	***Oniscus asellus* Linnaeus, 1758**	Spain, Andalusia	98
Trematoda			
	***Oniscus asellus* Linnaeus, 1758**	Europe	38
	***Porcellio scaber* Latreille, 1804**	Europe	38
	***Ligia oceanica* (Linnaeus, 1767)**	France	184, 185, 189
Plagiorchiida			
Dicrocoeliidae			
***Corrigia corrigia* (Braun, 1901)**	***Philoscia muscorum* (Scopoli, 1763)**	?	101
	***Porcellio scaber* Latreille, 1804**	?	101
***Corrigia* sp.**	***Hemilepistus fedtschenkoi* (Uljanin, 1875)** = *Porcellio fedtschencoi* Uljanin, 1875	Republic of Uzbekistan	95
	***Hemilepistus reductus* Borutzkii, 1945** = *Porcellio reductus* Borutzkii	Eastern Europe*, Republic of Uzbekistan	6, 95
***Lyperosomum petiolatum* (Railliet, 1900)**	***Ligia* sp.**	Republic of Poland	197
	***Porcellio scaber* Latreille, 1804**	Republic of Poland	197
***Platynosomum illiciens* (Braun, 1901)**	***Nagurus nanus* (Budde-Lund, 1908)**	Federative Republic of Brazil	59
	?	Federative Republic of Brazil, United States	59, 60
Microphallidae			
***Levinseniella* sp.**	***Ligia* sp.**	Western Pacific (general area)	106
***Maritrema linguilla* Jägerskiöld, 1908**	***Ligia oceanica* (Linnaeus, 1767)**	United Kingdom	107
***Maritrema* sp.**	***Ligia oceanica* (Linnaeus, 1767)**	Scotland	186
	***Ligia* sp.**	Western Pacific (general area)	106
***Megalophallus reamesi* Overstreet & Heard, 1955**	***Ligia baudiniana* Milne Edwards, 1840**	Turks and Caicos Islands, United States	108

* The original collection locality was in one of the following areas: Republic of Armenia, Republic of Azerbaijan, Republic of Belarus, Republic of Estonia, Georgia, Republic of Kazakhstan, Kyrgyz Republic, Republic of Latvia, Republic of Lithuania, Republic of Moldova, Russia, Republic of Tajikistan, Turkmenistan, Ukraine, and/or Republic of Uzbekistan

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(42) Poinar 1981; (43) Zimmermann 2010; (44) Baird 1999; (45) Baird *et al*. 1994; (46) Schwenck 1927; (47) Sixt *et al*. 2013; (48) Cordaux *et al*. 2007; (49) Kleespies *et al*. 2014; (50) Shay *et al*. 1985; (51) Drobne *et al*. 1999; (52) Wang *et al*. 2004b; (53) Wang *et al*. 2004a; (54) Fraune and Zimmer 2008; (55) Wang *et al*. 2007; (56) Eberl 2010; (57) Colloff and Hopkin 1986; (58) Wijnhoven 2001a; (59) Pinto *et al*. 2014; (60) Eckerlin and Leigh 1962; (61) Karasawa *et al*. 2012; (62) Ermin 1943; (63) Hess and Poinar 1985; (64) Schultz *et al*. 1982; (65) Lereboullet 1843; (66) Semenkeivitsch 1931; (67) Legrand 1948; (68) Fric 1872; (69) Vandel 1962; (70) Collinge 1918; (71) Standen 1917; (72) Schöbl 1880; (73) Norman and Brady 1911; (74) Sutton 1972; (75) Wijnhoven and Berg 1999; (76) Hopkin 1991; (77) Federici 1980; (78) Cole and Morris 1980; (79) Poinar *et al*. 1985; (80) Grosholz 1992; (81) Cutter 2006; (82) Barrière and Félix 2005; (83) Barrière and Félix 2007; (84) Petersen *et al*. 2015; (85) Nakao 2016; (86) Cordaux *et al*. 2012; (87) Langlois 2017; (88) Criado-Fernelio *et al*. 2013; (89) Cruz *et al*. 2019; (90) Vakarenko and Lisitsina 2001; (91) Krczal 1959; (92) Dey *et al*. 2012; (93) Matchanov *et al*. 1989; (94) Take and Hasegawa 2013; (95) Kabilov and Siddikov 1987; (96) Marchand and Grita-Timoulali 1991; (97) Ikramov 2002; (98) Cordero-del-Campillo *et al*. 1994; (99) Chowdhury 1994; (100) Ninni 1900; (101) The Natural History Museum [no date]; (102) Lisitsyna 1994; (103) Near *et al*. 1998; (104) Lisitsyna 1993; (105) Wesolowska and Okulewicz 2001; (106) Lester and Sewell 1989; (107) Hendow and James 1988; (108) Overstreet and Heard 1995; (109) von Roser 1840; (110) Vago *et al*. 1970; (111) Marden 2019; (112) Lichtwardt and Chen 1964; (113) Manier 1963; (114) Lichtwardt 1986; (115) Valle 2006; (116) Maessen 1955; (117) Scheer 1977; (118) Scheer 1976; (119) Chien and Hsieh 2001; (120) Lichtwardt and Williams 1990; (121) Valle and Santamaria 2009; (122) Poission 1929; (123) Léger and Duboscq 1906; (124) Poisson 1931; (125) Saikawa *et al*. 1997; (126) Kostanjšek *et al*. 2006; (127) Ulrich *et al*. 1993; (128) Ulrich *et al*. 1991; (129) Beerstecher *et al*. 1954; (130) Kostanjšek *et al*. 2002; (131) Jorgensen *et al*. 1997; (132) Margulis *et al*. 1998; (133) Ineson and Anderson 1985; (134) Hassall *et al*. 1987; (135) Lapanje *et al*. 2003; (136) Kostanjšek *et al*. 2004b; (137) Griffiths and Wood 1986; (138) Reyes and Tiedje 1976; (139) Márialigeti *et al*. 1984; (140) Kayang and Sharma 1999; (141) Kayang *et al*. 1996; (142) Cafaro 2002; (143) Cafaro 2005; (144) Lupetti *et al*. 2013; (145) Federici 1984; (146) Rousset *et al*. 1992; (147) Kostanjsek *et al*. 2007; (148) Coelho *et al*. 2022; (149) Valle and Cafaro 2008; (150) Manier 1969; (151) Suyama *et al*. 2021; (152) Tuzet and Manier 1950; (153) Tretter *et al*. 2014; (154) Lichtwardt 1960; (155) Lapanje *et al*. 2010; (156) Dittmer *et al*. 2016; (157) Bouchon *et al*. 2016; (158) Yousfi 1976; (159) Verhoeff 1942; (160) Tuzet and Manier 1947; (161) Bonnefoy and Marchal 1942; (162) Dogel and Fursenko 1920; (163) Remy 1928; (164) Němec 1895; (165) Matthes 1949; (166) Vandel 1960; (167) Bezzi and Stein 1907; (168) Thompson 1917; (169) Donisthorpe 1908; (170) Cram 1927; (171) Neveu-Lemaire 1936; (172) Piana 1897; (173) Hall 1929; (174) Legrand 1941; (175) Tuzet 1953; (176) Leidy 1853; (177) von Linstow 1882; (178) Richard 1899; (179) Jones 2023; (180) Webster 1949; (181) Omer-Cooper 1925; (182) Vandel 1955; (183) Brian 1932; (184) Villot 1875; (185) Villot 1879; (186) Lebour 1914; (187) Racovitza 1907; (188) Graeve 1914; (189) Cuénot 1891; (190) Poinar *et al*. 1980; (191) Boissevain 1919; (192) Manier 1950; (193) Verhoeff 1931; (194) Paliyenko and Boshko 2002; (195) Jones 2023; (196) Nguyen *et al*. 2021; (197) Hildebrand *et al*. 2019; (198) Takaku 2000; (199) Thanh *et al*. 2002; (200) Tang and Hyman 2007; (201) Piégu *et al*. 2014; (202) Rusconi *et al*. 2023; (203) Eng *et al*. 2005

Table 3.2 (following pages): Metazoan symbionts associated with terrestrial isopods, sorted by isopod host family and species. See Table C2 for a representative list of protists, bacteria, fungi, and viruses associated with terrestrial isopods. Associations that are supported only by experimental infection are not included, but associations found "accidentally" occurring in lab populations of isopods are included. Taxon names are listed in their most recent form, with alternative name(s) given in the original source(s) listed below the most recent name. Most often these are synonymies, but occasionally are due to misidentifications that were noted and corrected in later literature or to misspellings. Note that the localities listed for the associations are supported by a minimum of one of the listed references, but not necessarily by all of them. See Table 3.1 for the list of references.

Taxonomy (Host)	Symbiont family	Symbiont species	Localities	References
Unidentified terrestrial isopod (Oniscidea)				
	Acuariidae	***Dispharynx nasuta* (Rudolphi, 1819)** = *Acuaria nasuta* (Rudolphi, 1819) = *Acuaria spiralis* Molin, 1858 = *Dispharynx spiralis* (Molin, 1858) = *Dispharagus nasutus* (Rudolphi, 1819)	Ukraine	20
	Rhabditidae	***Caenorhabditis elegans* (Maupas, 1899) Dougherty, 1953** ***Caenorhabditis remanei* (Sudhaus, 1974) Andrássy, 1983** = *Caenorhabditis vulgaris* Baird *et al.*, 1994	France, Scotland Canada, Federal Republic of Germany, United States, People's Republic of China	81, 83 92
	Mermithidae	Mermithidae	Italy	144
	Dicrocoeliidae	***Platynosomum illiciens* (Braun, 1901)**	Federative Republic of Brazil, United States	59, 60
Agnaridae				
***Hemilepistus crenulatus* (Pallas, 1771)** = *Porcellio pectinatus*	Centrorhynchidae	***Sphaerirostris lancea* (Westrumb, 1821)** = *Centrorhynchus lanceoides* Petrochenko, 1949	Republic of Uzbekistan, Eastern Europe*	6, 95
	Acuariidae	***Acuaria* sp.**	Eastern Europe*	6
		***Dispharynx nasuta* (Rudolphi, 1819)** = *Acuaria nasuta* (Rudolphi, 1819) = *Acuaria spiralis* Molin, 1858 = *Dispharynx spiralis* (Molin, 1858) = *Dispharagus nasutus* (Rudolphi, 1819)	Eastern Europe*	6
***Hemilepistus fedtschenkoi* (Uljanin, 1875)** = *Porcellio fedtschencoi* Uljanin, 1875	Echinorhynchidae	***Pseudoacanthocephalus bufonis* (Shipley, 1903) Petrochenko, 1956**	Republic of Uzbekistan	97
	Plagiorhynchidae	***Plagiorhynchus cylindraceus* (Goeze, 1782)** = *Plagiorhynchus formosus* Van Cleave, 1918 = *Prosthorhynchus formosus* (Van Cleave, 1918) = *Prosthorhynchus cylindraceus* (Goeze, 1782) = *Prosthorhynchus transversus* (Rudolphi, 1819) = *Plagiorhynchus transversus* (Rudolphi, 1819)	Republic of Uzbekistan, Eastern Europe*	6, 7, 18, 93, 95
	Centrorhynchidae	***Sphaerirostris lancea* (Westrumb, 1821)** = *Centrorhynchus lanceoides* Petrochenko, 1949	Republic of Uzbekistan, Eastern Europe*	6, 93, 95
	Acuariidae	***Acuaria* sp.**	Republic of Uzbekistan, Eastern Europe*	6, 93
		***Dispharynx nasuta* (Rudolphi, 1819)** = *Acuaria nasuta* (Rudolphi, 1819) = *Acuaria spiralis* Molin, 1858 = *Dispharynx spiralis* (Molin, 1858) = *Dispharagus nasutus* (Rudolphi, 1819)	Republic of Uzbekistan, Eastern Europe*	6, 93
	Dicrocoeliidae	***Corrigia* sp.**	Republic of Uzbekistan	95
***Hemilepistus reductus* Borutzkii, 1945** = *Porcellio reductus* Borutzkii	Plagiorhynchidae	***Plagiorhynchus cylindraceus* (Goeze, 1782)** = *Plagiorhynchus formosus* Van Cleave, 1918 = *Prosthorhynchus formosus* (Van Cleave, 1918) = *Prosthorhynchus cylindraceus* (Goeze, 1782) = *Prosthorhynchus transversus* (Rudolphi, 1819) = *Plagiorhynchus transversus* (Rudolphi, 1819)	Republic of Uzbekistan, Eastern Europe*	6, 95
		***Sphaerirostris lancea* (Westrumb, 1821)** = *Centrorhynchus lanceoides* Petrochenko, 1949	Republic of Uzbekistan, Eastern Europe*	6, 93, 95
	Acuariidae	***Acuaria* sp.**	Republic of Uzbekistan	93
		***Dispharynx nasuta* (Rudolphi, 1819)** = *Acuaria nasuta* (Rudolphi, 1819) = *Acuaria spiralis* Molin, 1858 = *Dispharynx spiralis* (Molin, 1858)	Republic of Uzbekistan, Eastern Europe*	6, 93

		= *Dispharagus nasutus* (Rudolphi, 1819)		
	Dicrocoeliidae	***Corrigia* sp.**	Eastern Europe*, Republic of Uzbekistan	6, 95
***Lucasioides latus* (Uljanin, 1875)** = *Porcellio latus* Uljanin, 1875	Echinorhynchidae	***Pseudoacanthocephalus bufonis* (Shipley, 1903) Petrochenko, 1956**	Republic of Uzbekistan	97
	Centrorhynchidae	***Sphaerirostris scanensis* (Lundström, 1942)**	Republic of Uzbekistan	97
***Protracheoniscus politus* (Koch, 1841)** = *Protracheoniscus amoneus* Koch, 1841	Operculariidae	***Ballodora dimorpha* Dogiel & Furssenko, 1921**	Europe	165
	Rhinophoridae	***Paykullia maculata* (Fallén, 1815)** = *Chaetostevenia maculata* (Fallén, 1820) = *Plesina maculata* Fallén	Europe	26
Armadillidae				
***Armadillo officinalis* Duméril, 1816**	Rhinophoridae	***Phyto armadillonis* Kugler, 1978**	State of Israel	34
***Armadillo* sp.**	N/A (Arachnida: "Acari")	"Mite"	State of Libya	183
Armadillidiidae				
***Armadillidium assimile* Budde-Lund, 1885**	Mermithidae	***Mermis* sp.**	France	69
***Armadillidium nasatum* Budde-Lund, 1885**	Rhinophoridae	Rhinophoridae	France	27
		***Phyto melanocephala* (Meigen, 1824)**	France	26, 174
	Rhabditidae	***Caenorhabditis remanei* (Sudhaus, 1974) Andrássy, 1983** = *Caenorhabditis vulgaris* Baird *et al.*, 1994	United States	44, 45
***Armadillidium pallasii* Brandt, 1833** = *Armadillidium frontirostre* Budde-Lund, 1885	Rhinophoridae	***Stevenia signata* (Mik, 1866)**	Republic of Croatia	25, 29
***Armadillidium silvestrii* Verhoeff, 1931**	Rhinophoridae	***Phyto melanocephala* (Meigen, 1824)**	Europe	26
***Armadillidium versicolor* Stein, 1859**	Plagiorhynchidae	***Plagiorhynchus cylindraceus* (Goeze, 1782)** = *Plagiorhynchus formosus* Van Cleave, 1918 = *Prosthorhynchus formosus* (Van Cleave, 1918) = *Prosthorhynchus cylindraceus* (Goeze, 1782) = *Prosthorhynchus transversus* (Rudolphi, 1819) = *Plagiorhynchus transversus* (Rudolphi, 1819)	Ukraine	8
	Centrorhynchidae	***Sphaerirostris teres* (Rudolphi, 1819)**	Ukraine, Romania and/or Republic of Moldova	8, 102
	Rhinophoridae	***Phyto melanocephala* (Meigen, 1824)**	Europe	26
***Armadillidium vulgare* (Latreille, 1804)** = *Armadillidium pillularis* = *Armadillidium vulgaris* [sic]	Echinorhynchidae	Echinorhynchidae	Europe	38
		***Pseudoacanthocephalus bufonis* (Shipley, 1903) Petrochenko, 1956**	Republic of Uzbekistan	97
	Plagiorhynchidae	***Plagiorhynchus cylindraceus* (Goeze, 1782)** = *Plagiorhynchus formosus* Van Cleave, 1918 = *Prosthorhynchus formosus* (Van Cleave, 1918) = *Prosthorhynchus cylindraceus* (Goeze, 1782) = *Prosthorhynchus transversus* (Rudolphi, 1819) = *Plagiorhynchus transversus* (Rudolphi, 1819)	Republic of Bulgaria, Ukraine, France, United States, Republic of Poland	4, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 19, 103, 104, 105
	N/A (Arachnida: "Acari")	"Mite"	England	181
	N/A (Mesostigmata)	"Gamasides" (=Gamasida?)	Republic of Lebanon	182
	N/A (Oribatida)	Oribatida	United States	27
	Saproglyphidae	Saproglyphidae	France	27
	Rhinophoridae	***Phyto melanocephala* (Meigen, 1824)**	England, France	28, 38, 174
		***Stevenia signata* (Mik, 1866)**	Republic of Croatia	25, 29
	N/A (Nematoda)	Nematoda	France	27
	Acuariidae	***Dispharynx nasuta* (Rudolphi, 1819)** = *Acuaria nasuta* (Rudolphi, 1819) = *Acuaria spiralis* Molin, 1858	Spain, Andalusia	98, 171

		= *Dispharynx spiralis* (Molin, 1858)		
		= *Dispharagus nasutus* (Rudolphi, 1819)		
	N/A (Nematoda)	***Agamonematodum armadillonis pillularis* Leidy, 1853** incertae sedis	North America	176
		***Agamonematodum hospes* von Linstow, 1882** incertae sedis	Europe	177, 178
	Rhabditidae	***Caenorhabditis elegans* (Maupas, 1899) Dougherty, 1953**	Federal Republic of Germany	84
		***Caenorhabditis remanei* (Sudhaus, 1974) Andrássy, 1983**	Federal Republic of Germany	45, 84
		= *Caenorhabditis vulgaris* Baird *et al.*, 1994		
	Mermithidae	***Agamermis* sp.**	Oriental Republic of Uruguay, Argentine Republic	43, 202
		***Mermis* sp.**	France	69
		***Thaumamermis cosgrovei* Poinar, 1981**	United States	42, 63, 190, 200
	N/A (Cestoda)	Cestoda	United States	180
***Armadillidium* sp.**	Rhinophoridae	***Melanophora roralis* (Linnaeus, 1758)**	Federative Republic of Brazil	36
Balloniscidae				
***Balloniscus glaber* Araujo & Zaido, 1996**	Rhinophoridae	Rhinophoridae	Federative Republic of Brazil	24
Cylisticidae				
***Cylisticus convexus* (De Geer, 1778)**	Blattisociidae	***Lasioseius* cf. *(Crinidens) sp.***	Canada	This study
= *Cilisticus* [sic] *convexus*	Melicharidae	***Proctolaelaps* sp.**	Canada	This study
	Rhinophoridae	***Rhinomorinia sarcophagina* (Schiner, 1861)**	Republic of Poland	31
	Rhabditidae	***Caenorhabditis remanei* (Sudhaus, 1974) Andrássy, 1983**	United States	44
		= *Caenorhabditis vulgaris* Baird *et al.*, 1994		
		cf. *Oscheius myriophilus* (Poinar, 1986)	Canada	This study
		= *Rhabditis myriophila* Poinar 1986		
Ligiidae				
***Ligia baudiniana* Milne Edwards, 1840**	Microphallidae	***Megalophallus reamesi* Overstreet & Heard, 1955**	Turks and Caicos Islands, United States	108
***Ligia cinerascens* Budde-Lund, 1885**	N/A (Arachnida: "Acari")	"Mite"	Japan	94
	Eviphididae	***Thinoseius setifer* Takaku, 2000**	Japan	198
***Ligia oceanica* (Linnaeus, 1767)**	N/A (Nematoda)	Nematoda	France	189
	Rhabditidae	Rhabditidae	France	185
		***Rhabditis* sp.**	?	178
	N/A (Trematoda)	Trematoda	France	184, 185, 189
	Microphallidae	***Maritrema linguilla* Jägerskiöld, 1908**	United Kingdom	107
		***Maritrema* sp.**	Scotland	186
***Ligia* sp.**	Dicrocoeliidae	***Lyperosomum petiolatum* (Railliet, 1900)**	Republic of Poland	197
	Microphallidae	***Levinseniella* sp.**	Western Pacific (general area)	106
		***Maritrema* sp.**	Western Pacific (general area)	106
***Ligidium hypnorum* (Cuvier, 1792)**	Echinorhynchidae	***Acanthocephalus falcatus* (Frölich, 1789) Lühe, 1911**	Ukraine	90
= *Ligidium agile* (Persoon, 1793)				
***Ligidium japonicum* Verhoeff, 1918**	Echinorhynchidae	***Pseudoacanthocephalus toshimai* Nakao, 2016**	Japan	85
***Ligidium* sp.**	Mermithidae	Mermithidae	Japan	21
Oniscidae				
***Oniscus asellus* Linnaeus, 1758**	Neopygmephoridae	***Bakerdania elliptica* (Krczal, 1959)**	England, the Netherlands, Canada	57, 58, this study
= *Oniscus murarius* Cuvier, 1792	Rhinophoridae	***Melanophora roralis* (Linnaeus, 1758)**	United States	33
		***Paykullia maculata* (Fallén, 1815)**	Great Britain, England	28, 38
		= *Chaetostevenia maculata* (Fallén, 1820)		
		= *Plesina maculata* Fallén		
		***Phyto discrepans* (Pandellé, 1896)**	Great Britain	28
		= *Styloneuria discrepans* Pandelle, 1896		
		***Phyto melanocephala* (Meigen, 1824)**	England	38, 168
		***Stevenia atramentaria* (Meigen, 1824)**	Europe	109, 167
		= *Tachina atramentaria* Meigen, 1824		
		= *Rhinophora atramentaria*		

		The record of this species in association with *Oniscus asellus* may be incorrect (Wood *et al*. 2018)		
		***Stevenia umbratica* (Fallén, 1820)** = *Rhinophora umbratica* Fallén	?	109
		***Tricogena rubricosa* (Meigen, 1824)** = *Frauenfeldia rubricosa* (Meigen, 1824) = *Frauenfeldia trilineata* Meigen, 1824 = *Tricogena ribricosa* [sic]	?	69
	N/A (Nematoda)	Nematoda	The Netherlands, France	27, 58
	Rhabditidae	***Caenorhabditis elegans* (Maupas, 1899) Dougherty, 1953**	France, Federal Republic of Germany	82, 84
		***Caenorhabditis remanei* (Sudhaus, 1974) Andrássy, 1983** = *Caenorhabditis vulgaris* Baird *et al.*, 1994	Federal Republic of Germany	84
	Anoplocephalidae	***Oochoristica tuberculata* (Rudolphi, 1819)**	Spain, Andalusia	98
	N/A (Trematoda)	Trematoda	?	38
Philosciidae				
Philosciidae sp. Host resembled *Littorophiloscia vittata* (Say, 1818) (=*Philoscia vittata* Say 1818) but was thought to be a new species.	Oxyuridae	***Oniscicula oniscicula* Schwenk, 1927**	United States	46
***Atlantoscia floridana* (Van Name, 1940)**	Centrorhynchidae	***Centrorhynchus* sp.**	Federative Republic of Brazil	1
***Philoscia affinis* Verhoeff, 1908**	"muscides" (=Muscidae?) This may be a misidentification of Rhinophoridae; see the main text for details.	Muscidae	France	69, 193
	Rhinophoridae	***Stevenia atramentaria* (Meigen, 1824)** = *Tachina atramentaria* Meigen, 1824 = *Rhinophora atramentaria*	Europe	26
***Philoscia muscorum* (Scopoli, 1763)**	N/A ("Acanthocephala")	"Acanthocephala"	France	27
	Echinorhynchidae	Echinorhynchidae	Europe	38
	Dicrocoeliidae	***Corrigia corrigia* (Braun, 1901)**	?	101
Platyarthridae				
***Platyarthrus caudatus* Aubert & Dollfus, 1890**	Mermithidae	Mermithidae	Italy	159
***Platyarthrus hoffmannseggii* Brandt, 1833**	Mermithidae	***Mermis* sp.**	?	69
Porcellionidae				
***Porcellio laevis* Latreille, 1804**	Rhinophoridae	***Phyto luteisquama* Kugler, 1978**	State of Israel	34
	Acuariidae	***Dispharynx nasuta* (Rudolphi, 1819)** = *Acuaria nasuta* (Rudolphi, 1819) = *Acuaria spiralis* Molin, 1858 = *Dispharynx spiralis* (Molin, 1858) = *Dispharagus nasutus* (Rudolphi, 1819)	Spain, Andalusia	98, 170, 171, 172, 173, 178
	Tetrameridae	***Tetrameres mohtedai* (Bhalerao & Rao, 1944)**	Republic of India	99
	Mermithidae	***Thaumamermis cosgrovei* Poinar, 1981**	United States	63
***Porcellio scaber* Latreille, 1804**	Echinorhynchidae	Echinorhynchidae	Europe	38
	Plagiorhynchidae	***Plagiorhynchus cylindraceus* (Goeze, 1782)** = *Plagiorhynchus formosus* Van Cleave, 1918 = *Prosthorhynchus formosus* (Van Cleave, 1918) = *Prosthorhynchus cylindraceus* (Goeze, 1782) = *Prosthorhynchus transversus* (Rudolphi, 1819) = *Plagiorhynchus transversus* (Rudolphi, 1819)	United States, Canada	5, 11, this study
	Neopygmephoridae	***Bakerdania elliptica* (Krczal, 1959)**	Canada	This study
	Rhinophoridae	***Melanophora roralis* (Linnaeus, 1758)**	Great Britain, United States, England	28, 33, 37, 38
		***Paykullia maculata* (Fallén, 1815)**	Great Britain, England, France	28, 38

		= *Chaetostevenia maculata* (Fallén, 1820) = *Plesina maculata* Fallén		
		***Phyto discrepans* (Pandellé, 1896)** = *Styloneuria discrepans* Pandelle, 1896	Great Britain, England, France	28, 38
		***Phyto melanocephala* (Meigen, 1824)**	Great Britain, England, France	28, 38, 168, 174
		***Rhinophora lepida* (Meigen, 1824)**	Great Britain, England, France, the Netherlands	28, 38, 39
		***Stevenia atramentaria* (Meigen, 1824)** = *Tachina atramentaria* Meigen, 1824 = *Rhinophora atramentaria*	Swiss Confederation	38
		***Stevenia* sp.**	France	27
		***Tricogena rubricosa* (Meigen, 1824)** = *Frauenfeldia rubricosa* (Meigen, 1824) = *Frauenfeldia trilineata* Meigen, 1824 = *Tricogena ribricosa* [sic]	Republic of Poland, Ireland, Great Britain, England, France	28, 31, 35, 38
	N/A (Nematoda)	Nematoda	United States	203
	Acuariidae	***Dispharynx nasuta* (Rudolphi, 1819)** = *Acuaria nasuta* (Rudolphi, 1819) = *Acuaria spiralis* Molin, 1858 = *Dispharynx spiralis* (Molin, 1858) = *Dispharagus nasutus* (Rudolphi, 1819)	Spain, Andalusia	98, 171
	Diplogastridae	***Pristionchus* cf. *lheritieri / entomophagus***	Canada	This study
	Rhabditidae	***Caenorhabditis elegans* (Maupas, 1899) Dougherty, 1953**	Federal Republic of Germany, Scotland	81, 84
		***Caenorhabditis remanei* (Sudhaus, 1974) Andrássy, 1983** = *Caenorhabditis vulgaris* Baird *et al.*, 1994	United States, Federal Republic of Germany	44, 84
	Mermithidae	***Thaumamermis cosgrovei* Poinar, 1981**	United States	42, 190
	Trematoda	Trematoda	Europe	38
	Dicrocoeliidae	***Corrigia corrigia* (Braun, 1901)**	?	101
	Dicrocoeliidae	***Lyperosomum petiolatum* (Railliet, 1900)**	Republic of Poland	197
***Porcellio spinicornis* Say, 1818** = *Porcellio pictus* Brandt	Rhinophoridae	***Melanophora roralis* (Linnaeus, 1758)**	England	32
		***Phyto melanocephala* (Meigen, 1824)**	France	26, 174
	Aphelenchoididae	***Aphelenchoides* cf. *blastophthorus* Franklin 1952**	Canada	This study
	Rhabditidae	***Caenorhabditis elegans* (Maupas, 1899) Dougherty, 1953**	Scotland	81
***Porcellio* sp.**	Rhinophoridae	***Melanophora roralis* (Linnaeus, 1758)**	United States	40
		***Stevenia deceptoria* (Loew, 1847)**	Italy	30
	Mermithidae	***Mermis* sp.**	Italy	100
***Porcellionides pruinosus* (Brandt, 1833)**	Centrorhynchidae	***Centrorhynchus milvus* Ward, 1956**	Republic of Senegal	96
	Rhinophoridae	***Melanophora roralis* (Linnaeus, 1758)**	United States	37
		***Phyto angustifrons* (Rondani, 1856)** = *Cyrillia angustifrons* Rondani, 1856	France	38
		***Phyto discrepans* (Pandellé, 1896)** = *Styloneuria discrepans* Pandelle, 1896	France	38
	Acuariidae	***Dispharynx nasuta* (Rudolphi, 1819)** = *Acuaria nasuta* (Rudolphi, 1819) = *Acuaria spiralis* Molin, 1858 = *Dispharynx spiralis* (Molin, 1858) = *Dispharagus nasutus* (Rudolphi, 1819)	Federative Republic of Brazil	89
***Porcellionides sexfasciatus* (Budde-Lund, 1885)** = *Metoponorthus sexfasciatus* Budde-Lund, 1885	Mermithidae	***Mermis* sp.**	?	69
Trachelipodidae				
***Nagurus nanus* (Budde-Lund, 1908)**	Dicrocoeliidae	***Platynosomum illiciens* (Braun, 1901)**	Federative Republic of Brazil	59
***Trachelipus arcuatus* (Budde-Lund, 1885)**	Rhinophoridae	***Stevenia atramentaria* (Meigen, 1824)**	Europe	26

= *Porcellio arcuatus* Budde-Lund, 1885		= *Tachina atramentaria* Meigen, 1824 = *Rhinophora atramentaria*		
***Trachelipus rathkii* (Brandt, 1833)** = *Trachelipus rathkei* (Brandt)	cf. Acaridae (unkeyable nymph)	cf. Acaridae (unkeyable nymph)	Canada	This study
= *Tracheoniscus rathkei* (Brandt)	Stigmaeidae	Stigmaeidae	Canada	This study
	Rhinophoridae	***Paykullia maculata* (Fallén, 1815)** = *Chaetostevenia maculata* (Fallén, 1820) = *Plesina maculata* Fallén	The Netherlands	39
		***Stevenia atramentaria* (Meigen, 1824)** = *Tachina atramentaria* Meigen, 1824 = *Rhinophora atramentaria*	Great Britain, Republic of Poland	28, 31
		***Tricogena rubricosa* (Meigen, 1824)** = *Frauenfeldia rubricosa* (Meigen, 1824) = *Frauenfeldia trilineata* Meigen, 1824 = *Tricogena ribricosa* [sic]	Republic of Poland	31
	Alloionematidae	***Rhabditophanes* sp.**	Canada	This study
	Panagrolaimidae	***Panagrolaimus* cf. *rigidus* (Schneider 1866)**		
	Rhabditidae	***Caenorhabditis remanei* (Sudhaus, 1974) Andrássy, 1983** = *Caenorhabditis vulgaris* Baird *et al.*, 1994	United States	44
***Trachelipus ratzeburgii* (Brandt, 1833)** **=** *Tracheoniscus ratzeburgii*	Rhinophoridae	***Paykullia maculata* (Fallén, 1815)** = *Chaetostevenia maculata* (Fallén, 1820) = *Plesina maculata* Fallén	Federal Republic of Germany	26
***Trachelipus squamuliger* (Verhoeff, 1907)**	Plagiorhynchidae	***Plagiorhynchus cylindraceus* (Goeze, 1782)** = *Plagiorhynchus formosus* Van Cleave, 1918 = *Prosthorhynchus formosus* (Van Cleave, 1918) = *Prosthorhynchus cylindraceus* (Goeze, 1782) = *Prosthorhynchus transversus* (Rudolphi, 1819) = *Plagiorhynchus transversus* (Rudolphi, 1819)	Republic of Bulgaria	4
Trichoniscidae				
***Alpioniscus feneriensis* (Parona, 1880)** = *Trichoniscus dispersus* Racovitza, 1907	Rhabditidae	Rhabditidae	France	187
***Trichoniscus provisorius* Racovitza, 1908** = *Trichoniscus pusillus provisorius* Racovitza, 1908	Mermithidae	***Mermis* sp.**	?	166
***Trichoniscus pusillus* Brandt, 1833**	Mermithidae	***Mermis* sp.**	?	166
Tylidae				
***Tylos latreillei* Audouin, 1826** nom. dub.	N/A (Nematoda)	Nematoda	France	161
	Rhabditidae	***Matthesonema tylosa* Osche, 1955**	?	41

Table 3.3: Number of sowbugs examined for symbionts in this study. Multiple methods were used to recover symbionts, and several different methods were often used on the same individual (e.g. examination prior to dissection, followed by washing, followed by dissection, followed by Baermann funnel extraction). Sowbugs examined for iridovirus were either alive, dead (recent natural death), or preserved in ethanol; all other methods were performed on live or euthanized sowbugs (see Methods).

	Examined for iridovirus	Examined for internal and external symbionts without dissection	Dissected to look for internal symbionts	Washed prior to dissection to dislodge external nematodes	Tissues squashed between glass slides to look for encysted symbionts	Tissues used in Baermann funnel extraction post dissection (for nematodes)	Tissues put on seeded agar plate post dissection (for nematodes)
Porcellio spinicornis	592	311	61	78	37	25	-
Porcellio scaber	324	272	56	31	29	26	-
Trachelipus rathkii	403	302	51	67	15	22	8
Cylisticus convexus	160	138	27	10	13	12	-
Porcellio dilatatus	96	86	9	-	5	5	-
Oniscus asellus	266	77	21	18	10	14	-
Armadillidium nasatum	46	46	16	16	7	8	-
Nagurus cristatus	37	36	-	-	-	-	-
Philoscia muscorum	15	15	-	4	-	-	-
Armadillidium vulgare	23	5	-	1	-	-	-
Hyloniscus riparius	2	2	-	-	-	-	-
Trichoniscus pusillus	281	2	-	-	-	-	-
Porcellionides pruinosus	1	-	-	-	-	-	-
TOTAL	**2246**	**1292**	**241**	**225**	**116**	**112**	**8**

Table 3.4: Symbionts associated with sowbugs from Canada. All records were obtained from this study. Symbionts are recorded per individual sowbug rather than per population. Sowbugs and symbionts deposited in the E.H. Strickland Entomological Museum collections (University of Alberta) may be found under the accession numbers listed in the table.

HOST SPECIES	HOST RESEARCH ID / SEX SYMBIONT RESEARCH ID	COLLECTION LOCALITY / COORDINATES	PROPORTION OF SOWBUGS OF THIS SPECIES EXAMINED FROM THIS SITE WITH AT LEAST ONE SYMBIONT OF THE TYPE LISTED	NUMBER OF SYMBIONTS / LOCATION ON HOST	STRICKLAND ACCESSION NUMBER / PRESERVATION METHOD (H = host, S = symbiont)	SYMBIONT GENE(S) SEQUENCED	GENBANK ACCESSION NUMBER(S) FOR SYMBIONT SEQUENCE(S)	SYMBIONT IDENTITY BASED ON MORPHOLOGY	SYMBIONT IDENTITY BASED ON PHYLOGENY / PERCENT IDENTITY TO CLOSEST GENBANK MATCH / PERCENT IDENTITY TO CLOSEST BOLD MATCH
Trachelipus rathkii	018AAB, M	Canada, AB, Edmonton (wooded trail on Ronning Street) 53.476, -113.594	2/4 (50%)	Original number of nematodes unclear, location unclear (nematodes were recovered by placing each dissected sowbug on an agar plate seeded with *Escherichia coli*; plate was checked after 6 days).	S (ethanol): UASM407321 S (DESS): UASM407322; UASM407325	No amplification (two extractions with one nematode each)	-	Nematoda	-
Trachelipus rathkii	018AAA, M	Canada, AB, Edmonton (wooded trail on Ronning Street) 53.476, -113.594	2/4 (50%)	Original number of nematodes unclear, location unclear (nematodes were recovered by placing each dissected sowbug on an agar plate seeded with *Escherichia coli*; plate was checked after 6 days).	S (DESS): UASM407323; UASM407324	No amplification (two extractions with one nematode each)	-	Nematoda	-
Trachelipus rathkii	034, M (host) 034-1 (symbiont)	Canada, AB, Edmonton (wooded trail on Ronning Street) 53.476, -113.594	1/5 (20%)	2, location unclear (nematodes were recovered by placing each dissected sowbug on an agar plate seeded with *Escherichia coli*; plate was checked after 24 hours).	S (DESS): UASM407326	18S (one nematode)	PQ001363	Nematoda	*Rhabditophanes* sp. 99.76% *Rhabditophanes* sp. (GenBank LK995728.1) N/A (not COI)
Cylisticus convexus	047, 1M, 4F (host) 047-1 (symbiont) 047-2 (symbiont)	Canada, AB, Sherwood Park (from greenhouse) N/A (private business)	N/A	3 total from Baermann funnel extraction of 5 sowbugs	-	18S (two extractions with one nematode each)	PQ001364 PQ001365	Nematoda	cf. *Oscheius myriophilus* 99.77% Oscheius sp. / Rhabditis sp. (GenBank AF082994.1, U81588.1) N/A (not COI)
Porcellio scaber	058, 3M, 2F	Canada, BC, Vancouver Island (under rotting logs near Bamfield Marine Sciences Centre) 48.835, -125.136	N/A	1 total from Baermann funnel extraction of 5 sowbugs	-	No amplification (one nematode)	-	Nematoda	-
Trachelipus rathkii	071AAA, F	Canada, AB, Edmonton (under logs along trail in Goldbar Park) 53.558, -113.404	3/4 (75%)	6 on external surface of body	H (ethanol): UASM407076	No amplification (one nematode)	-	Nematoda	-
Trachelipus rathkii	071AAC, F (host) 071AAC (symbiont)	Canada, AB, Edmonton (under logs along trail in Goldbar Park) 53.558, -113.404	3/4 (75%)	1 on external surface of body	-	18S (one nematode)	PQ001367	Nematoda	*Panagrolaimus* cf. *rigidus / superbus* 97.4% *Panagrolaimus*

									rigidus (GenBank KC522706.1) but >95% match to other *Panagrolaimus* N/A (not COI)
Trachelipus rathkii	071AAD, F	Canada, AB, Edmonton (under logs along trail in Goldbar Park) 53.558, -113.404	3/4 (75%)	1 on external surface of body, 1 from Baermann funnel extraction	-	-	-	Nematoda	-
Porcellio spinicornis	074AAA, F (host) 074AAA (symbiont)	Canada, AB, Edmonton (in greenhouse in SE Edmonton) N/A (private business)	1/7 (14.3%)	1 on external surface of body	-	18S (one nematode)	PQ001366	Nematoda	*Aphelenchoides* cf. *blastophthorus* 97.92% *Aphelenchoides* sp. (GenBank JQ957884.1) N/A (not COI)
Trachelipus rathkii	091AAD, F	Canada, AB, Edmonton (from pitfall trap in Kinsmen Park) 53.527, -113.514	1/11 (9.1%)	1 on external surface of body	H (ethanol): UASM407357	-	-	Nematoda	-
Porcellio scaber	092, 4M, 1F	Canada, BC, Bamfield (under planters and pots) N/A (private residence)	N/A	7 total from Baermann funnel extraction of 5 sowbugs	S (ethanol): UASM407316	-	-	Nematoda	-
Porcellio scaber	092AAG, M	Canada, BC, Bamfield (under planters and pots) N/A (private residence)	5/8 (62.5%)	2 on external surface of body	H (ethanol): UASM407358	-	-	Nematoda	-
Porcellio scaber	092AAF, M	Canada, BC, Bamfield (under planters and pots) N/A (private residence)	5/8 (62.5%)	3 on external surface of body	H (ethanol): UASM407359	-	-	Nematoda	-
Porcellio scaber	092AAC, F (host) 092-3 (symbiont)	Canada, BC, Bamfield (under planters and pots) N/A (private residence)	5/8 (62.5%)	12 on external surface of body	H (ethanol): UASM407360 S (ethanol): UASM407319 The nematodes in this sample are different individuals than those used for DNA sequencing, but originate from the same host	18S (three nematodes in single extraction)	PQ001368	Nematoda	*Pristionchus* cf. *lheritieri / entomophagus* 99.55% and 99.88% *Pristionchus entomophagus* (GenBank KT188843.1) but >99% match to other *Pristionchus* N/A (not COI)
Porcellio scaber	092AAD, F	Canada, BC, Bamfield (under planters and pots) N/A (private residence)	5/8 (62.5%)	3 on external surface of body	S (ethanol): UASM407318	-	-	Nematoda	-

Porcellio scaber	092AAA, F (host) 092AAA (symbiont)	Canada, BC, Bamfield (under planters and pots) N/A (private residence)	5/8 (62.5%)	>100 on external surface of body	H (ethanol): UASM407361 S (ethanol): UASM407317 The nematodes in this samples are different individuals than those used for DNA sequencing, but originate from the same host	18S (10 nematodes in single extraction)	PQ001369	Nematoda	*Pristionchus* cf. *lheritieri / entomophagus* 99.55% *Pristionchus entomophagus* (GenBank KT188843.1) but >99% match to other *Pristionchus* N/A (not COI)
Porcellio scaber	057AAA, M	Canada, BC, Parksville (wooded area) 49.304, -124.259	1/29 (3.5%)	1 in body cavity	S (slide): UASM407308	-	-	Acanthocephala: cf. Plagiorhynchidae	-
Porcellio scaber	092AAK, F (host) 092AAK (symbiont)	Canada, BC, Bamfield (under planters and pots) N/A (private residence)	1/76 (1.3%)	1 in body cavity	H (ethanol): UASM407125 S (ethanol): UASM407314	COI	PQ002160	Acanthocephala: Plagiorhynchidae	N/A 98.80% *Plagiorhynchus cylindraceus* (=*transversus*) (GenBank NC_029767.1) 92.86% *Plagiorhynchus cylindraceus* (=*transversus*) (BOLD GBMNA12672-19)
Porcellio scaber	106AAA, M (host) 106AAA (symbiont)	Canada, BC, Bamfield (around house) N/A (private residence)	1/9 (11.1%)	1 in body cavity	H (ethanol): UASM407151 S (ethanol): UASM407315	COI	PQ002161	Acanthocephala: Plagiorhynchidae	N/A 98.95% *Plagiorhynchus cylindraceus* (=*transversus*) (GenBank NC_029767.1) 92.93% *Plagiorhynchus cylindraceus* (=*transversus*) (BOLD GBMNA12672-19)
Trachelipus rathkii	013, M	Canada, AB, Edmonton (in pitfall trap in urban yard in SW Edmonton) N/A (private residence)	1/60 (1.7%)	1 mobile mite on sternites	S (slide): UASM407300	-	-	cf. Acaridae (unkeyable nymph)	-
Cylisticus convexus	047AAA, F	Canada, AB, Sherwood Park (from greenhouse) N/A (private business)	1/40 (2.5%)	1 mobile mite on cephalon between antennae	S (slide): UASM407298	-	-	Blattisociidae: *Lasioseius* cf. (*Crinidens*) sp.	-
Cylisticus convexus	047AAB, F	Canada, AB, Sherwood Park (from greenhouse) N/A (private business)	1/40 (2.5%)	1 mobile mite on cephalon between antennae	S (slide): UASM407299	-	-	Melicharidae: *Proctolaelaps* sp.	-

Porcellio scaber	058AAB, M	Canada, BC, Vancouver Island (under rotting logs near Bamfield Marine Sciences Centre) 48.835, -125.136	3/36 (8.3%)	1 mite on center of 7th pereonite	S (slide): UASM407303	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	058AAA, F	Canada, BC, Vancouver Island (under rotting logs near Bamfield Marine Sciences Centre) 48.835, -125.136	3/36 (8.3%)	1 mite on 6th sternite near basis of left pereiopod, 1 mite on 7th sternite near basis of left pereiopod	S (slide): UASM407304	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	058AAC, F	Canada, BC, Vancouver Island (under rotting logs near Bamfield Marine Sciences Centre) 48.835, -125.136	3/36 (8.3%)	1 mite on 6th sternite near basis of left pereiopod	H (ethanol): UASM407042 S (slide): UASM407305	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Trachelipus rathkii	073a-4C, F	Canada, AB, Edmonton (under concrete debris in Hermitage Park) 53.587, -113.374	1/71 (1.4%)	1 immobile on pereiopod	S (slide): UASM407297	-	-	Stigmaeidae	-
Oniscus asellus	1081A4, M	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	7/25 (28%)	2 mites on 7th sternite near basis of left pereiopod	S (slide): UASM407306	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	
Oniscus asellus	108-1C1, M	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	7/25 (28%)	1 mite at center of 7th sternite	H (ethanol): UASM407362	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Oniscus asellus	108-1C2, M	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	7/25 (28%)	1 mite on 7th sternite near basis of right pereiopod	H (ethanol): UASM407144 S (ethanol): UASM407309	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Oniscus asellus	108-1C3, M	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	7/25 (28%)	1 mite on 7th sternite near basis of right pereiopod	H (ethanol): UASM407363	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Oniscus asellus	108-2A1, F	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	7/25 (28%)	3 mites on center of 6th sternite	S (slide): UASM407306	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Oniscus asellus	1082A4, F	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	7/25 (28%)	2 mites on 7th sternite near basis of left leg, 1 mite on center of 7th sternite	H (ethanol): UASM407364 S (ethanol): UASM407312	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Oniscus asellus	108-2B4, F	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	7/25 (28%)	1 mite on 5th sternite near basis of left leg, 1 mite on 6th sternite near basis of left leg, 1 mite on 7th sternite near basis of left leg, 2 mites on center of 7th sternite, 1 mite on 6th sternite near basis of right leg, 1 mite on 7th sternite near basis of right leg	S (ethanol): UASM407311	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	108-2C3, F	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	10/53 (18.9%)	1 mite on 6th sternite near basis of left leg	H (ethanol): UASM407147	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-

Porcellio scaber	108-3A3, M	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	10/53 (18.9%)	1 mite on center of 6th sternite	S (ethanol): UASM407313	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	108-3A4, M	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	10/53 (18.9%)	1 mite on center of 7th sternite	H (ethanol): UASM407146	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	108-3B2, F	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	10/53 (18.9%)	1 mite on 7th sternite near basis of right leg	-	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	108-4A4, F	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	10/53 (18.9%)	1 mite on center of 7th sternite, 1 mite on 7th sternite near basis of left leg	S (ethanol; samples from multiple hosts in one vial): UASM407310	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	108-4B4, M	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	10/53 (18.9%)	1 mite on center of 7th sternite	H (ethanol): UASM407295 S (ethanol; samples from multiple hosts in one vial): UASM407310	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	108-4C1, M	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	10/53 (18.9%)	2 mites on center of 7th sternite	S (ethanol; samples from multiple hosts in one vial): UASM407310	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	108-4C3, F	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	10/53 (18.9%)	1 mite on 7th sternite near basis of right leg	S (ethanol; samples from multiple hosts in one vial): UASM407310	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	108-5B2, M	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	10/53 (18.9%)	1 mite on center of 7th sternite, 1 mite on 7th sternite near basis of left leg	S (ethanol; samples from multiple hosts in one vial): UASM407310	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	108-5B4, M	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	10/53 (18.9%)	1 mite on center of 7th sternite	S (ethanol; samples from multiple hosts in one vial): UASM407310	-	-	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	-
Porcellio scaber	10801 (symbiont) 10802 (symbiont) The two *Bakerdania elliptica* mites used for COI sequencing came from a vial containing mites from six of the *Porcellio scaber* individuals listed above (108-4A4, 108-4B4, 108-4C1, 108-4C3, 108-5B2 and 108-5B4). Sequencing was successful for only one of the two mites.	Canada, BC, Vancouver (Stanley Park) 49.304, -123.144	N/A (see note in research ID column)	N/A (see note in research ID column)	S (mite 10801; slide): UASM407301 S (mite 10802; slide): UASM407302	COI (mite 10802)	PQ008649	Neopygmephoridae: *Bakerdania elliptica* (Krczal, 1959)	80.24% Pygmephoridae sp. (GenBank MF749028.1) 81.01% Pygmephoridae sp. (BOLD CNGIH195-13)

Porcellio scaber	0591C, F	Canada, AB, Edmonton (University of Alberta Botanic Gardens, warm temperate greenhouse) 53.407, -113.761	N/A	Multiple structures resembling a yeast ascus were associated with a growth on the ovary that resembled hepatopancreatic tissue	-	-	-	Ascomycota (?)	-

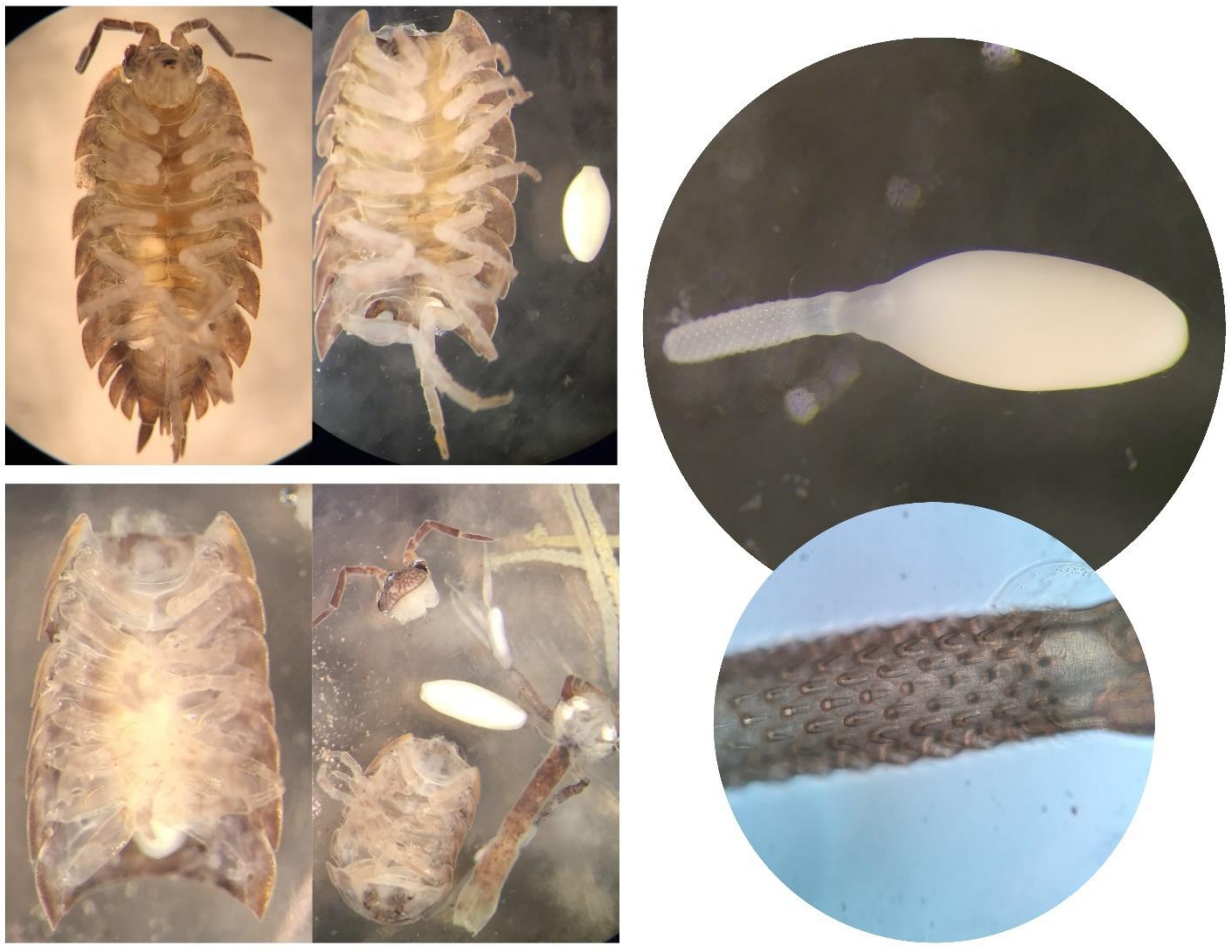


Figure 3.1: Acanthocephalans obtained in this study from *Porcellio scaber* from British Columbia, Canada. Images on the left show cystacanths *in situ* in the sowbug hosts. The cystacanths are visible through the translucent sternites. Middle images show the size of the cystacanth relative to the sowbug host. Images on the right show an everted cystacanth and the hooks on the proboscis.

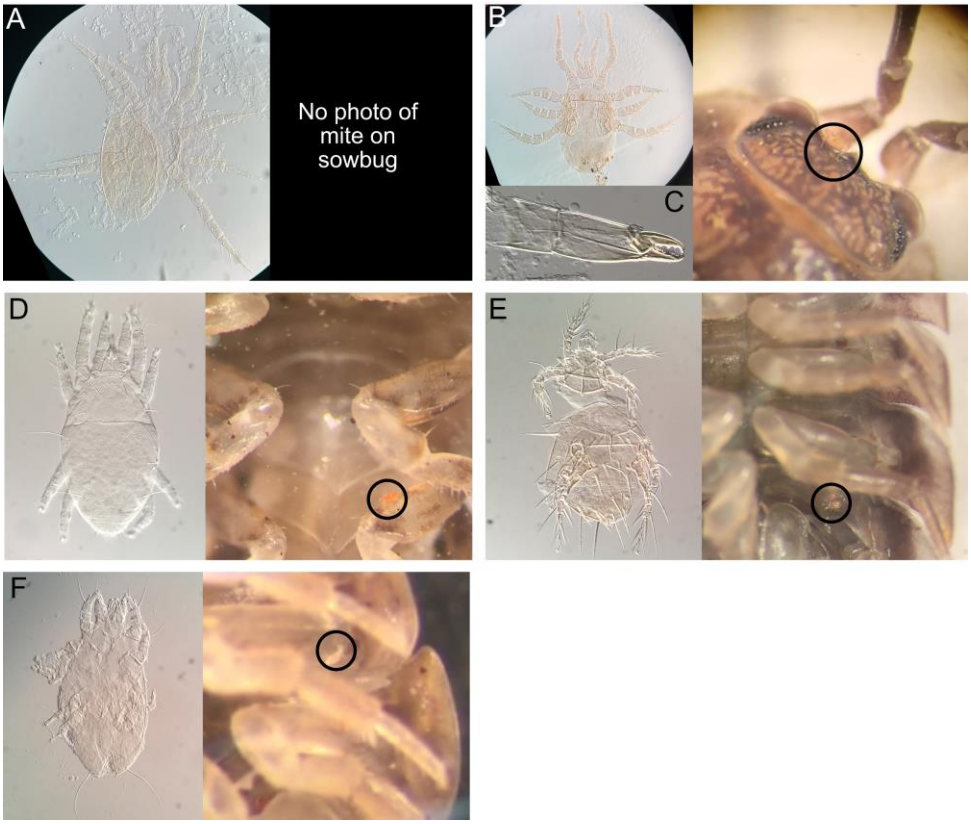


Figure 3.2: Mites obtained in this study from sowbugs from British Columbia, Canada and Alberta, Canada (See Table 3.4 for host/locality information). Each mite is shown *in situ* on the host, with the mite circled, and is also pictured after clearing and slide-mounting. Mites are not shown to scale relative to each other. **A**: *Proctolaelaps* sp., found actively moving on the head of the host between the antennae. **B**: *Lasioseius* cf. (*Crinidens*) sp., found actively moving on the head of the host between the antennae. **C**: Chelicera of *Lasioseius* cf. (*Crinidens*) sp. shown in B. **D**: Stigmaeidae sp., found inactive on the 7th pereiopod of the host. **E**: *Bakerdania elliptica*, found inactive on the posterior pereion sternites of the host. **F**: cf. Acaridae sp. (unkeyable nymph) found actively moving on the sternites of the host.

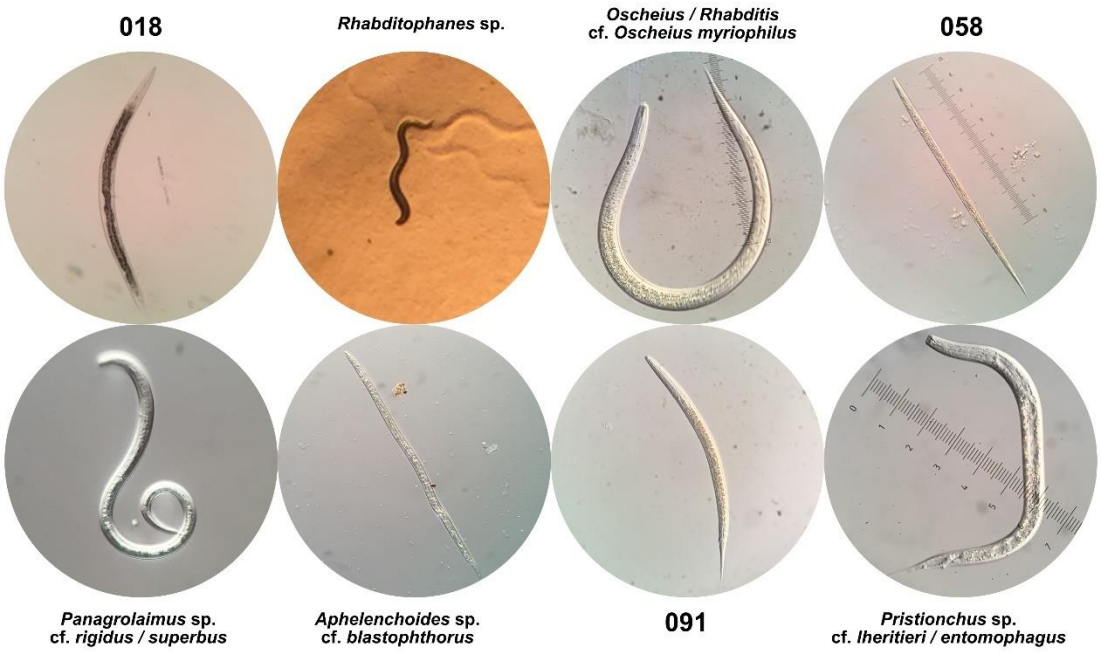


Figure 3.3: Nematodes obtained in this study from sowbugs from British Columbia, Canada and Alberta, Canada (See Table 3.4 for host/locality information). Labels indicate the collection number rather than the species identity if identification via partial 18S sequencing was unsuccessful (see Table 3.4).

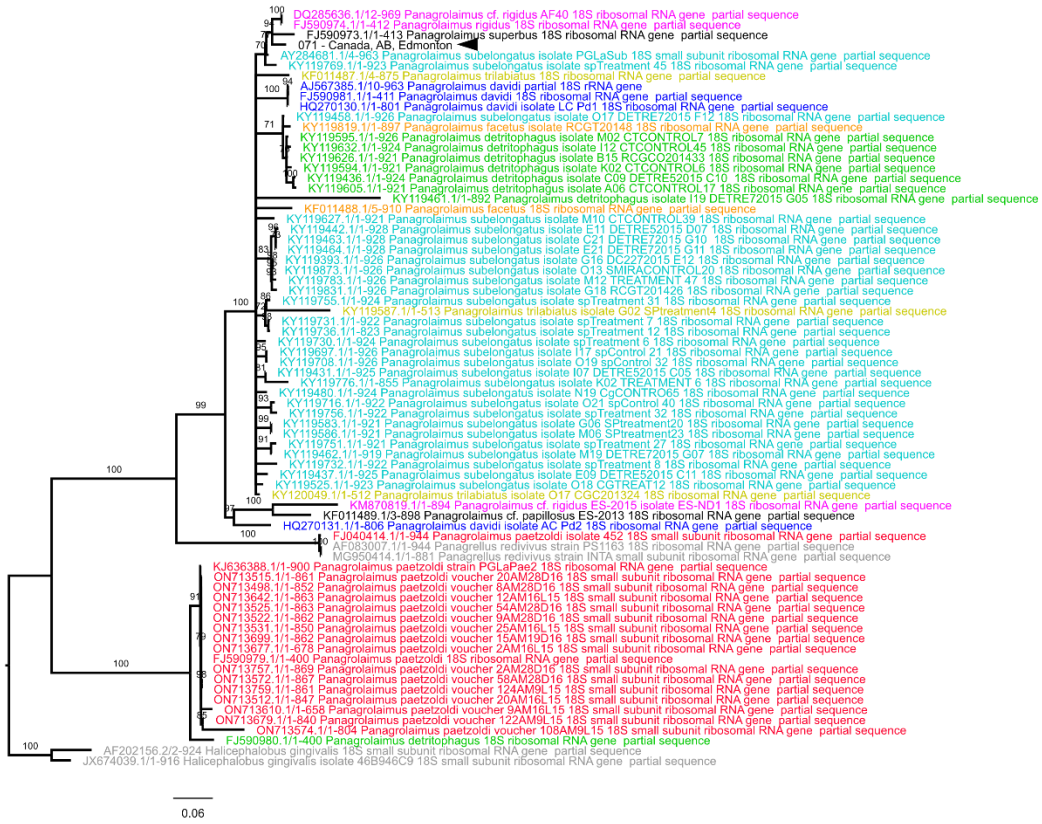


Figure 3.4: Maximum likelihood phylogeny of *Panagrolaimus* partial 18S sequences. Zoom for details. Species represented by multiple sequences are assigned a unique color; outgroup sequences are grey. The sequence from this study is indicated with a black arrow. Numbers above the nodes indicate ultrafast bootstrap support; clades with <70% support are collapsed. Names of the sequences obtained from GenBank reflect the names given when the sequences were deposited, and may not be in accordance with currently-accepted taxonomy.

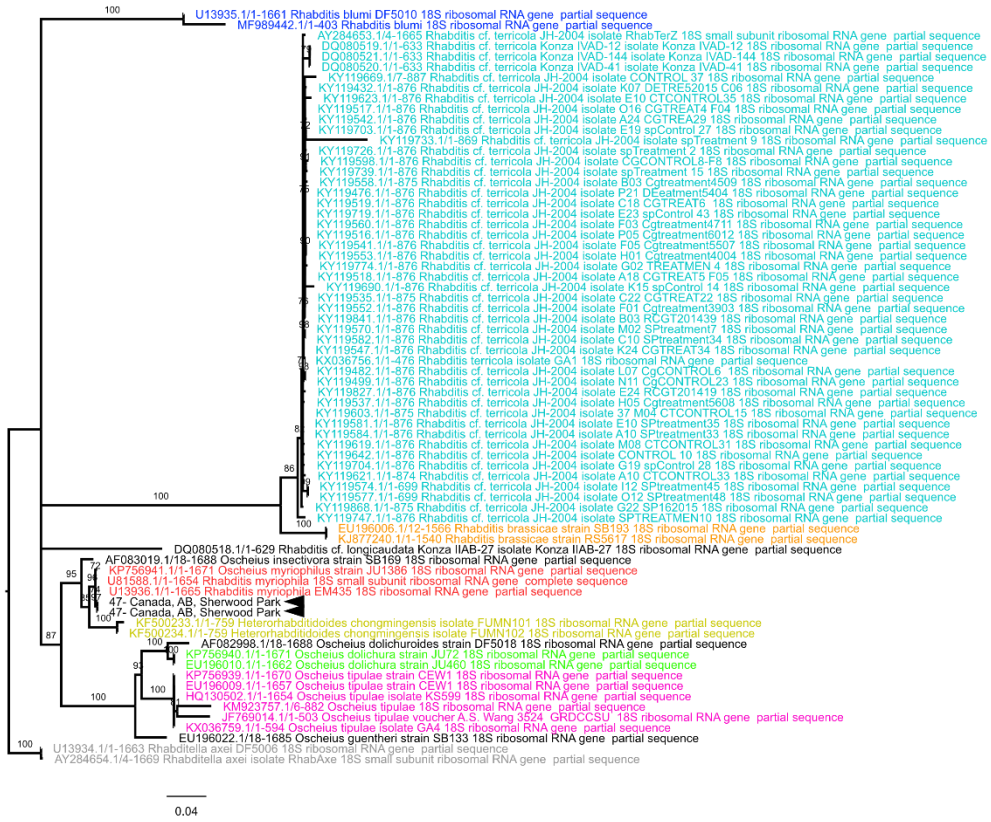


Figure 3.5: Maximum likelihood phylogeny of *Oscheius* and *Rhabditis* partial 18S sequences. Zoom for details. Species represented by multiple sequences are assigned a unique color; outgroup sequences are grey. Sequences from this study are indicated with black arrows. Numbers above the nodes indicate ultrafast bootstrap support; clades with <70% support are collapsed. Names of the sequences obtained from GenBank reflect the names given when the sequences were deposited, and may not be in accordance with currently-accepted taxonomy.

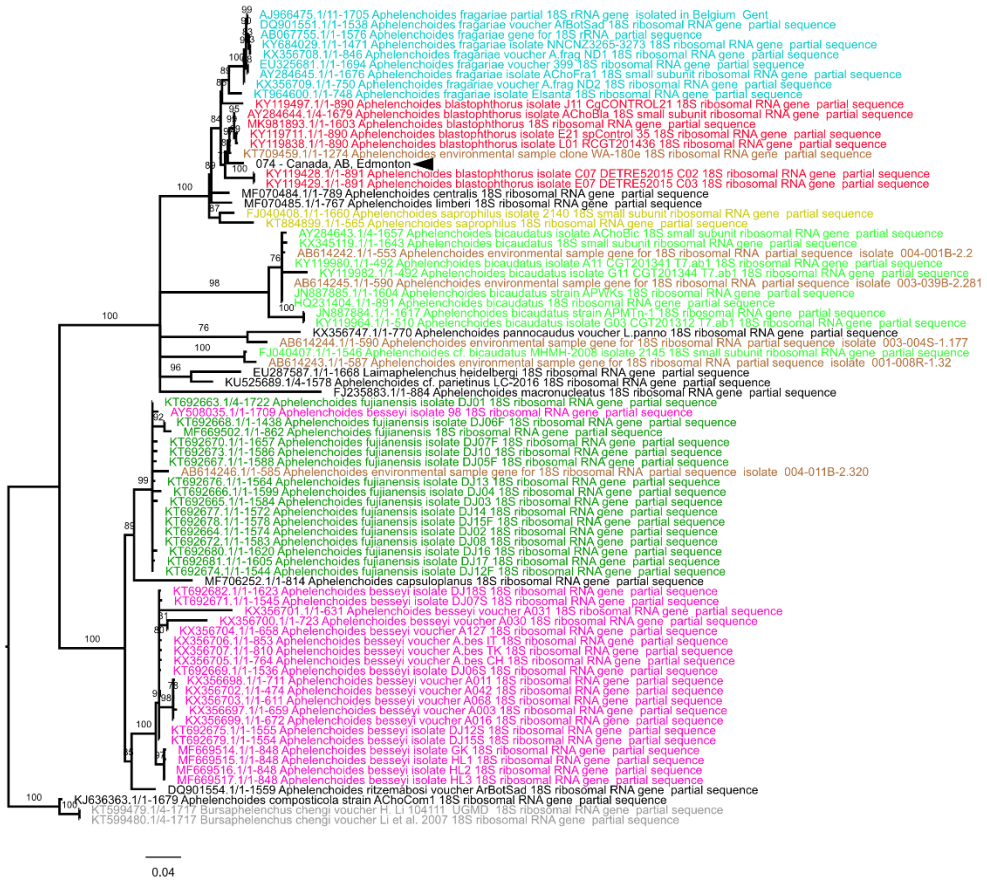


Figure 3.6: Maximum likelihood phylogeny of *Aphelenchoides* partial 18S sequences, including unidentified *Aphelenchoides* environmental samples. Zoom for details. Species represented by multiple sequences are assigned a unique color; outgroup sequences are grey. The sequence from this study is indicated with a black arrow. Numbers above the nodes indicate ultrafast bootstrap support; clades with <70% support are collapsed. Names of the sequences obtained from GenBank reflect the names given when the sequences were deposited, and may not be in accordance with currently-accepted taxonomy.



Figure 3.7: Maximum likelihood phylogeny of *Pristionchus* partial 18S sequences. Zoom for details. Species represented by more than two sequences are assigned a unique color; outgroup sequences are grey. Sequences from this study are indicated with black arrows. Numbers above the nodes indicate ultrafast bootstrap support; clades with <70% support are collapsed. Names of the sequences obtained from GenBank reflect the names given when the sequences were deposited, and may not be in accordance with currently-accepted taxonomy.

Chapter 4.

Population structure of a non-native terrestrial isopod (*Porcellio spinicornis* Say) in Alberta, Canada: multiple introductions, intercontinental bottleneck, and role of greenhouses as sites of introduction

4.1. Introduction

4.1.1. Introduced sowbugs

Terrestrial isopods, also known as sowbugs, are crustaceans belonging to the suborder Oniscidea (Schmidt 2008). With over 3700 named species, sowbugs form the largest isopod suborder (Schmalfuss 2004; Sfenthourakis and Taiti 2015) and are one of the few groups of crustaceans with fully terrestrial members (Richardson and Araujo 2015). Sowbugs are readily transported to new areas via human activity, and some species have established populations in many different parts of the world (Jass and Klausmeier 2000; Schmalfuss 2004; Szlavecz *et al*. 2018). Sowbugs from Europe have been introduced extensively across North America (Hatch 1947; Jass and Klausmeier 2000). In Canada, native oniscideans are almost entirely limited to the coasts, with sowbugs in non-coastal provinces consisting mostly of non-native species (Chapter 2). Sowbugs in non-coastal areas of Canada have received little research attention, and historical records of sowbugs in the Prairie Provinces of Canada (Alberta, Saskatchewan, Manitoba) are even more scarce. As of 2014 there had been no published records of sowbugs from any of the Prairie Provinces (Snyder 2014) and the first and only published peer-reviewed record of a sowbug from this area was for *Trachelipus rathkii* (Brandt) from a single site in Edmonton, Alberta (Li 2022).

However, a greater diversity of oniscideans from these provinces has been reported in non-peered reviewed publications (Stormer and Proctor 2021, 2022) and as photos on citizen science websites (Chapter 2). Based on such records, sowbugs have been present in the Prairie Provinces for at least two decades: citizen science websites such as iNaturalist and BugGuide include many unambiguous photographs of sowbugs from Alberta, Saskatchewan, and Manitoba (iNaturalist 2023a, 2023b, 2023c; BugGuide 2023a, 2023b, 2023c) and two unpublished GBIF records list sowbugs from this area (GBIF 1804315867; GBIF 2633738084). Including these sources, the earliest record of a sowbug from the Prairie Provinces is *Porcellio spinicornis* Say from Edmonton, Alberta in 2005 (BugGuide 33837). Anecdotal evidence from long-term residents in Alberta also suggest that sowbugs may be a relatively recent introduction, as they seem to have been absent from the province until the late 1970s (pers. obs., HP; pers. comm., John Acorn, University of Alberta). The limited historical records of sowbugs from provinces and states contiguous with the Prairie Provinces also suggest a relatively early date of introduction: the earliest sowbug record from Ontario is 1871 (Stuxberg 1873); from British Columbia, 1905 (Richardson 1905); from Minnesota, 1932 (Arcangeli 1932); and from Montana, 1939 (Hatch 1939). To the best of my knowledge no published records of sowbugs exist for North Dakota or the Northwest Territories (Jass and Klausmeier 2001).

Initial introductions of sowbugs to North America may have occurred through transport of soil ballast on ships (Lindroth 1957), and present-day introduction may take place through sale of sowbugs as pet food (Cochard *et al*. 2010) or as pets themselves (e.g. Jungle Jewel Exotics 2023), through shipment of building materials (Slabber and Chown 2002) and gravel (McQueen 1976), or via shipment of soil, plants, and other gardening supplies to greenhouses and gardens (Hatch 1947; Jass and Klausmeier 2000; Vilisics and Hornung 2009; Cochard *et al*.

2010; De Smedt *et al*. 2017). The importance of greenhouses as sites of sowbug introduction has been proposed by several researchers. Sowbug diversity is typically high in greenhouses (De Smedt *et al*. 2017) even when compared with natural areas such as parks and forests (Korsós *et al*. 2002). Sowbugs were present in 66/67 greenhouses examined in North America in the Pacific Northwest (Hatch 1947) and 7/7 greenhouses surveyed in Britain (Gregory and Lugg 2020). Some species of sowbugs may be entirely restricted to greenhouses in colder parts of their non-native range (Hatch 1947; Rapp 2001; Schmalfuss 2004; Gregory 2014). Greenhouses may therefore be sites of primary introduction for sowbugs, from which multiple secondary introductions may originate. However, the role of greenhouses as 'invasion hubs' (Acevedo-Limón *et al*. 2020) for sowbug introduction has never been examined with molecular methods.

4.1.2. Molecular investigation of introduced species

An introduced population of a non-native species may originate directly from a region to which it is native (primary introduction) or be derived from an already introduced population (secondary introduction) (Michaelides *et al*. 2015). Introduction of a subset of a population to a new area usually acts as a bottleneck, expressed as reduced genetic diversity in the founding population when compared to the source population (founder effect) (Dlugosch and Parker 2008; Pérez-Portela *et al*. 2012). Loss of genetic diversity correlates with number of individuals introduced, with more severe bottlenecks resulting in a greater reduction in genetic diversity (Spencer *et al*. 2000). As a population originating from a secondary introduction may have undergone an additional bottleneck compared to populations at primary introduction sites, a population with high genetic diversity compared to other sites is often considered to represent a primary introduction site (Pérez-Portela *et al.* 2012; Lacoursière-Roussel *et al*. 2012; Leo *et al*. 2015; Cao *et al*. 2017). Such geographic variation in genetic diversity in introduced species may

also develop via gradual range expansion following initial introduction, which typically produces a cline in which diversity decreases with increasing distance from the original introduction site (White *et al*. 2013, Acevedo-Limón *et al*. 2020). However, clines in genetic diversity may not be observed if new sites are reached by passive dispersal (e.g. human-mediated dispersal; see following paragraph). In some circumstances source and founding populations may have similar levels of genetic diversity. Multiple introductions may add genetic diversity (Dupont *et al.* 2003), particularly if introductions originate from different source populations (Kolbe *et al*. 2004). Similar levels of diversity in source and founding populations may also be explained by rapid population growth following introduction (Zeisset and Beebee 2003), or a high mutation rate (Kaňuch *et al*. 2021). Even populations secondarily introduced from primarily introduced populations can maintain high levels of genetic diversity (Zeisset and Beebee 2003; Kolbe *et al*. 2004). However, genetic diversity may still decline at least temporarily (Kaňuch *et al*. 2021), even in populations originating from multiple introductions (Dlugosch and Parker 2008).

Active and passive dispersal may affect patterns of relatedness between populations of an introduced species within its introduced range. Limited dispersal may lead to a pattern of isolation by distance (IBD), where a positive correlation exists between genetic and geographic distances among populations (Wright 1943). The scale at which IBD exists is related to dispersal capacity: weakly-dispersing species may lack this pattern over large spatial scales but exhibit it over smaller scales (Peterson and Denno 1998; Aguillon *et al*. 2017). Sowbugs are generally considered to be poor active dispersers (Hornung 2011; Lee *et al*. 2014; Szlavecz *et al*. 2018; Dimitriou *et al*. 2022), especially those with highly convex bodies that protect themselves by rolling up (= conglobation) (Schmalfuss 1984). However, field studies suggest that some sowbug species may be capable of travelling considerable distances. The desert-dwelling *Hemilepistus*

reaumurii Milne Edwards can cover over 1000 m in a single year (Baker 2004) and even *Armadillidium vulgare* (Latreille), a conglobating species, has been observed to travel 1.3 - 6.4 m/day (Paris 1965; Furukawa *et al*. 2017), and could theoretically travel up to 150 m/day (Furukawa *et al*. 2017). Sowbug dispersal may be biased by sex: both sexes of *H. reaumurii* disperse long distances (Baker 2004), but *A. vulgare* exhibits male-biased dispersal, leading to IBD over a scale of <100 meters for females only (Durand *et al*. 2019). On a larger scale, evidence of IBD is present in the nuclear genome of *A. vulgare* across 10s of kilometers in France (Verne *et al*. 2012). Active dispersal by sowbugs in an area to which they are introduced could therefore lead to isolation by distance within a single city, assuming sufficient time has elapsed and that no there are no significant barriers that would inhibit gene flow between closely situated populations. However, patterns of IBD can be disrupted by intermittent long-range dispersal (Wright 1943). IBD may not be observed when human-mediated passive dispersal plays a role in transporting individuals between distant localities (Pérez-Portela *et al*. 2012; Acevedo-Limón *et al*. 2020). Given the many documented introductions of terrestrial isopods to new areas via human activity, passive dispersal in non-native sowbugs may play a major role in establishing new populations via secondary introductions, and IBD may be absent if sowbugs are frequently passively transported between sites.

4.1.3. Population structure of *Porcellio spinicornis*

I chose *Porcellio spinicornis* Say (Isopoda: Oniscidea: Porcellionidae) as a model species to study the population structure of introduced sowbugs in Alberta because it was present in multiple greenhouse and non-greenhouse sites in Alberta (Chapter 2), whereas other species were uncommon in one of the two site types. To my knowledge the population structure of *P. spinicornis* has never been studied in either its native or introduced range. *Porcellio spinicornis*

is native to Europe (Schmalfuss 2004) but has been introduced to North America (Jass and Klausmeier 2000). It is one of the most common sowbug species in Alberta (Chapter 2), in North America (Jass and Klausmeier 2000) and in urban areas worldwide (Szlavecz *et al*. 2018). *Porcellio spinicornis* prefers relatively dry calcareous substrates (Harding and Sutton 1985) and can be found in greenhouses (Harding and Sutton 1985; Gregory *et al*. 2009). In Ontario (Canada), *P. spinicornis* typically lives for one year, with young from the previous autumn overwintering and producing a brood in summer, which then breed in autumn (McQueen 1976). A small percentage of individuals may live two years (McQueen 1976).

In this study I investigate the population genetic structure of an introduced sowbug (*Porcellio spinicornis*) in Alberta using ddRADseq, which yields short sequences from many random locations throughout the genome (Peterson *et al.* 2012). First, I assess the genetic variation of populations within a city (i.e. Edmonton) and provincially across several localities in Alberta. I also determine whether genetic variation is correlated with geographic distance locally (e.g. within a city) and/or between cities. Since passive dispersal has likely played a major role in establishing sowbug populations in Alberta, my *a priori* expectation was that there would be weak or no signals of isolation by distance both within and between cities. Due to bottlenecks associated with primary introduction and/or because founders originated from more than one source, populations in different greenhouses will likely differ substantially from each other, especially if greenhouses receive goods from different suppliers (i.e. different sowbug source populations). Non-greenhouse populations will also likely differ from each other for the same reason (i.e. different greenhouse source populations and/or bottlenecks associated with secondary introduction). Overall, populations of *P. spinicornis* within the same city may therefore be as differentiated from each other as from populations in a different city.

Secondly, I assess whether genetic evidence supports the role of greenhouses as primary introduction sites for *P. spinicornis* in Edmonton. While greenhouses have often been assumed to represent primary introduction sites for introduced sowbugs in general, this has never been tested with molecular methods. If greenhouses are the primary sites of introduction, greenhouse populations of *P. spinicornis* should have higher levels of genetic diversity compared to populations outside of greenhouses. Lower genetic diversity outside of greenhouses may be either due to bottlenecks and subsequent loss of genetic diversity with secondary introductions from greenhouses to other sites, or from range expansion via active dispersal of sowbugs away from greenhouses. Finally, I use partial COI sequences to make a preliminary investigation into the relationships between *P. spinicornis* populations in Alberta, in the rest of North America, and in Europe. Through investigation of *P. spinicornis* populations I hope to understand more about the movement and history of introduced sowbug populations in Alberta.

4.2. Methods - ddRADseq

Porcellio spinicornis lacks a published genome, and there are currently no genomes available for any species in the family Porcellionidae. Most insect genomes are less than 1 Gbp (Hanrahan and Johnston 2011; Alfsnes *et al*. 2017) but crustacean genomes tend to be larger (Alfsnes *et al*. 2017). Sowbug genomes are large (1 – 10 Gbp) (Jeffrey 2015; Becking *et al*. 2019; Chebbi *et al*. 2019; Russell *et al*. 2021; Yuan *et al*. 2023) which made whole-genome sequencing prohibitively expensive. ddRADseq was chosen to investigate the population structure of *P. spinicornis* because no reference genome is required (Peterson *et al*. 2012; Andrews *et al*. 2016), the data can be used to study recent divergence (Carter *et al*. 2023) and ddRADseq has been used previously to investigate sowbug population structure (Dimitriou *et al*. 2022).

4.2.1. Sowbug collections

I collected *Porcellio spinicornis* specimens from 2021-2023. My collections were augmented by specimens provided by T. Pike, K. Floate, H. Carcamo, H. Proctor, C. Crooks, B. Grappone, B. Tonn and C. Paszkowski (Chapter 2). Collecting efforts focused on the greater Edmonton area (Alberta) and parts of southern Alberta, with smaller opportunistic collections from Ontario and Saskatchewan (Fig. 4.1, 4.2; Table 4.1). Sowbugs were collected in the spring, summer, and fall from a variety of urban areas, disturbed natural areas (e.g. nature trails in residential localities), and relatively undisturbed natural areas (e.g. trails in rural localities). In addition to outdoor collections, I also searched for sowbugs at greenhouses located within a 70 km radius of Edmonton, Alberta with permission from greenhouse managers. I initially contacted greenhouses at random, but after having consistently failed to find sowbugs at greenhouses with dry concrete flooring, I thereafter selected greenhouses based on presence of suitable sowbug habitat as shown in social media images (e.g. gravel substrate, outdoor area with pots resting on the

ground, plant displays with soil substrate). I searched for sowbugs in the immediate area surrounding the greenhouses and in greenhouse buildings. Collection methods were similar across all types of collection sites: I hand-collected sowbugs by turning over gravel and mulch and lifting items on the ground, and obtained smaller sowbugs from Tullgren funnel extractions of leaf piles and soil. I temporarily housed all live-collected sowbugs in containers with a damp paper towel prior to photographing them, determining their sex (Hopkin 1991), and identifying them morphologically (Chapter 2), after which I euthanized them with carbon dioxide gas and preserved them in 95% ethanol for DNA extraction and molecular identification (Chapter 2) or in 70% ethanol as morphological vouchers.

4.2.2. Sample preparation

Briefly, I extracted total genomic DNA from 130 *Porcellio spinicornis* using a DNeasy Blood and Tissue Kit (Qiagen) according to the manufacturer's instructions, with the following modifications designed to increase DNA yield from poorly-preserved samples: (1) tissue was ground with a pestle after adding buffer ATL; (2) incubation time was three hours after adding proteinase K; (3) 4 µl of RNAse A was added after incubation. The entire body was used for DNA extraction when sowbugs measured 5 mm in length or less (cephalon to telson tip), the entire pereion for sowbugs between 5-10 mm, and the first 4-5 pereion segments for sowbugs >10 mm. In the latter two cases the head and pleon were kept as morphological vouchers, as many of the features necessary for sowbug species identification are found in these areas (e.g. second antennae, ommatidia, telson and uropods, male pleopods). The gut was removed prior to extraction when sowbugs were >4 mm in length. Residual tissues (when available) and/or conspecifics from the same collection sites were deposited in the E.H. Strickland Entomological Museum collections (University of Alberta) (Table 4.1) under accession numbers UASM407006

- UASM407368. Following extraction, I measured DNA concentration with a Qubit 2.0 fluorometer and evaluated DNA purity with a Nanodrop spectrophotometer. The raw DNA extract often contained a pink pigmentation; I cleaned the 45 pinkest samples with a OneStep™ PCR Inhibitor Removal Kit (Cedarlane) which removed the pigmentation. Based on the quantity of DNA yield as assessed by Qubit, I chose up to five individuals per site for ddRADseq, resulting in an initial 120 samples from 35 sites. Finally, I normalized each sample to 20 ng/µl with a minimum of 200 ng of DNA and assessed DNA quality and normalization success with gel electrophoresis. As expected, many of the samples stored in 70% ethanol exhibited severe DNA degradation and were removed from further analysis. The final sample set contained 72 individuals covering five greenhouses and 23 non-greenhouse sites with 1-4 individuals per site (median three individuals per site). ddRADseq library preparation and sequencing was performed by the University of Alberta Molecular Biology Service Unit (MBSU). Library preparation followed MacDonald (2020) with the following modifications: (1) the restriction enzymes were EcoR1 and Pst1; (2) all sixteen i5 adaptors were used, but subpools were made with 10 µl of eight sample ligations instead of 5 µl of 16 samples (step 3); (3) purification of the final pool was done with a 1:1 ratio of Seramag Select beads following the manufacturer's protocol; 4) size range of the final pool was 400-2000 (average 1000 bp). Sequencing was performed using a NextSeq 500 (Illumina) and a 75-cycle high output kit.

4.2.3. Restriction enzyme choice

ddRADseq has been performed only once for a sowbug species (Dimitriou *et al*. 2022). The species used in that study was from the family Armadillidae rather than Porcellionidae, and so the restriction enzyme pair used by Dimitriou *et al*. (2022) would not necessarily be ideal for *Porcellio spinicornis*. To estimate the number of fragments produced for different enzyme

combinations, I used the Sim RAD R package (Lepais and Weir 2014) to perform in silico digestions of four sequenced sowbug genomes (*Trachelipus rathkii* (Brandt) (GenBank GCA_015478945.1), *Ligia exotica* Roux (GenBank GCA_002091915.1), *Armadillidium nasatum* Budde-Lund (GenBank GCA_009176605.1), *Armadillidium vulgare* (Latreille) (GenBank GCA_004104545.1)) and two simulated *Porcellio spinicornis* genomes. I chose a fragment size selection window of 150-1500 bp, which is the typical fragment size distribution resulting from ddRADseq library preparation at the University of Alberta Molecular Biology Service Unit (MBSU). I set the length of the simulated *P. spinicornis* genomes to 3.48 Gbp based on the estimated genome size of this species (Gregory 2023), and assigned one *P. spinicornis* genome a G/C content of 25.5%, and the other 35.5% (the lowest and highest content of the four sequenced sowbug genomes). I digested all six genomes in silico with all the enzyme combinations available at the MBSU (Msp1/Pst1, Msp1/Sbf1, EcoR1/Pst1, EcoR1/Sbf1) resulting in 24 genome/enzyme combinations. To shorten the computation time the *T. rathkii* genome was digested five times using a random selection of 20% of the genome, and the results were averaged. Similarly, each of the two simulated *P. spinicornis* genomes were digested twice using a random selection of 50% of the genome each time, and the results were averaged for each genome individually. Multiple digestions produced identical results for the other three sowbug genomes. This analysis resulted in estimates of the number of fragments (i.e. ddRADseq loci) produced from the *Porcellio spinicornis* genome with each restriction enzyme combination. I used these estimates to calculate the expected read depth with each enzyme combination by accounting for the number of *Porcellio spinicornis* individuals used in the analysis and the expected number of reads produced by sequencing with a NextSeq 500 (Ilumina).

4.2.4. Data preparation and filtering

Preparation for data analysis roughly followed Rochette and Catchen (2017). The scripts and pipeline that I used for data preparation and most analyses (PCA, DAPC, ADMIXTURE, F_{ST} calculation) were modified from scripts written by Dr. Erin Campbell (Canadian Food Inspection Agency, Ottawa) and from examples of Dr. Campbell's scripts that were modified by Leah Jackson (University of Alberta). Reads were demultiplexed and filtered for quality with Stacks v 2.64 (Rochette *et al*. 2019) with further filtering in fastP v 0.23.1 (Chen *et al*. 2018) to remove enzyme cut sites and Illumina adaptor sequences. Read statistics and quality were visualized with FastQC (Andrews 2010) and MultiQC (Ewels *et al*. 2016). FastQC detected an Illumina Universal Adaptor sequence (AGATCGGAAGAG) that was not present in the list of adaptors that fastP automatically removes, so I manually specified this sequence for removal (-a AGATCGGAAGAG). During initial exploration of the dataset it became evident that a sample from a non-greenhouse site in Edmonton had 99.98% missing data and exhibited aberrant characteristics in FastQC (elevated GC content and percentage of overrepresented sequences compared to all other samples). I removed this sample from further analysis, leaving 71 samples remaining. Reads were assembled into loci using the de novo pipeline in Stacks v 2.64 (Rochette *et al*. 2019). I selected values for the M, m, and n parameters based on the number of loci and number of SNPs per locus using the r80 method (Paris *et al*. 2017). I tested values of M 0-5, n 0-6, and m 1-6 while other values were held at their default (M2, m3, n0), with additional tests of n 0-6 when M=4, and M=n for values 1-6. The population map included all samples in same population for both parameter testing and final de novo locus assembly with the chosen parameters, as there was no prior expectation for a particular population structure. Finally, VCFtools (Danecek *et al*. 2011) was used to filter the dataset for minimum genotype quality

(minGQ=30), minimum allele frequency (maf=0.01), and missing data (20% missing data allowed) to create dataset 1, which included all SNPs. Both STRUCTURE and ADMIXTURE assume unlinked loci by default (Pritchard *et al*. 2000; Alexander *et al*. 2009) and so Stacks v. 2.64 was used to select one random SNP per locus prior to filtering in VCFtools, after which the dataset was filtered with VCFtools as stated previously to create dataset 2. File conversions throughout this pipeline were completed using PLINK v 1.9 (Chang *et al*. 2015) and the R package gwscaR (https://github.com/spflanagan/gwscaR).

4.2.5. PCA and DAPC

I constructed a PCA and DAPCs for dataset 1 using the R package adegenet v 2.1.0 (Jombart and Collins 2015). I also completed the same analyses for a subset of dataset 1 that included only the samples from Edmonton. Samples with a high percentage of missing data may form a cluster at the origin of a PCA plot (Yi and Latch 2022). I colored individuals in the plot by percentage of missing data to determine whether missing data may have influenced the clustering observed. The percentage of missing data per individual was obtained using the --missing-indv flag in VCFtools (Danecek *et al*. 2011). I also colored individuals in the plot by sex to assess whether sex may have played a role in the clustering patterns observed. I used K-means clustering and a-score optimization (as implemented in adegenet) to select the number of clusters and the number of principal components to retain for the DAPCs. As the K-means clustering and DAPC results varied in duplicate runs, K-means clustering and DAPC construction was repeated 10 times for K-values 2 and 3 for each dataset for a total of 40 DAPCs.

4.2.6. ADMIXTURE analysis

I performed a hierarchical population structure analysis on dataset 2 using ADMIXTURE v 1.3 (Alexander *et al*. 2009), where clusters found in the initial analysis were re-analysed individually

to see if substructure was present. I tested K-values from 2-10 for each analysis with 20 replicates per K-value. Initial exploration of the dataset was conducted with K-values from 2-30, one replicate per K, and 10-fold cross validation as implemented in ADMIXTURE to assess the preferred K-value(s). Additionally, I used both STRUCTURE v 2.3.4 (Pritchard *et al*. 2000) and ADMIXTURE to construct a K=2 plot for a preliminary version of dataset 2 to compare the results generated by these algorithms. STRUCTURE analysis was conducted with 100,000 burn-in and 100,000 post burn-in iterations. The plot generated by STRUCTURE was identical to the plot made with ADMIXTURE (Fig. D1) but was produced approximately 15 times slower, and so ADMIXTURE was used for subsequent analyses. I used CLUMPAK (Kopelman *et al*. 2015) to investigate major and minor modes for each K-value for each analysis and to produce plots for each K-value. Preferred K-value(s) for each analysis were assessed with 10-fold cross-validation as implemented in ADMIXTURE, and for the initial analysis (all samples included) the choice of K was assessed further with STRUCTURESELECTOR (Li and Liu 2018). STRUCTURESELECTOR runs several different methods for estimating the preferred K-value, including the choose K algorithm (Raj *et al*. 2014), the "Evanno method" (ΔK, or delta-K) (Evanno *et al*. 2005), and the four estimates of K proposed by Puechmaille (2016). The latter four estimates require input from the user to group the samples into populations. Because a threefold division of the total sample set was indicated by the initial ADMIXTURE analysis, the SNP phylogeny, and the PCA (see Results), I grouped the samples into three populations (Edmonton, northern Calgary, and "mixed"). Finally, I visualized ADMIXTURE results with STRUCTURE PLOT (Ramasamy *et al*. 2014) and QGIS v 3.14.16 (QGIS.org 2023).

Unbalanced sampling can affect the output generated by genetic clustering algorithms (e.g. ADMIXTURE, STRUCTURE) (Kalinowski 2011; Puechmaille 2016; Lawson *et al*. 2018).

To assess population structure with balanced sampling, I created 10 datasets that each contained a random set of eight samples from Edmonton as well as all twelve samples from non-Edmonton sites (N=4 northern Calgary, N=8 southern Alberta) and ran 10 replicates for each K-value from 2-10. I used CLUMPAK (Kopelman *et al*. 2015) to visualize the results and to produce plots for each K-value.

4.2.7. Phylogenetic analysis

I constructed a maximum likelihood phylogeny of dataset 1 with IQTree (Nguyen *et al*. 2015) using ModelFinder (Kalyaanamoorthy *et al*. 2017) to select the best model. I removed ambiguously-constant sites (e.g. sites for which some samples lacked sequence information, but all sequenced samples had the same nucleotide) and applied the ascertainment bias correction option (+ASC). The phylogeny was assessed with 1000 ultrafast bootstrap replicates (Hoang *et al*. 2018). Finally, I used FigTree (Rambaut 2009) and TreeGraph2 (Stöver and Müller 2010) to visualize the phylogenies.

4.2.8. Isolation by distance

To test for isolation by distance (IBD) I created five datasets ('allsites 1-5') by choosing three individuals from each site that had sequences from at least three individuals. For sites that had four individuals, a subset of three sequences was chosen per site to maximize differences between the first four datasets (e.g. 1st, 2nd, and 3rd individuals in the first dataset, 1st, 2nd, and 4th for the second dataset, 2nd, 3rd, and 4th for the third dataset, etc.). The fifth dataset consisted of applying each selection pattern in sequence (e.g. 1st, 2nd, and 3rd individuals from the first site, 1st, 2nd, and 4th for the second site, 2nd, 3rd, and 4th for the third site, etc.). I then removed all non-Edmonton samples from the five datasets to make an additional five datasets ('Edmonton 1-5') to test for IBD within Edmonton. Each of the allsites and Edmonton datasets were created by

rerunning the populations module of Stacks v 2.64 (Rochette *et al*. 2019) with the same Stacks parameters used to create dataset 1 and using a population map that treated each site as a separate population. I filtered each allsites and Edmonton dataset separately using VCFtools (Danecek *et al*. 2011) with the same parameters that were used to create dataset 1. I then performed Mantel tests separately for each of the five allsites datasets and each of the five Edmonton datasets using the vegan R package (Oksanen *et al*. 2007) with 9999 permutations. I used $\log_{10}$ Haversine distance and raw Haversine distance (i.e. great-circle distances) for the geographic distance matrices, which were calculated using the geosphere R package (Hijmans *et al*. 2017), and I used the graph4lg R package (Savary *et al*. 2021) to calculate F_{ST}, linearized F_{ST} and Euclidean genetic distance matrices. I performed Mantel tests for all six combinations of genetic and geographic distances for each of the ten datasets (five Edmonton datasets, five allsites datasets). Finally, I produced average genetic and geographic distance matrices for all five Edmonton datasets combined and for all five allsites datasets combined, and performed Mantel tests for each dataset using all six combinations of the averaged matrices.

4.2.9. Kinship and ploidy assessment

To determine whether any observed population structure might be kin-level (e.g. parent-offspring) rather than population-level (Rodriguez-Ramilo and Wang 2012), I performed a kinship analysis using KING (Manichaikul *et al*. 2010) to detect close relatives, using default settings as implemented in PLINK v 2.0 (Chang *et al*. 2015). I performed the kinship analysis on both dataset 1 and dataset 2 separately. Two terrestrial isopod species formerly considered to be subspecies exhibit ploidy differences and also overlap in distribution (*Trichoniscus pusillus* Brandt and *Trichoniscus provisorius* Racovitza) (Frankel *et al*. 1981; Harding and Sutton 1985; Schmalfuss 2004). To confirm uniform ploidy across all samples in the dataset, I used the R

package vcfR (Knaus and Grünwald 2018) to assess the ploidy of each individual *P. spinicornis* in dataset 1 and to calculate ploidy for all individuals combined. The vcfR package uses the ratio of the sequencing frequency of alleles to infer ploidy from VCF data (Knaus and Grünwald 2018).

4.2.10. Population statistics

To compare measures of genetic diversity between greenhouse and non-greenhouse sites and to assess gene flow among sites, I created five datasets by selecting three individuals semi-randomly from all non-greenhouse and greenhouse sites that had at least three individuals (the allsites datasets – see the isolation by distance section). I passed each filtered VCF file for each of the five datasets through the Stacks v 2.64 population module (Rochette *et al*. 2019) using the -fstats option to calculate average nucleotide diversity per variable site (π) and number of private alleles per population for each dataset. I used the R package dartR (Mijangos *et al*. 2022) to calculate the inbreeding coefficient (F_{IS}), observed heterozygosity, observed minus expected heterozygosity, and observed minus unbiased expected heterozygosity for each population. Finally, I used the R package stAMMP (Pembleton *et al*. 2013) to calculate pairwise F_{ST} matrices with bootstrapped p-values. I then calculated the average of each of these values for each population across all five datasets.

4.3. Methods - COI sequencing

4.3.1. COI sequencing

I selected 27 *Porcellio spinicornis* specimens used for ddRADseq to sequence the cytochrome c oxidase subunit I (COI) barcode region (Fig. 4.1; Table 4.1). Samples were selected based on the groups formed in the SNP phylogeny and ADMIXTURE analysis so that a variety of clades and clusters were represented. For PCR and Sanger sequencing I used the primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and either HC02198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') or IsoCoiRint (5'-GCYCCYGCYAAWACAGGKARDGA-3') (Folmer *et al*. 1994; Dimitriou and Sfenthourakis 2022). The latter primer is designed specifically for sowbugs and usually resulted in successful amplification of samples that produced a poor sequence with the LCO1490/HC02198 primer pair. PCR reactions had a total volume of 20 µl and contained 5 µl of template DNA (leftover non-normalized DNA extracts that had been prepared for ddRADseq), 0.5 µl of each primer (10 µM concentration), 10 µl of AccuStart II GelTrack® PCR SuperMix (Quantabio) and 4 µl of water. For the LCO1490/HC02198 primer pair, the amplification conditions consisted of initial denaturation at 94˚C for three minutes, followed by 35 cycles of 94˚C for 45 seconds, 48˚C for 45 seconds, and 72˚C at 60 seconds, and a final extension at 72˚C for seven minutes. Amplification with the LCO1490/IsoCoiRint primers followed the "strict" protocol in Dimitriou and Sfenthourakis (2022). I cleaned amplified DNA with a column-based PCR cleanup kit (Truin Science) and submitted the samples to the University of Alberta Molecular Biology Service Unit (MBSU) for bidirectional Sanger sequencing. I manually trimmed and aligned the forward and reverse reads in JalView (Waterhouse *et al*. 2009) to create consensus sequences for each sample.

All COI sequences obtained in this study are deposited in GenBank under accession numbers UASM407006 - UASM407368.

4.3.2. Haplotype diversity

I combined the 27 COI sequences from Alberta *Porcellio spinicornis* with COI sequences from one *P. spinicornis* from Saskatchewan and two from Ontario (Chapter 2) and all available *Porcellio spinicornis* sequences from BOLD (Ratnasingham and Hebert 2007) and GenBank (https://www.ncbi.nlm.nih.gov/nucleotide/). The BOLD and GenBank sequences originated primarily from Ontario, with additional samples from Alberta, Minnesota, Germany, and Luxembourg. Since all but one of the GenBank sequences (DQ889123.1) were also included in BOLD along with their GenBank reference number, the final dataset included only the 24 sequences from BOLD and one sequence from GenBank (DQ889123.1). In total, the final COI dataset included 55 *P. spinicornis* COI sequences, which I manually aligned and trimmed in JalView (Waterhouse *et al*. 2009). I used DnaSP6 (Rozas *et al*. 2017) to convert the COI dataset to NEXUS format and to calculate summary statistics, and used PopART (Leigh and Bryant 2015) to create haplotype networks. I used all six available network construction methods to explore the relationship between haplotypes when additional nodes (i.e. unsampled haplotypes) were inferred (median joining (Bandelt *et al*. 1999), TCS (Clement *et al*. 2002), integer NJ, and tight span walker networks) and when only the sampled haplotypes were included (minimum spanning network).

4.3.3. Phylogenetic analysis

I constructed a maximum likelihood phylogeny for the COI dataset with IQTree (Nguyen *et al*. 2015) using ModelFinder (Kalyaanamoorthy *et al*. 2017) to select the best model. The phylogeny was assessed with ultrafast bootstrap (Hoang *et al*. 2018) using 5000 replicates (-B 5000) and

allowing up to 5000 bootstrap iterations (-nm 5000). Finally, I used FigTree (Rambaut 2009) and TreeGraph2 (Stöver and Müller 2010) to format the phylogenies for viewing.

4.4. Results - ddRADseq

4.4.1. Sowbug collections from greenhouse and non-greenhouse sites

My colleagues and I searched for sowbugs in 118 sites in Alberta, two in Ontario, and one in Saskatchewan. Of the 118 sites in Alberta, 15 were greenhouses. Sowbugs were present at 67/103 non-greenhouse sites and 11/15 greenhouses. In total, I identified 2382 sowbugs to the level of species (Chapter 2). Greenhouse and non-greenhouse sites in Alberta differed in relative species prevalence. In non-greenhouse sites, *Porcellio spinicornis* and *Trachelipus rathkii* were by far the most common species (44/103 and 35/103 sites) followed by *Cylisticus convexus* (De Geer) (8 sites). In greenhouses, *Armadillidium nasatum* was the most common species (6/15 sites) followed by *Porcellio spinicornis* and *Cylisticus convexus* (five sites each) (Fig. 4.3). Species evenness appears to be greater in greenhouse than in non-greenhouse sites (Fig. 4.3) but I did not make a statistical comparison of species evenness since I lack a consistent measure of species abundance (I did not record all sowbugs observed at each site). Overall, seven species were found in non-greenhouse sites in Alberta and seven were found in greenhouses, and the proportion of sites with sowbugs present was slightly higher for greenhouses than for non-greenhouse sites (73.3%, 11/15 vs 65.0%, 67/103). The 67 non-greenhouse sites with at least one sowbug had an average of 1.4 species, and the 11 greenhouses that contained at least one sowbug had an average of two species. Two species were unique to greenhouses (*Porcellio dilatatus* Brandt and *Nagurus cristatus* (Dollfus)) and two were unique to non-greenhouse sites (*Porcellionides pruinosus* (Brandt) and *Armadillidium vulgare*).

4.4.2. Restriction enzyme choice

As expected, the enzyme pairs with longer cutting sites produced fewer fragments, and longer genomes and genomes with a lower G/C content tended to produce more fragments (Fig. D2). I chose the enzyme pair EcoR1/Pst1 to balance both the number of loci and the read depth based on (1) the number of fragments produced from in silico digestion with this enzyme; (2) the number of samples; and (3) the number of reads the NextSeq 500 typically yields per sequencing run. Theoretically, EcoR1/Pst1 would result in ~100,000-200,000 loci with a read depth between 24-68 depending on the G/C content of the *Porcellio spinicornis* genome.

4.4.3. Data preparation and filtering

ddRADseq using EcoR1/Pst1 resulted in 277,428,476 single-end 76 bp reads (read length includes 8 bp Illumina adaptor and 5 bp enzyme cutting site). Based on the r80 method I chose the Stacks parameter values M=3, m=3, and n=3 for de novo locus assembly (Fig. D3). Prior to filtering in VCFtools, dataset 1 contained 19,330 total loci, of which 15,472 were polymorphic, and contained 51,853 SNPs, with an average weighted per-sample coverage of 37.9 reads (range 8.4-82.2). Loci contained between 0-17 SNPs with an average of 4.69 SNPs per locus. Mean depth per locus was 44.7 reads (range 7.8-524.3). After filtering in VCFtools, dataset 1 contained 13,262 polymorphic loci with 39,978 SNPs and an average of 4.29 SNPs per locus.

4.4.4. PCA

The PCA plot made with all samples in dataset 1 contained three well-separated clusters, corresponding to a group of four sowbugs from northern Calgary, a group of three sowbugs from greenhouse 3 (Edmonton), and a group containing all remaining samples (Fig. D4). The latter cluster contained two sub-clusters. One contained all sowbugs from Edmonton except the three from greenhouse 3, and the other contained all sowbugs from southern Alberta except the four

from northern Calgary (Figs. 4.4, D5). PC1 explained 4.21% of the variance (Fig. D4) and separated sowbugs from Edmonton, southern Alberta and northern Calgary, although one sample from northern Calgary grouped with southern Alberta (Figs. 4.4, D5). PC2 explained 2.36% of the variance (Fig. D4) and differentiated between three sowbugs from greenhouse 3 and all other samples, with the remaining fourth sowbug from greenhouse 3 grouping with Edmonton (Fig. 4.4). Samples from greenhouses 1, 4, and 5 fell within the Edmonton cluster with minimal overlap between each greenhouse (Fig. 4.4), whereas greenhouse 2 (from northeast Edmonton) and greenhouse 3 (from southeast Edmonton) each formed a group distinct from all other samples, except for one sample from greenhouse 3 that fell within the Edmonton cluster (Fig. 4.4). The PCA using only samples from Edmonton also showed greenhouses 3 and 2 as distinct clusters, but greenhouse 5 and a site from southwest Edmonton (non-greenhouse site 6) also each formed a distinct cluster (Fig. 4.5). As expected, samples with high levels of missing data (>20%, N=3) were plotted near the origin of the plot, but samples with <20% missing data (all other samples) did not show obvious signs of bias towards the origin, and instead clustered according to sampling site (Fig. 4.4). Clusters were composed of a mix of males and females, and both sexes appeared evenly distributed across the plot (Fig. 4.4).

4.4.5. DAPC

When all samples in dataset 1 were included, the number of clusters chosen with K-means clustering was two, with eight PCs retained. There were two patterns for K=2: (1) four samples from Northern Calgary were split from all other samples; (2) N=1 sample from southern Calgary, the sample from Lethbridge, and all samples from Edmonton were grouped together apart from all other samples (Fig. D6). Increasing K to 3 resulted in a variety of different patterns where several samples from Edmonton (greenhouse 2, non-greenhouse site 6, N=3 samples from

greenhouse 3, N=1 from greenhouse 1) and two samples from southern Alberta (Lethbridge, N=1 from southern Calgary) varied in whether they were grouped with Edmonton, with southern Alberta, together, or separated (Fig. D7).

When only samples from Edmonton were included, the number of clusters chosen with K-means clustering was two, and six PCs were retained. When K=2, either three samples from greenhouse site 3 were split from the rest of Edmonton, or greenhouse 2 and non-greenhouse site 6 were split from the rest of Edmonton (Fig. D8). Increasing K to 3 resulted in a variety of patterns where several samples (greenhouse 2, non-greenhouse site 6, N=3 from greenhouse 3, non-greenhouse site 1, non-greenhouse site 13) were variously grouped with the rest of Edmonton, separately, or with each other (Fig. D9).

4.4.6. ADMIXTURE analysis

The filtered dataset used for ADMIXTURE analysis (dataset 2) contained one SNP per locus and had 11,800 SNPs. The preferred K-value for the first level of the hierarchical analysis was K=2 according to CV error and the choose K method, but K=3 was preferred according to the four measures proposed by Puechmaille (2016) and according to ΔK. Both the K=2 and K=3 plots contained three main clusters: (1) four samples from northern Calgary; (2) all samples from Edmonton, including all five greenhouses; (3) samples from various locations in southern Alberta (Lethbridge (N=1), Coaldale (N=2), Claresholm (N=1), Drumheller (N=1), southern Calgary (N=2), northern Calgary (N=1)). Hereafter these clusters will be referred to as the "northern Calgary", "Edmonton", and "mixed" clusters. The K=2 plot assigned Edmonton and northern Calgary each to a separate cluster, with the remaining individuals from southern Alberta forming a third admixed cluster (Fig. 4.6). The K=3 plot assigned northern Calgary and the remainder of southern Alberta each to a separate cluster, while Edmonton samples contained

admixture between southern Alberta and a third population (Fig. 4.6). Increasing K to four added a fourth population to Edmonton, allowing greater differentiation between sampling sites: mapping the K=4 admixture components showed that individuals from the same site often shared similar component proportions, although greenhouse 3 and non-greenhouse site 11 (northern Calgary) each had a single individual with very different components from the others at the same site (Figs. 4.1, 4.2). There was no substructure observed in the Edmonton cluster or in the mixed cluster, but separate analysis of the four individuals in the northern Calgary group resulted in two clusters. One cluster consisted of two individuals that had been identified as second-degree relatives in the kinship analysis. Analysis of the mixed and northern Calgary clusters together resulted in their assignment to separate populations with almost no admixture between them, and analysis of the mixed and Edmonton clusters together showed admixture from the mixed cluster in the Edmonton cluster, with two samples from greenhouse 3 exhibiting 100% assignment to the same population as the mixed cluster, but almost no admixture from Edmonton in the mixed cluster.

Similar results were obtained in the K=3 ADMIXTURE plots produced from datasets containing all non-Edmonton samples and only eight samples from Edmonton. Samples from Edmonton, four samples from northern Calgary, and all other samples each formed a cluster (Fig. D10). However, Edmonton exhibited almost no admixture, in contrast to the extensive admixture observed when all samples from Edmonton were included in the dataset (Fig. 4.6). Admixture from the Edmonton cluster was present in a sample (149-1) from southern Calgary when only eight samples from Edmonton were included, when all samples in the dataset were included, and when the four samples from northern Calgary were excluded from the dataset (Figs. D10, 4.6).

4.4.7. Phylogenetic analysis

The best model for the maximum likelihood phylogeny of dataset 1 was SYM+R4. After retaining only non-constant sites (i.e. discarding sites that were ambiguously constant), 30,706 SNPs remained in the dataset. The phylogeny contained two major clades: one clade contained all samples from Edmonton, and the other contained all samples from southern Alberta (Fig. 4.7). Inside the latter clade was a separate clade on long branch containing all but one of samples from northern Calgary. Most of the terminal clades were well-supported, and samples from the same site tended to cluster together: ten of the sampling sites (N=2 greenhouses, N=8 non-greenhouse sites) each formed a single site-specific clade. Except for one sample, all samples from greenhouse 3, greenhouse 4, and non-greenhouse site 2 also each formed a single clade (Fig. 4.7).

4.4.8. Isolation by distance

One site from northern Calgary and 15 from Edmonton had at least three individuals and so were included in the dataset to test isolation by distance (IBD). Five of the sites from Edmonton were from greenhouses, and ten were from non-greenhouse sites. When Calgary was included in the Mantel tests, there was significant IBD with all combinations of genetic and geographic measures except for those that used the Euclidean genetic distance measure (Fig. 4.8). The later result was likely due to one of the Edmonton sites (greenhouse site 5) that had a high Euclidean genetic distance from all other sites in the dataset. There was no significant IBD for any of the Mantel tests conducted on the Edmonton samples alone (Calgary excluded) (Fig. 4.9).

4.4.9. Kinship and ploidy assessment

Kinship analysis of dataset 1 detected fewer related individuals than analysis of dataset 2, but in both cases the highest level of relatedness were second-degree relatives (e.g. half siblings) (Fig.

D11). These consisted of two sowbugs from greenhouse site 3 (southeast Edmonton) that were both second-degree relatives (kinship coefficient 0.174-0.176), and a pair of sowbugs from non-greenhouse site 11 (northern Calgary) that were second degree relatives (kinship coefficient 0.1704-0.1797). Three other pairs of sowbugs had kinship coefficients between 0-0.011, while kinship coefficients between all other individuals were negative (Fig. D11), indicating unrelatedness and suggesting that individuals originate from different populations (Manichaikul *et al*. 2010).

The predicted ploidy for all samples combined was 2 (diploid) (Fig. D12). Ploidy for individual samples varied from 2-3, but was closely linked to read depth, where samples with low read depth were often predicted to be triploid, and samples with higher read depth were predicted to be diploid. This relationship can be demonstrated with logistic regression, where the ploidy of a sample is significantly predicted by the average weighted read depth ($p = 0.0026$) (Fig. D13). This makes sense given that alleles in heterozygous loci represented by only a few reads are likely to occur in uneven ratios, even if the organism is diploid (e.g. with only three reads, alleles can only be present in ratios of 1:2; with only five, alleles can only be present in ratios of 1:4 or 2:3; with only seven reads, the ratios must be 1:6, 2:5 or 3:4; etc.). The ploidy of individual *Porcellio spinicornis* samples with low read depth therefore cannot be estimated with confidence using this method. However, 10/13 of the samples estimated to be triploid had conspecifics from the same sampling site that were estimated to be diploid (the remaining 3/13 samples had no conspecifics collected from their respective sampling sites) and so it is likely that all individuals in the dataset are diploid.

4.4.10. Population statistics

Eleven non-greenhouse sites (10 from Edmonton, one from northern Calgary) and five greenhouse sites from Edmonton each had at least three individuals and were used to calculate population statistics. Both greenhouse and non-greenhouse sites exhibited a range of genetic diversity as measured by the number of private alleles, nucleotide diversity and observed heterozygosity in each population (Fig. 4.10). There were no obvious differences in diversity between greenhouse and non-greenhouse sites for any of these measures. Non-greenhouse site 11 (northern Calgary) had more private alleles than any other site, but was the only site included in the analysis that was not from Edmonton. Greenhouse site 3 and non-greenhouse site 11 (northern Calgary) each contained a single individual that greatly affected most measures of genetic diversity depending on whether it was included in the analysis. Greenhouse and non-greenhouse sites also exhibited a range of F_{IS} (inbreeding coefficient) values, with average F_{IS} per site ranging from -0.014 to 0.108. Observed heterozygosity was higher than the unbiased expected heterozygosity for all sites, but was lower than the expected heterozygosity (Fig. 4.10). F_{ST} values were highest between Calgary and all other sites (0.1022 – 0.1786), while F_{ST} between populations in Edmonton ranged from 0.0054 – 0.1259 (Table 4.2). Apart from Calgary, the three sites with the highest overall F_{ST} values were greenhouse sites (greenhouses 2, 3, and 5). Almost all sites were significantly differentiated based on F_{ST} values (Table 4.2). The site with the lowest overall F_{ST} values was non-greenhouse site 5, which was not significantly differentiated from greenhouse 1 and two non-greenhouse sites despite being geographically distant from these areas (Table 4.2; Fig. D14). Non-greenhouse site 5 also had the highest genetic diversity of any non-greenhouse site in Edmonton (Fig. 4.10).

4.5. Results – COI sequences

4.5.1. Haplotype diversity

Porcellio spinicornis sequences from BOLD, GenBank, and this study included seven haplotypes, of which three were unique to North America and four were unique to Europe (Germany and Luxembourg). No haplotypes were shared between Europe and North America. Haplotype variation was identical for both the 28 sequences from Alberta and for all 46 sequences from North America (eight segregating sites, eight parsimony-informative sites) and was much lower than the haplotype variation for the seven sequences from Europe (35 segregating sites, 28 parsimony-informative sites). The haplotype network showed a close relationship between two of the North American haplotypes (Fig. 4.11) which were separated by only a single nucleotide difference. Two of the European haplotypes were also separated by only a single difference, and this pair exhibited 4.3-5.0% nucleotide divergence from the other five haplotypes in the dataset. All networks showed a similar relationship between the haplotypes, with few inferred nodes for the methods that implemented this feature (Fig. D15). North American haplotypes were not unique to particular localities (Fig. D15).

4.5.2. Phylogenetic analysis

The maximum likelihood tree constructed with *Porcellio spinicornis* COI sequences from Europe and North America had a large clade containing a haplotype from Germany and clades for each of the three haplotypes from North America (Fig. 4.11). The remaining three European haplotypes formed a polytomy with this larger clade. None of the North American haplotypes were limited to a particular cluster observed in the SNP analyses of *Porcellio spinicornis* from Alberta (Fig. 4.7). Instead, all three North American haplotypes were present in Edmonton and in

the “mixed” cluster (southern Alberta), and two of the three haplotypes also appeared in the “northern Calgary” cluster (Fig. 4.7).

4.6. Discussion

4.6.1. Multiple introductions to Alberta

At least three distinct populations of *Porcellio spinicornis* are present in Alberta. The PCA, DAPC, phylogeny, and ADMIXTURE plots created from the SNP data obtained from ddRADseq all indicated that northern Calgary contains a *P. spinicornis* population that is highly genetically distinct from all other populations in Alberta, and that populations from other areas in southern Alberta are distinct from both Edmonton and northern Calgary. The presence of multiple genetically differentiated groups of an introduced species can be interpreted as evidence that more than one introduction has occurred (Johnson and Starks 2004; Lacoursière-Roussel *et al*. 2012). Additional support for this interpretation includes the correspondence of each genetically differentiated group to sites that are geographically distant (Cao *et al*. 2017) and/or to sites where primary introductions are known to have occurred (Acevedo-Limón *et al*. 2020). Historical evidence regarding sowbug introduction to Alberta is extremely scarce, but given the geographic distance between Edmonton, northern Calgary, and other sites in southern Alberta, the populations at these sites likely represent at least three separate introductions. However, it is possible that the actual number of introductions is far greater. Most samples in this study originated from Edmonton, with relatively few samples from other sites. Unbalanced sampling can affect the output generated by genetic clustering algorithms (e.g. ADMIXTURE, STRUCTURE) and typically results in in poorly-sampled populations being clustered together rather than assigned their own clusters (Kalinowski 2011; Puechmaille 2016; Lawson *et al*. 2018), while an over-sampled population may form a single large cluster (Kalinowski 2011) and exhibit a lot of admixture (Puechmaille 2016). This fits the pattern observed in the ADMIXTURE plot for *Porcellio spinicornis* in Alberta, where almost all samples from southern

Alberta were clustered together despite having originated from geographically-distant sampling sites, whereas samples from Edmonton formed a single large cluster with varying degrees of admixture (Figs. 4.1, 4.6). It is therefore possible that southern Alberta contains multiple distinct populations that were not detected in this study, which would suggest an even greater number of introductions.

It is difficult to determine whether the distinct populations of *Porcellio spinicornis* in Alberta represent multiple primary introductions from the same source, multiple primary introductions from multiple sources, multiple secondary introductions from a single primary introduction (i.e. "invasion hub") or a combination of these. Due to bottlenecks followed by genetic drift, introduced populations originating from the same source may exhibit genetic differentiation, even if there is no differentiation in the source population (Acevedo-Limón *et al*. 2020). This would then resemble the pattern that would result from multiple introductions (i.e. multiple genetically differentiated groups). Similarly, bottlenecks associated with secondary introductions from a single primary introduction could also lead to population differentiation, again resulting in a similar pattern (Chapter 1, Fig. 1.1). Comparison between populations in Alberta and potential source populations (e.g. Europe and other parts of North America) may provide support for multiple introductions having occurred if two or more populations in Alberta are found to correspond genetically to different source populations.

4.6.2. Homogeneity in Edmonton

Unexpectedly, there was no evidence for isolation by distance or substructure among *Porcellio spinicornis* populations in Edmonton, and F_{ST} between most sites was relatively low (<0.05) despite samples originating from sites up to 30 km apart. Absence of both genetic structure and IBD in an introduced species can sometimes be attributed to high gene flow among sites

(Dalmon *et al*. 2007). However, sowbugs are generally considered to be poor dispersers (Hornung 2011; Lee *et al*. 2014; Szlavecz *et al*. 2018; Dimitriou *et al*. 2022). It is also unlikely that they would undergo frequent active dispersal over 25 km to populations at opposite ends of the city, especially as the North Saskatchewan River would pose a significant barrier to dispersal. Alternatively, non-native species may not exhibit IBD due to human-mediated transport among localities (Leo *et al*. 2015; Acevedo-Limón *et al*. 2020), especially when the species involved has a high probability of 'hitch-hiking' despite low intrinsic dispersal capacity (Pérez-Portela *et al*. 2012; Cao *et al*. 2017). Sowbugs are readily transported by human activity (Wang and Schreiber 1999), and so gene flow between sites might theoretically be maintained via passive dispersal. Some of the lowest F_{ST} values in Edmonton occurred between sites at opposite ends of the city (e.g. NG2, NG5, G1: $F_{ST} < 0.007$), whereas many adjacent sites exhibited relatively high F_{ST} values (e.g. NG10, NG7, NG6: $F_{ST} > 0.05$), and most sampling sites were located in residential areas rather than in greenhouses. While occasional exchange of objects with associated sowbugs (e.g. plants, lawn decorations) may occur between homeowners, it is difficult to explain why these objects would be transported frequently enough to homogenize populations in Edmonton, and why this would apparently take place less frequently for sites within the same area. It is therefore unlikely that frequent gene flow among sites via active and/or passive dispersal can account for the lack of IBD and distinct population clusters in Edmonton.

An alternative explanation for the homogeneity and lack of isolation by distance among *Porcellio spinicornis* populations in Edmonton is that these populations originate from introductions from the same source population (or from several similar source populations) and that some populations originate from other Edmonton populations. If *Porcellio spinicornis* was introduced to Edmonton recently, populations may have not had sufficient time to diverge from

each other: a lack of population structure would be expected in cases where introduction or expansion into an area is recent (Chen *et al*. 2006; Myburgh *et al*. 2007; Campbell *et al*. 2020). Alternatively, it is possible that these introductions took place many decades ago, but that populations exhibit limited divergence from each other because the founding populations were large. A relatively recent introduction of *Porcellio spinicornis* to Edmonton would be consistent with the limited historical records available from areas contiguous with the Prairie Provinces, from which the first recorded sowbugs date from 1871-1939 (see Introduction). Additional evidence of a recent introduction would include reduced genetic diversity compared to the original population (Leo *et al*. 2015; Oberhänsli *et al*. 2021), but without data from potential source populations it is difficult to conclude whether *P. spinicornis* in Alberta have also experienced a reduction in genetic diversity.

Determining the active dispersal ability of introduced sowbugs is crucial to understanding their potential to spread into new areas. However, it is difficult to determine what role active dispersal has played in the movement of sowbugs among sites in Edmonton due to the lack of information about source populations for *Porcellio spinicornis* in Alberta. The relatively low F_{ST} values among many sites in Edmonton (<0.05) could be attributed to high gene flow, but may instead result from a common origin for these populations, with recent introduction dates and/or large founding populations resulting in low differentiation among sites (see above). If introduction of *Porcellio spinicornis* to Edmonton has occurred recently and if the species is in fact capable of widespread active dispersal, it could expand outside of introduction sites (i.e. urban areas) in the coming years. Continued monitoring of introduced sowbug populations would determine if this is the case. Field studies of the dispersal behaviour of *P. spinicornis* and/or evaluating its tolerance to desiccation and low temperatures would help determine

whether active dispersal of *P. spinicornis* in Alberta may be limited by abiotic factors (e.g. absence of suitable overwintering habitat).

4.6.3. Greenhouses as introduction sites

Although both greenhouse and non-greenhouse sites showed a range of genetic diversity and species richness, these factors unexpectedly did not differ overall between the two types of sites. When there are no clear differences in genetic diversity it is difficult to identify probable sites of introduction (Wostenberg 2015). Populations in three of the five greenhouses appeared somewhat dissimilar to each other and to other populations in Edmonton in the PCA and ADMIXTURE plots, but were more similar to the rest of Edmonton than they were to sites in other parts of Alberta, suggesting they may share a common source population. This could result from non-greenhouse populations having originated from greenhouses (e.g. via purchase of items), by greenhouse populations having originated from non-greenhouse sites (e.g. via return of purchased items to greenhouses, or from import of stock from a primary introduction site), or by introduction to both greenhouse and non-greenhouse sites from the same source population (e.g. via shipment of building supplies to both sites). Without a difference in genetic diversity between the two site types, it is not possible to determine whether introductions likely occurred from greenhouses to non-greenhouse sites or vice versa. Similarly, the fact that some greenhouses populations differed from other populations in Edmonton could be explained by bottlenecks associated with secondary introduction from a non-greenhouse site to the greenhouses (Fig. 1.1), or to successful secondary introductions from greenhouses to non-greenhouse sites having been more frequent for some greenhouses than other. I cannot rule out the possibility that sowbug populations in Alberta may have originated from greenhouses, but neither can I confirm that greenhouses play a role in sowbug introduction. Analysis of potential

source populations may aid in identifying sites of primary introduction, with evidence for greenhouses as sites of primary introduction if source populations are found to be more similar to populations in greenhouses than in other site types.

One exception to the problem of determining the origin of sowbug populations in greenhouses is the population of *Porcellio spinicornis* collected from the Biological Sciences greenhouse at the University of Alberta (greenhouse site 5 (G5)). Sowbugs inside this greenhouse were dissimilar from all other sites, but were by far the most similar to non-greenhouse site 4 (NG4), which was the population collected in the vicinity of the Biological Sciences building. It is likely that one of these populations was the source for the other given the genetic similarity and close proximity of the two sites (130 m). The site with highest genetic diversity likely represents the source population (Pérez-Portela *et al.* 2012; Lacoursière-Roussel *et al*. 2012; Leo *et al*. 2015; Cao *et al*. 2017). Genetic diversity in the G5 population was substantially lower than NG4, so the greenhouse population likely originated from NG4 rather than vice versa. The greenhouse is located four floors above the ground (approximately 18 m) and has gaps in the panels for ventilation (pers. obs., HS). While it is not impossible that sowbugs could have actively dispersed up the side of the building and into the greenhouse, initial introduction to the greenhouse was likely via human-mediated dispersal. Despite being the closest genetic matches, the NG4 and G5 populations were significantly differentiated, so gene flow between the two populations is probably infrequent. *Porcellio spinicornis* are occasionally seen wandering the halls of the fourth floor of the Biological Sciences building and other buildings in the vicinity (pers. obs., HP, HS). One of these individuals (144001) was included in this study. It was more similar to the NG4 population than to G5, suggesting it originated from the NG4 population (outside the building), which is consistent with the indoor greenhouse

population having originated from entry of outdoor populations. The reduction in genetic diversity observed for the G5 population and its differentiation from the probable source population suggests introduction was associated with a bottleneck, and may also indicate a recent introduction (Leo *et al*. 2015; Oberhänsli *et al*. 2021).

4.6.4. A North American bottleneck

Data obtained from COI sequences of *Porcellio spinicornis* indicated considerably reduced genetic diversity in North American populations compared to native European populations. *Porcellio spinicornis* from all North American samples combined (47 from Canada and one from Minnesota) had fewer COI haplotypes and far less haplotype variation than Europe, even though North America had almost seven times the number of samples from Europe and all European samples originated from only two contiguous countries (Germany and Luxembourg). Excluding Alberta, North America had only two haplotypes, and extensive sampling in Alberta revealed only one additional haplotype, which differed from an existing North American haplotype by only a single nucleotide (Fig. 4.11). Variation in cytochrome c oxidase subunit I (COI) has been linked to climate adaptation in mites (Tixier *et al*. 2022) and fish (Grant *et al*. 2006), and so it is possible that the few haplotypes present in Canada represent climate-associated selection. This could be assessed by testing the lower lethal temperature limit and desiccation tolerance for sowbugs with different haplotypes. Alternatively, the low diversity could also be the result of bottlenecks. Introduction of a small number of individuals may lead to a loss of diversity in non-native populations of a species (Dlugosch and Parker 2008; Pérez-Portela *et al*. 2012), and bottlenecks could occur both with initial introduction of sowbugs from Europe and from subsequent secondary introductions from these populations. Given the apparently high haplotype diversity in European populations of *P. spinicornis* and the homogeneity of haplotypes in North

America, it seems unlikely that the current North American populations of *P. spinicornis* originated from multiple introductions from a variety of European localities. Instead, North American populations may be derived from other North American populations (e.g. secondary introduction from the United States to Canada, or from coastal populations into the interior), or from a small number of primary introductions from Europe, or from many primary introductions from a limited number of European localities. The possibility of populations having originated via extensive secondary introduction could be determined by more intensive sampling from the United States and from populations on the eastern coastline, and by use of more informative genetic markers.

The apparently reduced haplotype diversity in North American populations of *Porcellio spinicornis* contrasts with the lack of evidence for a founder effect in a comparison of European and North American *Armadillidium vulgare* populations using allozyme markers (Garthwaite *et al.* 1995). It is possible that the introduction history of *A. vulgare* in North America (i.e. size and/or frequency of introductions) is different than *P. spinicornis* such that only *P. spinicornis* has experienced a founder effect. While *A. vulgare* is common in England, including many localities along the coast, *P. spinicornis* has a spotty distribution (Harding and Sutton 1985), which may have led to more frequent or larger introductions of *A. vulgare* than *P. spinicornis*. Alternatively, it is possible that a reduction in genetic diversity for North American *P. spinicornis* has only occurred for mitochondria and not for nuclear loci (e.g. selective sweep for particular mitochondrial haplotypes due to *Wolbachia* bacterial infection; see Graham and Wilson 2012; Deng *et al*. 2021). Comparison of nuclear loci in North American and European *P. spinicornis* populations would provide evidence as to whether the apparent bottleneck for North American populations is also reflected in nuclear loci.

Since *Porcellio spinicornis* is native to Europe (Schmalfuss 2004), it is surprising that Europe and North America did not share any haplotypes. It is possible that North American haplotypes may be present in Europe in areas for which sequences were not available - particularly those that likely played a major role in historical sowbug introduction to North America via ship ballast (e.g. England) (Lindroth 1957). If native haplotypes are diverse and limited to specific areas in the native range of a species, the probable location(s) of origin for introduced populations can be determined (Kolbe *et al*. 2004). Therefore, it may be possible to determine the probable origin(s) of North American *Porcellio spinicornis* simply by sampling COI haplotypes from multiple areas of its native European range. This information could then be used to select localities for further investigation with more informative markers. Alternatively, it is possible that North American haplotypes are unique to North America, but since introduction of *Porcellio spinicornis* to North America likely occurred within the last 500 years (Lindroth 1957), evolution would have had to take place extremely rapidly, with strong selective pressure resulting in a very small number of present-day North American haplotypes (all currently-known European haplotypes are 1-5% divergent from North American haplotypes). Finally, North American *P. spinicornis* may represent a cryptic species, and are therefore not conspecific with the sequenced populations from Germany and Luxembourg. The high divergence (5%) observed between two of the European haplotypes and the remaining European and North American haplotypes would seem to support this hypothesis. However, an interspecific divergence of 5% is relatively low compared to the high interspecific COI divergences observed for other sowbug species (3-29%) (Raupach *et al*. 2022) and falls within the 3-5% range observed previously for *P. spinicornis* (Raupach *et al*. 2022).

4.7. Conclusion

The population structure of *Porcellio spinicornis* in Alberta is complex, and it is likely that multiple primary and/or secondary introductions have occurred. Surprisingly, populations in Edmonton were genetically homogenous, suggesting they may have originated from recent and/or large founding populations from the same source population(s). A recent introduction of *P. spinicornis* to Alberta agrees with anecdotal evidence and historical data regarding sowbugs from contiguous provinces and states. Unexpectedly, patterns in genetic diversity and species richness neither supported nor contradicted the hypothesis that greenhouses are sites of primary introduction for sowbugs in Alberta, but at least one greenhouse population appears to have originated via introduction from a nearby non-greenhouse site. North American populations of *P. spinicornis* have remarkably low COI diversity, suggesting introduction of this species to North America was associated with a severe bottleneck and that many North American populations may have originated from secondary introductions from other North American localities. Future investigation into the primary introduction sites for *P. spinicornis* in Alberta should involve sampling from probable source localities in Europe, particularly France and the United Kingdom, and on the eastern coast of North America.

4.8. References

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4.9. Tables and figures

Table 4.1 (following pages)**:** Collection information for *Porcellio spinicornis* individuals used in this study for ddRADseq and/or COI sequencing. Sample 098AAA1 was removed from the ddRADseq analysis because it had a high percentage of missing data (see main text). Samples 184A1, 185C1A, and 191-1 were only used for COI sequencing and were not included in the ddRADseq analysis. Coordinates are replaced with a locality description for sites that represent a private residence or business. Residual tissues (when available) and/or additional conspecifics from the same collection site are deposited in the E.H. Strickland Entomological Museum collections (University of Alberta) under the accession numbers listed in the table. The list of conspecifics includes only individuals not already listed in the table.

SAMPLE ID	SITE ID	SEX	GENBANK ID (COI)	STRICKLAND ACCESSION NUMBER	SITE NAME	SITE COORDINATES / LOCATION
066AAA	G1	M		UASM407069	Canada: Alberta, Edmonton (Greenhouse in northeast Edmonton)	Northeast Edmonton
066AAB	G1	F	PQ015341	UASM407070	Canada: Alberta, Edmonton (Greenhouse in northeast Edmonton)	Northeast Edmonton
066AAC	G1	F		UASM407328	Canada: Alberta, Edmonton (Greenhouse in northeast Edmonton)	Northeast Edmonton
070AAA	G2	F	PP995881	UASM407075	Canada: Alberta, Edmonton (Greenhouse in northeast Edmonton)	Northeast Edmonton
070AAB	G2	M		UASM407329	Canada: Alberta, Edmonton (Greenhouse in northeast Edmonton)	Northeast Edmonton
070AAC	G2	F		UASM407330	Canada: Alberta, Edmonton (Greenhouse in northeast Edmonton)	Northeast Edmonton
074AAG	G3	M		UASM407092	Canada: Alberta, Edmonton (Greenhouse in southeast Edmonton)	Southeast Edmonton
074AAH	G3	F	PQ015342	UASM407331	Canada: Alberta, Edmonton (Greenhouse in southeast Edmonton)	Southeast Edmonton
074AAI	G3	F		UASM407093	Canada: Alberta, Edmonton (Greenhouse in southeast Edmonton)	Southeast Edmonton
074AAJ	G3	M	PQ015343	UASM407332	Canada: Alberta, Edmonton (Greenhouse in southeast Edmonton)	Southeast Edmonton
086AAA	G4	F	PQ015345	UASM407102	Canada: Alberta, Edmonton (Greenhouse in northeast Edmonton)	Northeast Edmonton
086AAB	G4	M		UASM407333	Canada: Alberta, Edmonton (Greenhouse in northeast Edmonton)	Northeast Edmonton
086AAC	G4	F		UASM407334	Canada: Alberta, Edmonton (Greenhouse in northeast Edmonton)	Northeast Edmonton
086AAD	G4	M	PQ015346	UASM407103	Canada: Alberta, Edmonton (Greenhouse in northeast Edmonton)	Northeast Edmonton
1331C1	G5	M		UASM407234 Conspecific: UASM407235	Canada: Alberta, Edmonton (University of Alberta Biological Sciences Greenhouse)	53.52896283179059, -113.52607556703111
1331C2	G5	M		UASM407287 Conspecific: UASM407235	Canada: Alberta, Edmonton (University of Alberta Biological Sciences Greenhouse)	53.52896283179059, -113.52607556703111
138-1	G5	M	PQ015354	UASM407236 Conspecific: UASM407235	Canada: Alberta, Edmonton (University of Alberta Biological Sciences Greenhouse)	53.52896283179059, -113.52607556703111
098AAA1	N/A	M		No residual tissue No conspecifics	Canada: Alberta, Edmonton ("Haddow Dr. Trail")	53.456829, -113.597853
184A1	N/A	M	PP995884	UASM407253 Conspecifics: UASM407254 UASM407255 UASM407256	Canada: Ontario, Port Hope (Private residence)	Port Hope
185C1A	N/A	M	PP995885	UASM407264	Canada: Ontario, Port Hope (Fish ladder)	Port Hope
191-1	N/A	F	PP995886	UASM407276	Canada: Saskatchewan, Regina (Private residence)	43.96791904910919, -78.29586674466525
048AAB	NG1	M		UASM407007	Canada: Alberta, Edmonton (Jackson Homesteaders)	53.578006449906084, -113.27229778666883

				Conspecifics: UASM407006 UASM407008 UASM407009		
048AAE	NG1	M		UASM407335 Conspecifics: UASM407006 UASM407008 UASM407009	Canada: Alberta, Edmonton (Jackson Homesteaders)	53.578006449906084, -113.27229778666883
048AAF	NG1	F		UASM407336 Conspecifics: UASM407006 UASM407008 UASM407009	Canada: Alberta, Edmonton (Jackson Homesteaders)	53.578006449906084, -113.27229778666883
048AAG	NG1	M	PQ015336	UASM407337 Conspecifics: UASM407006 UASM407008 UASM407009	Canada: Alberta, Edmonton (Jackson Homesteaders)	53.578006449906084, -113.27229778666883
050AAD	NG2	F		UASM407027 Conspecific: UASM407026	Canada: Alberta, St. Albert (St. Albert Botanic Park)	53.65183547945506, -113.60051889795554
050AAE	NG2	M	PQ015337	UASM407028 Conspecific: UASM407026	Canada: Alberta, St. Albert (St. Albert Botanic Park)	53.65183547945506, -113.60051889795554
050AAF	NG2	F	PQ015338	UASM407029 Conspecific: UASM407026	Canada: Alberta, St. Albert (St. Albert Botanic Park)	53.65183547945506, -113.60051889795554
052AAJ	NG3	F		UASM407025 Conspecifics: UASM407022 UASM407023 UASM407024	Canada: Alberta, Edmonton (Private residence, southwest Edmonton)	Southwest Edmonton
052AAK	NG3	M	PQ015339	UASM407338 Conspecifics: UASM407022 UASM407023 UASM407024	Canada: Alberta, Edmonton (Private residence, southwest Edmonton)	Southwest Edmonton
052AAM	NG3	F		UASM407339 Conspecifics: UASM407022 UASM407023 UASM407024	Canada: Alberta, Edmonton (Private residence, southwest Edmonton)	Southwest Edmonton
052AAN	NG3	F		UASM407340	Canada: Alberta, Edmonton (Private residence, southwest Edmonton)	Southwest Edmonton

				Conspecifics: UASM407022 UASM407023 UASM407024		
144001	NG4	F		UASM407238	Canada: Alberta, Edmonton (University of Alberta North Campus Indoors)	53.52675809079533, -113.52712098861218
064AAB	NG4	F		UASM407066	Canada: Alberta, Edmonton (University of Alberta North Campus outdoors)	53.52854965868851, -113.52471333801123
064AAC	NG4	M		UASM407341	Canada: Alberta, Edmonton (University of Alberta North Campus outdoors)	53.52854965868851, -113.52471333801123
065AAA	NG4	F	PQ015340	UASM407342	Canada: Alberta, Edmonton (University of Alberta North Campus outdoors)	53.52854965868851, -113.52471333801124
085AAA	NG5	F	PQ015344	UASM407106	Canada: Alberta, Edmonton ("Sobeys Southbrook")	53.42233509159471, -113.51454359560968
085AAB	NG5	F		UASM407343	Canada: Alberta, Edmonton ("Sobeys Southbrook")	53.42233509159471, -113.51454359560968
085AAC	NG5	M		UASM407107	Canada: Alberta, Edmonton ("Sobeys Southbrook")	53.42233509159471, -113.51454359560968
085AAD	NG5	M		UASM407344	Canada: Alberta, Edmonton ("Sobeys Southbrook")	53.42233509159471, -113.51454359560968
087AAA	NG6	F		UASM407345	Canada: Alberta, Edmonton (Private residence, southwest Edmonton)	Southwest Edmonton
087AAB	NG6	M		UASM407109	Canada: Alberta, Edmonton (Private residence, southwest Edmonton)	Southwest Edmonton
087AAC	NG6	F	PQ015347	UASM407346	Canada: Alberta, Edmonton (Private residence, southwest Edmonton)	Southwest Edmonton
087AAE	NG6	F		UASM407110	Canada: Alberta, Edmonton (Private residence, southwest Edmonton)	Southwest Edmonton
093AAA	NG7	M		UASM407347	Canada: Alberta, Edmonton ("Ramsay Heights Lookout trail")	53.47984191322757, -113.59036506200589
093AAB	NG7	F		UASM407121	Canada: Alberta, Edmonton ("Ramsay Heights Lookout trail")	53.47984191322757, -113.59036506200589
093AAC	NG7	M	PQ015349	UASM407122	Canada: Alberta, Edmonton ("Ramsay Heights Lookout trail")	53.47984191322757, -113.59036506200589
095AAB	NG8	F		UASM407348 Conspecifics: UASM407129 UASM407130	Canada: Alberta, Edmonton (Whitemud Creek Community Centre)	53.463572, -113.563351
095AAC	NG8	F	PQ015350	UASM407349 Conspecifics: UASM407129 UASM407130	Canada: Alberta, Edmonton (Whitemud Creek Community Centre)	53.463572, -113.563351
095AAD	NG8	F		UASM407350 Conspecifics: UASM407129 UASM407130	Canada: Alberta, Edmonton (Whitemud Creek Community Centre)	53.463572, -113.563351
099AAK	NG9	F		UASM407351 Conspecific: UASM407127	Canada: Alberta, Edmonton ("Haynes Close rock river")	53.460899, -113.596278
099AAL	NG9	F		UASM407128 Conspecific: UASM407127	Canada: Alberta, Edmonton ("Haynes Close rock river")	53.460899, -113.596278

099AAN	NG9	M		UASM407352 Conspecific: UASM407127	Canada: Alberta, Edmonton ("Haynes Close rock river")	53.460899, -113.596278
100AAA	NG10	F		UASM407114	Canada: Alberta, Edmonton ("Ronning Street Trail")	53.475769, -113.593809
100AAB	NG10	F		UASM407353	Canada: Alberta, Edmonton ("Ronning Street Trail")	53.475769, -113.593809
100AAC	NG10	M		UASM407115	Canada: Alberta, Edmonton ("Ronning Street Trail")	53.475769, -113.593809
159-3	NG11	M	PQ015356	UASM407279	Canada: Alberta, Calgary (Private residence, Edgemont)	Edgemont
160-1	NG11	F	PQ015357	UASM407193	Canada: Alberta, Calgary (Private residence, Edgemont)	Edgemont
160-2	NG11	F		UASM407204	Canada: Alberta, Calgary (Private residence, Edgemont)	Edgemont
162-1	NG11	M	PQ015359	UASM407216	Canada: Alberta, Calgary (Private residence, Edgemont)	Edgemont
089AAB	NG12	F		UASM407354	Canada: Alberta, Edmonton (Kinsmen Park)	53.52691556520977, -113.51398893351357
090AAA	NG13	F	PQ015348	UASM407111	Canada: Alberta, Edmonton (Private residence, northwest Edmonton)	Northwest Edmonton
090AAC	NG13	M		UASM407112	Canada: Alberta, Edmonton (Private residence, northwest Edmonton)	Northwest Edmonton
096AAA	NG14	M		UASM407113	Canada: Alberta, Edmonton ("Burton Rd. trail")	53.476782, -113.565659
097AAB	NG15	M		UASM407131	Canada: Alberta, Edmonton ("66th Ave River Loop Trail")	53.499196, -113.577757
101AAA	NG16	M	PQ015351	UASM407136 Conspecific: UASM407137	Canada: Alberta, Edmonton (Private residence, southwest Edmonton)	Southwest Edmonton
101AAB	NG16	F		UASM407355 Conspecific: UASM407137	Canada: Alberta, Edmonton (Private residence, southwest Edmonton)	Southwest Edmonton
104AAF	NG17	M		UASM407356 Conspecifics: UASM407138 UASM407139	Canada: Alberta, Coaldale (Private residence)	Coaldale
104AAH	NG17	F	PP995882	UASM407296 Conspecifics: UASM407138 UASM407139	Canada: Alberta, Coaldale (Private residence)	Coaldale
105A1A	NG18	M	PQ015352	UASM407226	Canada: Alberta, Lethbridge (Private residence)	Lethbridge
111-11	NG19	M	PQ015353	UASM407212 Conspecifics: UASM407197 UASM407208 UASM407188 UASM407181	Canada: Alberta, Claresholm	50.023641, -113.581900
148-22	NG20	F		UASM407213	Canada: Alberta, Calgary (Private residence, North Glenmore)	North Glenmore

				Conspecifics: UASM407196 UASM407207 UASM407220 UASM407209 UASM407368		
149-1	NG21	F	PP995883	UASM407200	Canada: Alberta, Calgary (Private residence, Haysboro)	Haysboro
155-13	NG22	M	PQ015355	UASM407223 Conspecifics: UASM407233 UASM407205 UASM407228 UASM407230 UASM407219 UASM407214 UASM407224 UASM407246	Canada: Alberta, Drumheller (Private residence)	Drumheller
161-1	NG23	F	PQ015358	UASM407215	Canada: Alberta, Calgary (Private residence, Coventry Hills)	Coventry Hills

Table 4.2: Pairwise F_{ST} values (upper right) and associated p-values (lower left) for populations of *Porcellio spinicornis* from 5 greenhouses (G) and 11 non-greenhouse sites (NG) in Alberta. All sites are located in Edmonton except NG11 (northern Calgary). F_{ST} values are sorted and colored by magnitude, and are averaged from five datasets that subsampled three individuals per site from all sites with at least three individuals (see main text). P-values less than 0.001 are shown as "0"; larger p-values are colored darker orange. The highest and lowest p-value for each of the five datasets is shown when applicable.

	NG9	NG2	NG5	G1	NG4	NG8	G4	NG10	NG3	NG1	NG7	NG6	G3	G2	G5	NG11
NG9	NA	0.007	0.006	0.006	0.012	0.015	0.013	0.019	0.023	0.031	0.031	0.044	0.055	0.064	0.051	0.115
NG2	0 - 0.01	NA	0.005	0.013	0.015	0.023	0.022	0.024	0.034	0.041	0.032	0.047	0.073	0.068	0.062	0.12
NG5	0 - 0.217	0 - 0.674	NA	0.006	0.017	0.017	0.017	0.029	0.029	0.04	0.036	0.039	0.062	0.069	0.057	0.113
G1	0.001 - 0.01	0	0 - 0.132	NA	0.015	0.027	0.019	0.019	0.021	0.035	0.036	0.039	0.063	0.066	0.059	0.102
NG4	0	0	0 - 0.001	0 - 0.001	NA	0.031	0.03	0.033	0.032	0.044	0.041	0.054	0.075	0.077	0.033	0.12
NG8	0	0	0	0	0	NA	0.031	0.029	0.037	0.056	0.037	0.062	0.08	0.074	0.073	0.137
G4	0	0	0 - 0.044	0	0	0	NA	0.039	0.037	0.049	0.05	0.048	0.076	0.076	0.066	0.133
NG10	0	0	0	0	0	0	0	NA	0.043	0.052	0.054	0.059	0.09	0.076	0.074	0.139
NG3	0	0	0	0	0	0	0	0	NA	0.053	0.06	0.064	0.086	0.086	0.076	0.138
NG1	0	0	0	0	0	0	0	0	0	NA	0.07	0.069	0.097	0.098	0.09	0.143
NG7	0	0	0	0	0	0	0	0	0	0	NA	0.077	0.095	0.096	0.074	0.143
NG6	0	0	0	0	0	0	0	0	0	0	0	NA	0.1	0.1	0.104	0.126
G3	0	0	0	0	0	0	0	0	0	0	0	0	NA	0.126	0.125	0.162
G2	0	0	0	0	0	0	0	0	0	0	0	0	0	NA	0.11	0.167
G5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	NA	0.179
NG11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	NA

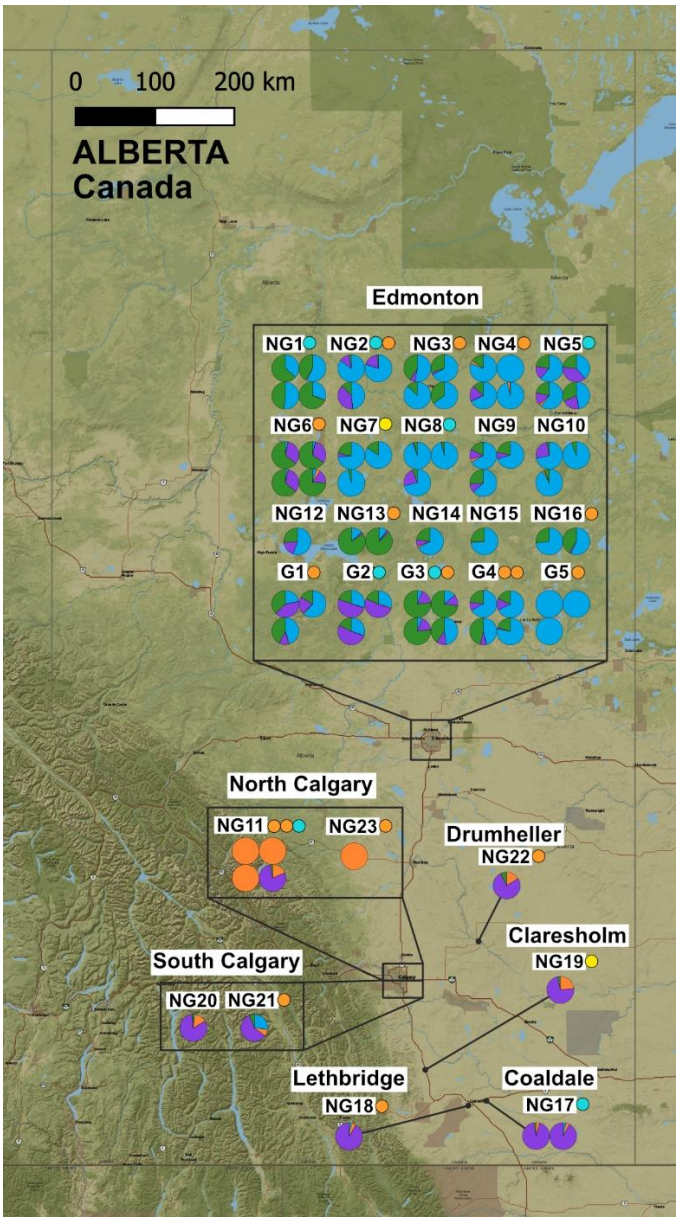


Figure 4.1: Collection localities, COI haplotypes, and ADMIXTURE components for 71 *Porcellio spinicornis* in Alberta. NG = non-greenhouse site, G = greenhouse site. Pie charts show K=4 ADMIXTURE components for each sowbug individual. Colored circles by the site name shows the COI haplotype(s) for individuals from that site. The three possible haplotypes are shown in orange, blue, and yellow. The basemap is the ESRI Street map (https://server.arcgisonline.com/arcgis/rest/services/World_Street_Map/MapServer).

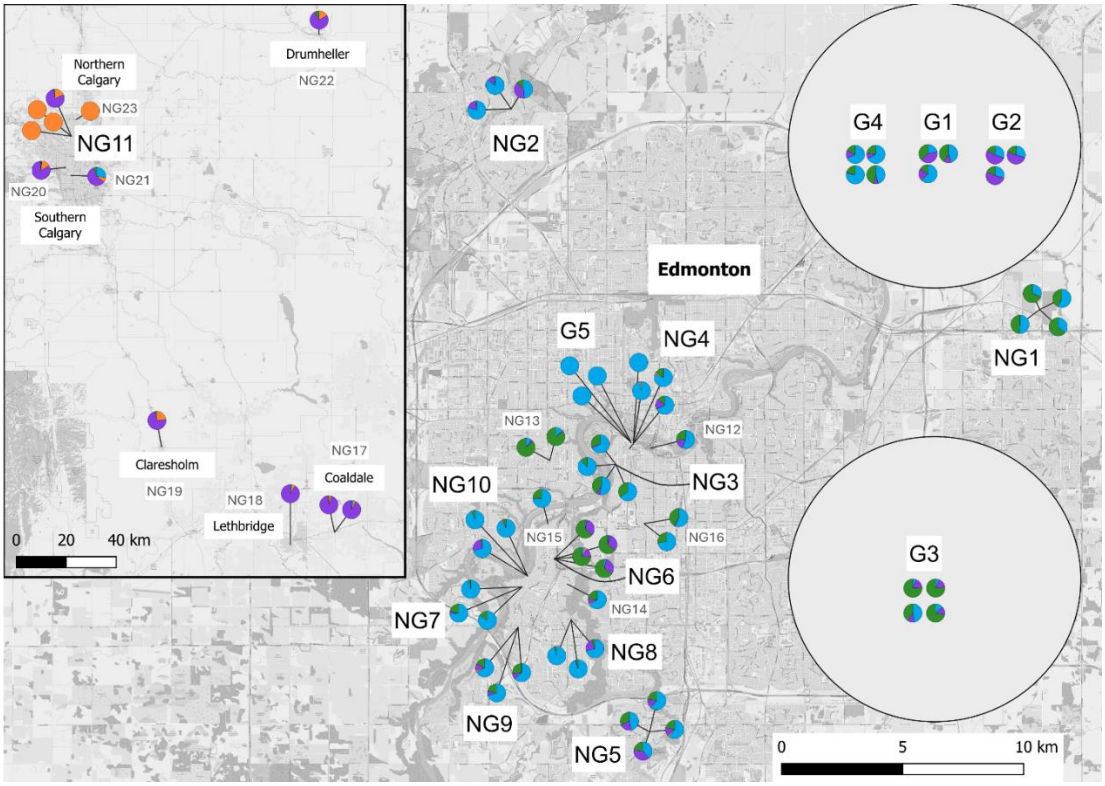


Figure 4.2: Collection localities for 71 *Porcellio spinicornis* samples from Alberta, with pie charts showing K=4 ADMIXTURE components for each individual. Individuals collected from the same site are joined by lines centered on the collection site. Southern Alberta is shown in the upper left inset with labelled localities. Greenhouse and non-greenhouse sites used in Mantel tests and for population-level statistics are labelled with large labels; other sites have smaller labels (NG = non-greenhouse site, G = greenhouse site). Locations are obscured for greenhouses 1 to 4.

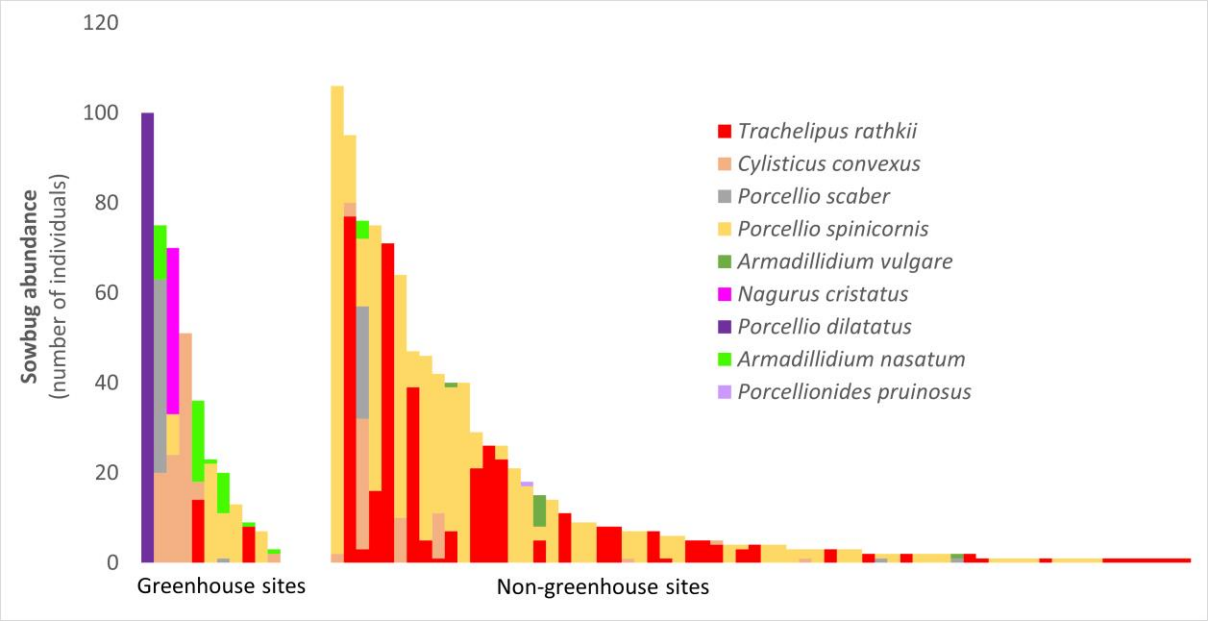


Figure 4.3: Species of sowbugs (Isopoda: Oniscidea) found in 11 greenhouse and 67 non-greenhouse sites in Alberta.

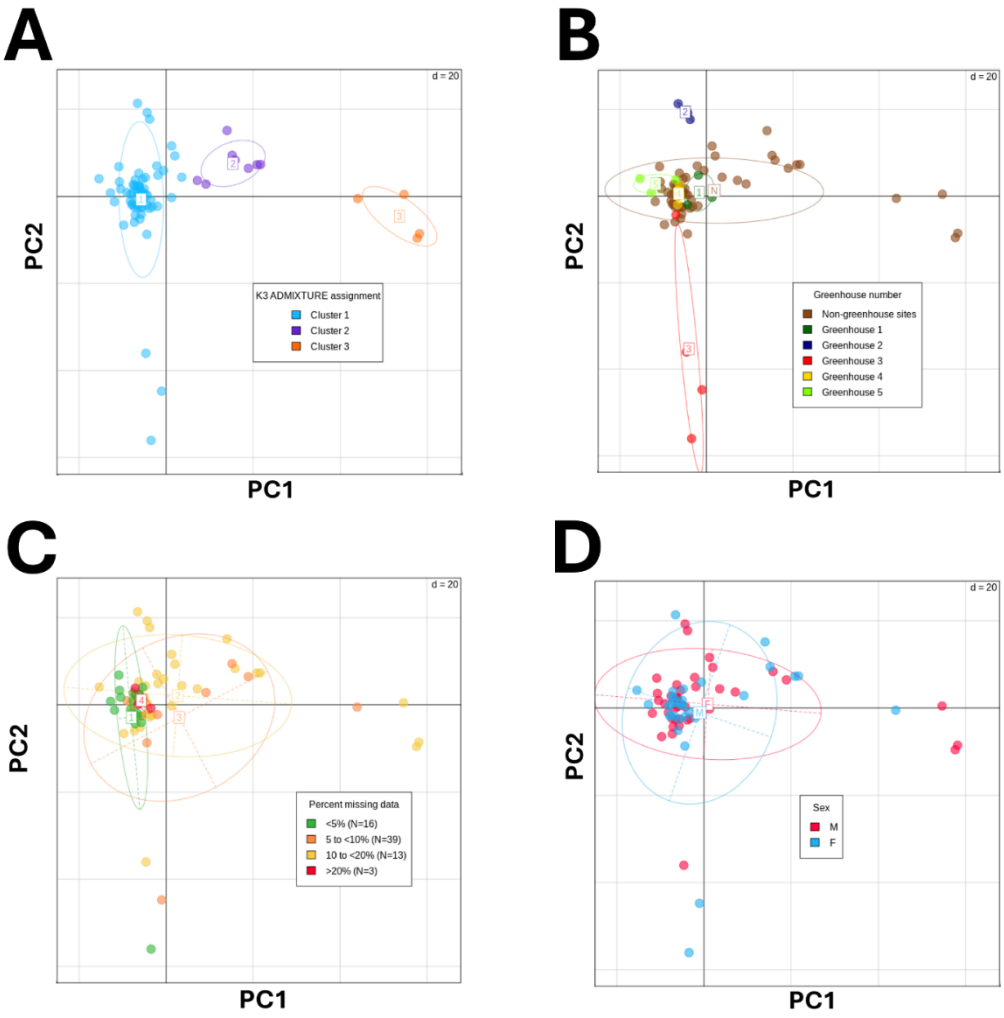


Figure 4.4: PCA plots produced with 39,978 SNPs from 71 *Porcellio spinicornis* from Alberta. Individuals are colored by (A) K=3 ADMIXTURE assignment, where cluster 1 includes all samples from Edmonton, cluster 2 includes N=1 sample from northern Calgary and samples from all other localities in southern Alberta, and cluster 3 includes N=4 samples from northern Calgary (Fig. 4.1); (B) greenhouse site; (C) percentage of missing data per individual; (D) sex. Greenhouses each form a separate cluster in (B).

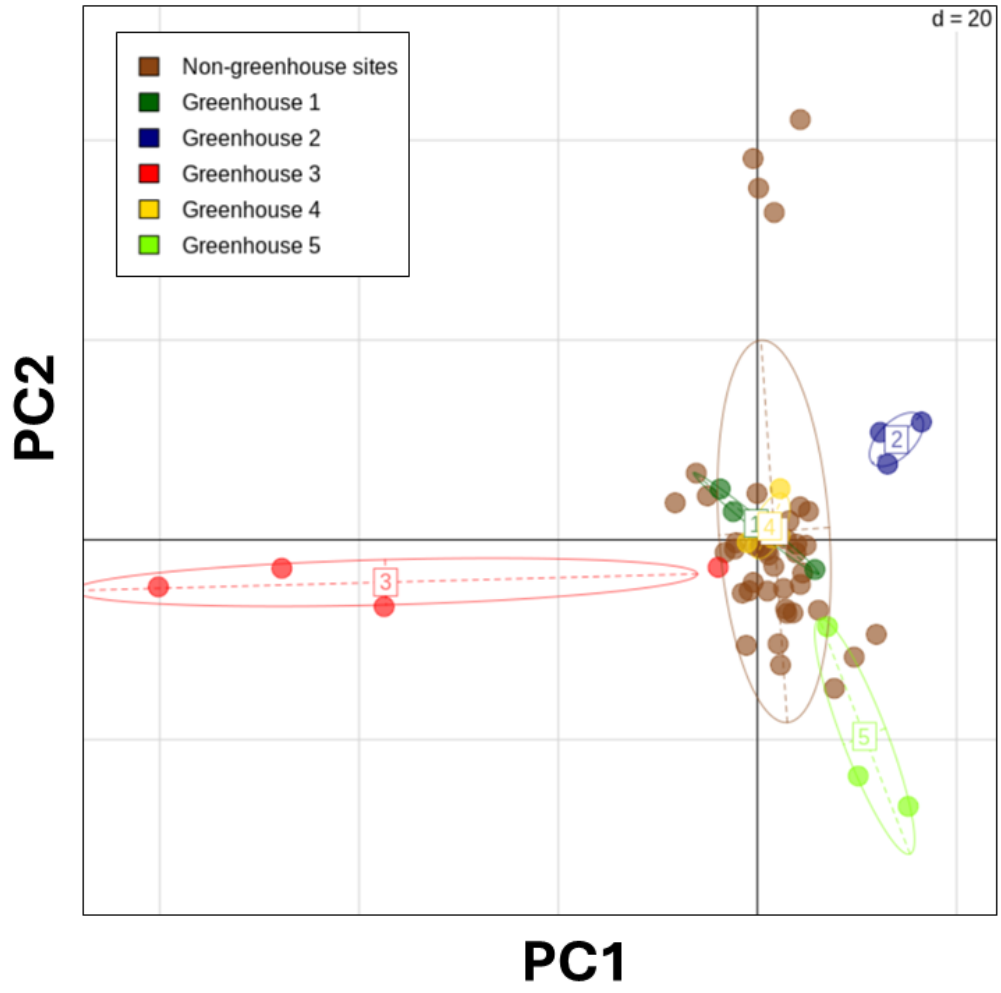


Figure 4.5: PCA plot produced with 39,978 SNPs from 59 *Porcellio spinicornis* from Edmonton, Alberta. Non-greenhouse individuals are brown while others are colored by greenhouse site. The cluster of four individuals at the top of the plot corresponds to four individuals from a site from southwest Edmonton (non-greenhouse site 6).

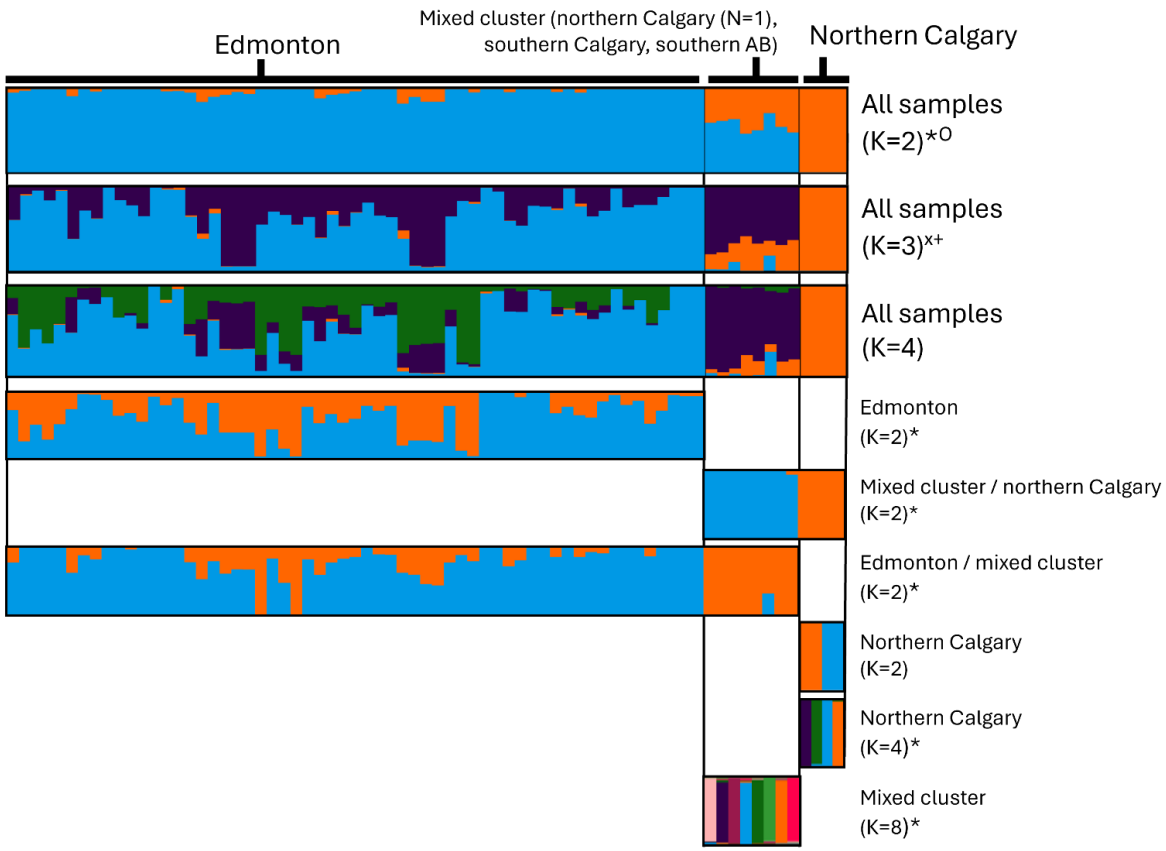


Figure 4.6: Hierarchical ADMIXTURE analysis of *Porcellio spinicornis* from Alberta. ^{X} indicates the K-value chosen based on the four measures proposed by Puechmaille (2016), * indicates the K-value chosen based on CV error, $^{+}$ indicates the K-value chosen according to ΔK (Evanno *et al*. 2005), and ^{O} indicates the K-value chosen based on the choose K algorithm (Raj *et al*. 2014). Plots for some additional K-values are also shown.

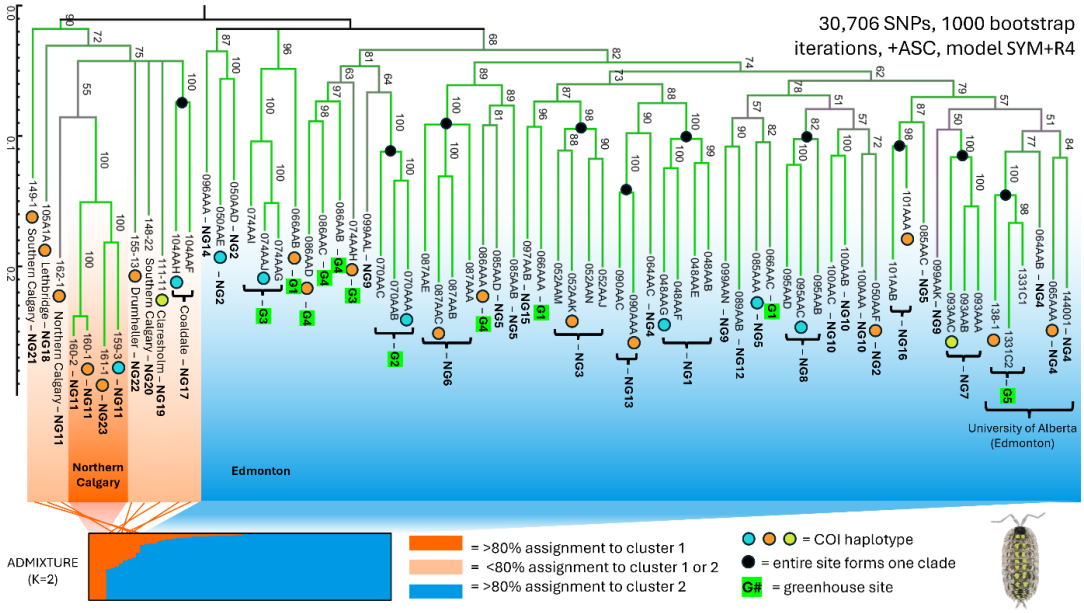


Figure 4.7: Maximum likelihood phylogeny of 71 *Porcellio spinicornis* from Alberta constructed with 30,706 SNPs, with comparison to the ADMIXTURE K=2 plot (Fig. 4.6). Zoom for details. Numbers by nodes indicate ultrafast bootstrap support; phylogeny color indicates bootstrap support, where greener areas have higher support. All sites in cluster 1 are from Edmonton; other localities are listed below the corresponding sample. Individuals are labelled by sample code and by site number: NG# = non-greenhouse site, G# = greenhouse site (highlighted). See Figs. 4.1 and 4.2 for collection maps.

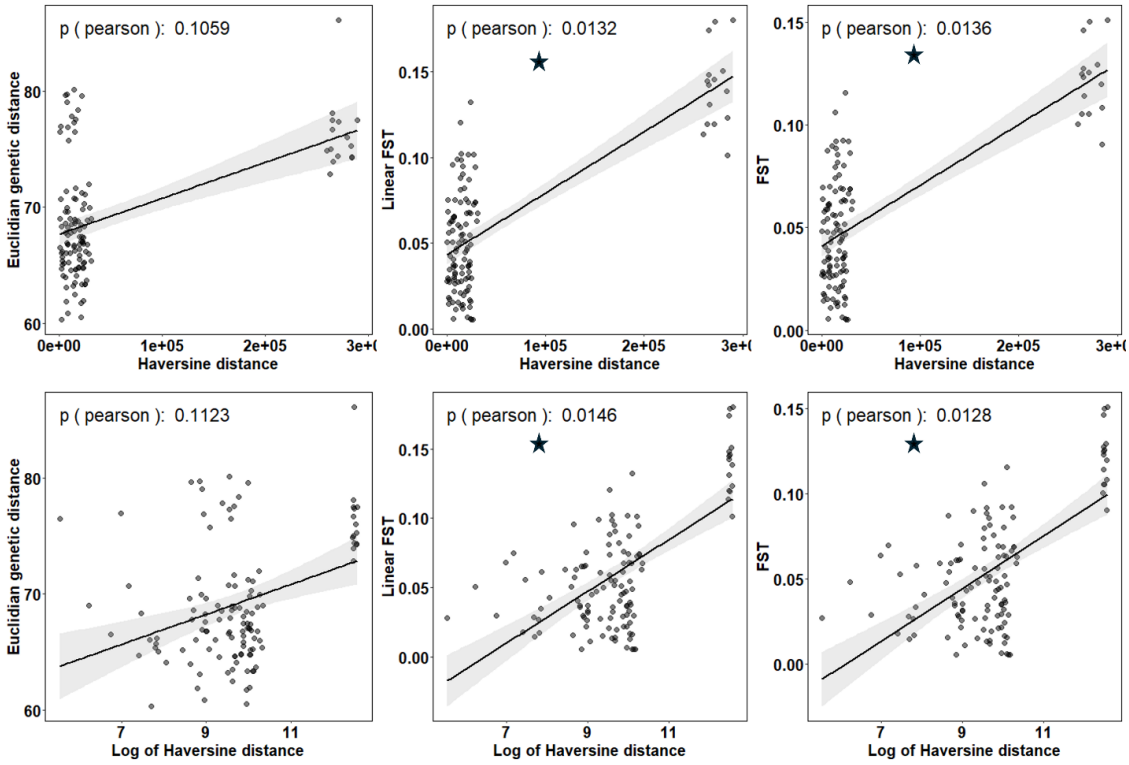


Figure 4.8: Mantel tests for *Porcellio spinicornis* from Alberta using two measures of geographic distance and three measures of genetic distance. Plots that show significant isolation by distance are marked with a star. Geographic and genetic distance matrices used for these plots were averaged from five datasets that subsampled three individuals per site from all sites with at least three individuals (see main text).

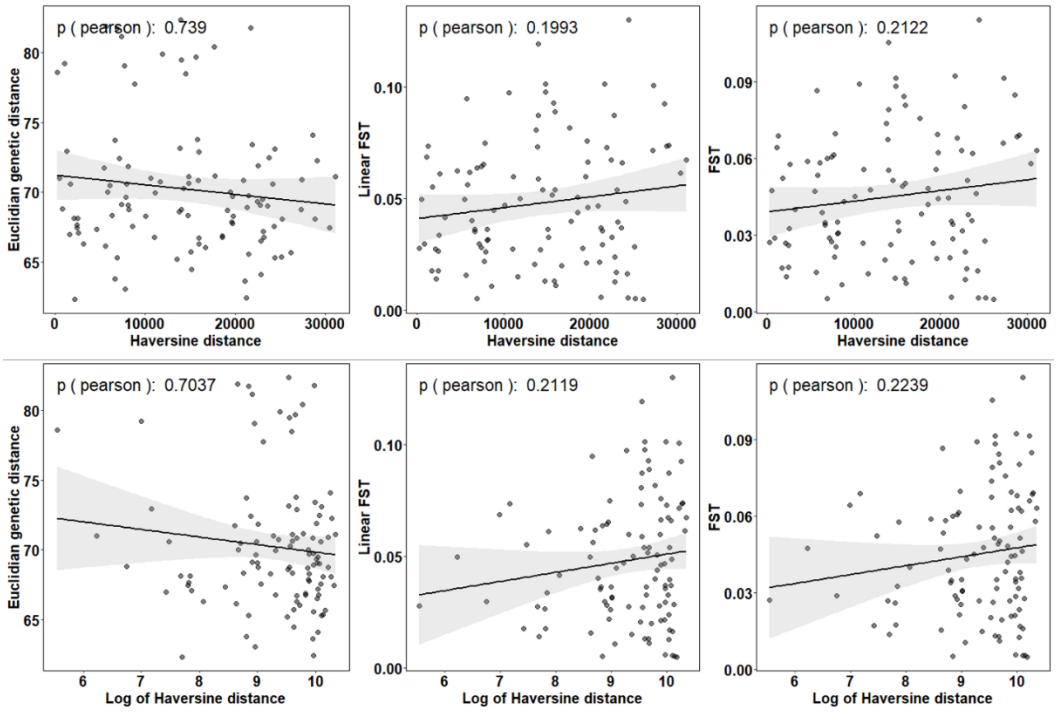


Figure 4.9: Mantel tests for *Porcellio spinicornis* from Edmonton using two measures of geographic distance and three measures of genetic distance. None of the plots show significant isolation by distance. Geographic and genetic distance matrices used for these plots were an averaged from five datasets that subsampled three individuals per site from all sites with at least three individuals (see main text).

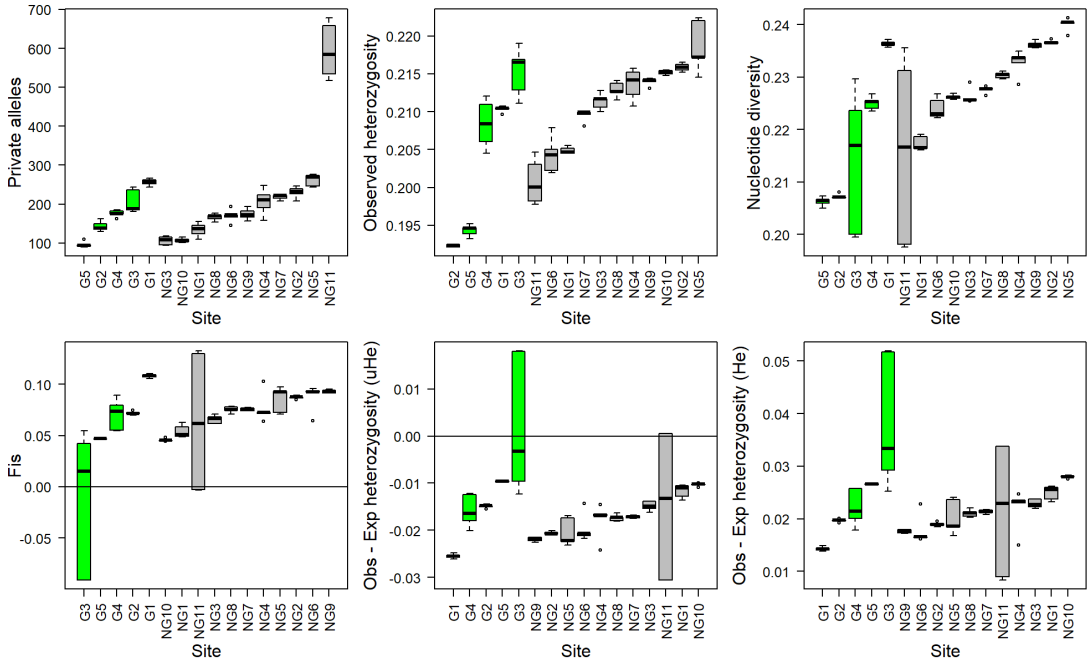


Figure 4.10: Boxplots of population-level statistics for *Porcellio spinicornis* from 11 non-greenhouse sites (N=10 from Edmonton, N=1 (NG11) from northern Calgary) and 5 greenhouses from Edmonton. Statistics were calculated for three individuals per site. If sites had more than three individuals, the values were averaged over 5 datasets with different combinations of individuals (see main text). Greenhouse site 3 (G3) and non-greenhouse site 11 (NG11) each had a single individual that greatly influenced the values when included.

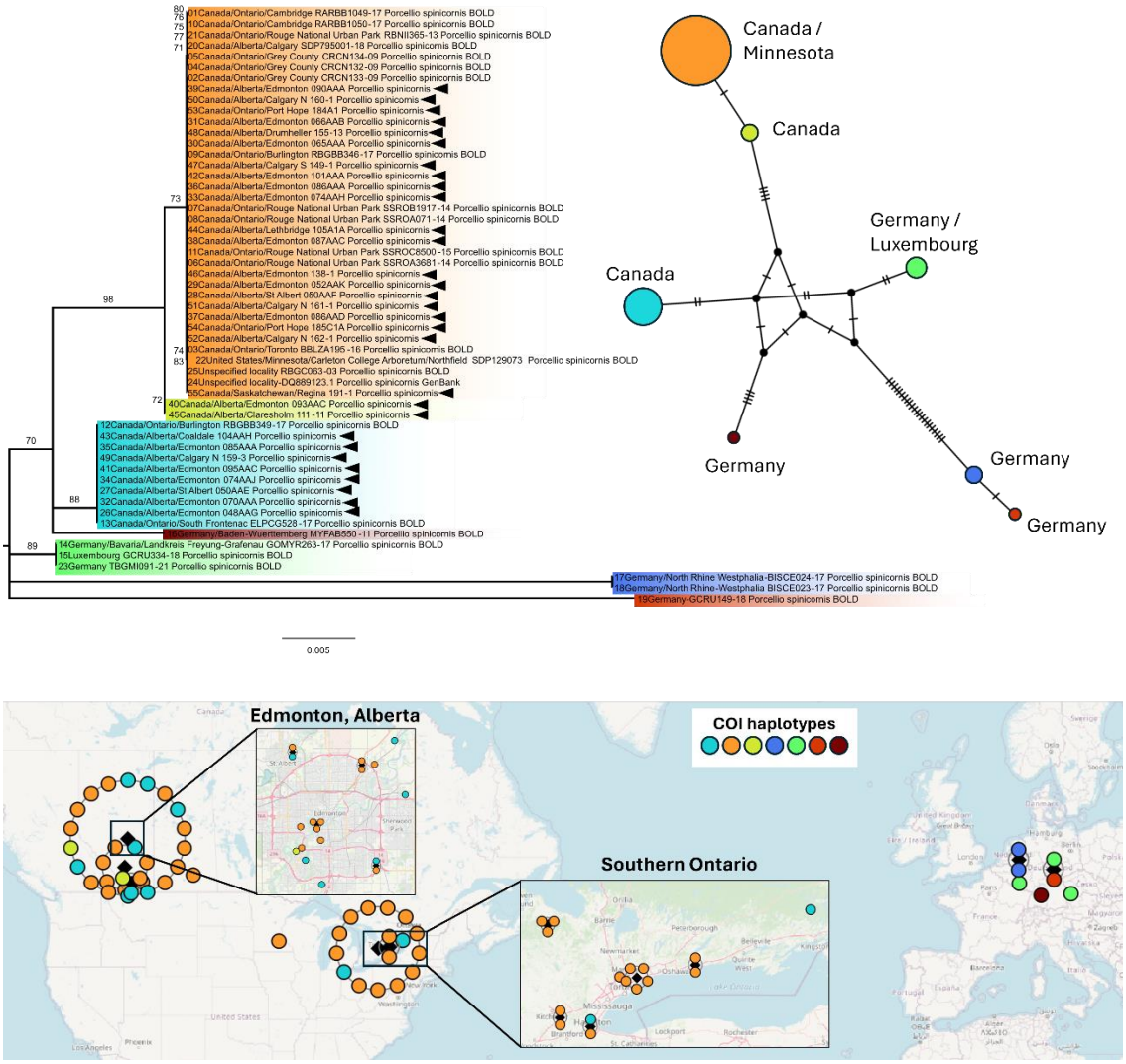


Figure 4.11: Maximum likelihood phylogeny, haplotype network, and map of 55 *Porcellio spinicornis* COI barcode sequences from North America (Canada and Minnesota) and Europe (Germany and Luxembourg). Zoom for detail. Samples collected in this study are indicated in the phylogeny with arrows, with clades colored based on haplotype. The network was made with the Tight Span Walker algorithm as implemented in PopART (Leigh and Bryant 2015).

Chapter 5.

General discussion

5.1. Summary of findings

The goal of my thesis research was to document a neglected component of Alberta's biodiversity and to provide a foundation for understanding the potential impact of introduced sowbugs in this region. When I began my thesis work there were no published peer-reviewed records mentioning the occurrence of sowbugs in Alberta. The recent publication by Li (2022) includes only one species from a single site in Alberta. This first thorough survey of sowbugs in Alberta (Chapter 2) has greatly expanded our knowledge of the distribution and diversity of sowbugs in this province. At least nine species of sowbugs occur in Alberta, of which one (*Nagurus cristatus* (Dollfus)) had never been recorded from Canada, and one (*Porcellio dilatatus* Brandt) had never been recorded from western Canada. Previous records of symbionts associated with sowbugs in Canada were also scarce, consisting of only a single record: *Caenorhabditis remanei* Sudhaus from unidentified sowbugs in Ontario (Dey *et al*. 2012). Ten sowbug-associated taxa were recovered in this study from sowbugs in Alberta and British Columbia (Chapter 3) including eight symbiont taxa that had never been recorded in association with sowbugs and the first record of the mite *Bakerdania elliptica* (Krczal) in North America. Molecular barcodes obtained in this study from sowbug and symbiont species include the first sequence data for *Bakerdania elliptica* (COI) and *Nagurus cristatus* (partial 18S), which will aid in identification of these taxa in the future. Prior to my thesis research, the role of greenhouses in sowbug introduction had never been assessed with molecular methods, and the scarcity of historical records for sowbugs

in Alberta made it impossible to determine the history and movements of sowbugs in the province. With the molecular evidence I obtained (Chapter 4), it is now possible to state that populations of the sowbug *Porcellio spinicornis* Say in Alberta originated from at least three separate introductions to different parts of the province, likely from populations in other parts of North America, and that genetic evidence is consistent with a relatively recent introduction. Evidence for greenhouses as primary introduction sites was inconclusive, and so it is possible that other routes may play an equal or more frequent role in passive dispersal of sowbugs (e.g. movement of landscaping materials, transportation with outdoor décor when these items are moved between properties, etc.).

Overall, none of the evidence collected from this study suggests that sowbugs currently pose a threat to Alberta's ecology, economy, or human health. Competition between introduced and native sowbug species is not a concern at present, as all species recovered from the province were non-native. Co-introduction or increased transmission of potentially damaging symbiotic species also does not appear to merit concern: sowbugs in Alberta are remarkably symbiont-free, with the few recovered symbionts consisting almost entirely of phoretic or necromenic species rather than parasitic taxa. The only exception was a single *Aphelenchoides* nematode that may represent the facultative plant parasitic species *Aphelenchoides blastophthorus* Franklin. However, this association seems to be uncommon, as only a single *Aphelenchoides* nematode was recovered. Only two sowbug species are common in Alberta (*Porcellio spinicornis* and *Trachelipus rathkii* (Brandt)), and only a single symbiont was recovered from the most common species (*Aphelenchoides* from *Porcellio spinicornis*). However, the species diversity of sowbug-associated symbionts may change over time if introductions are ongoing and/or if symbiont species in Alberta begin to associate with sowbugs. Similarly, the impact of sowbugs in Alberta

may also change over time due to range expansion: if sowbug introductions are very recent and/or if sowbugs are capable of frequent active dispersal around cities (Chapter 4), sowbugs may have yet to occupy all accessible and habitable areas. Range expansion of introduced sowbug populations, especially into less-disturbed areas, may lead to unwanted ecological effects due to sowbug decomposition activity. The spread of introduced earthworms in forests in North America has led to changes in plant communities (Bohlen *et al*. 2004), and earthworms and sowbugs share similar ecological niches (soil-dwelling decomposers of plant matter) (Bouchon *et al*. 2016). There may be a delay between when a species is first introduced and when problematic impact occurs (Crooks 2005), so it is important to continue to monitor introduced sowbug populations to assess whether their impact is changing.

5.2. Monitoring and surveying sowbugs in Alberta

While only a single species of sowbug from one site in the province was reported in a published, peer-reviewed venue (Li 2022), I found that records from citizen scientists provided a much more comprehensive picture, highlighting the value of citizen science initiatives in documenting and monitoring sowbug diversity. As of 10 December 2023, seven of the nine species recorded from Alberta in this study had also been documented from the province at least once on iNaturalist (iNaturalist 2023) and/or BugGuide (BugGuide 2023), with sowbug records originating from many different parts of Alberta (Chapter 2). As many sowbugs are identifiable to species based on photos alone (personal observation, HS; Gregory 2022), using citizen science to monitor introduced populations of sowbugs would be an excellent way to track range expansion and to document the arrival of additional species. For many smaller species (e.g. Trichoniscidae), identification to particular species may not be possible with photos alone, but observations of this group would still be useful in detecting morphotypes that do not match any

known species in an area, documenting readily-visible sowbug symbionts (e.g. iridovirus), and identifying sowbug populations that could be sampled in the future for identification purposes or for research. However, while most of the sowbug species identifications for observations on iNaturalist and BugGuide were a good match for the associated image(s), some identifications were doubtful or clearly inaccurate (Chapter 2). It is important to critically evaluate records obtained from citizen science initiatives to ensure identifications are reasonable, particularly for observations that record species in unusual localities. Species identifications should also be assessed by detailed morphological examination and molecular data from collected specimens whenever possible, both to confirm the identification (especially for newly documented species) and to provide material for future studies.

Although I am reasonably confident that I have documented the distribution and diversity of sowbugs in urban and suburban areas of central Alberta, much remains to be learned. There are several areas in the province from which collections were not made (e.g. northern Alberta; western Alberta near the Rocky Mountains) as well as habitats that were not investigated (e.g. caves, agricultural areas, boreal forest, badlands, foothills). Caves may be a particularly important area to survey, since native sowbug species in Alberta may be most likely to occur in caves: the only known native species of aquatic isopod in the province is thought to have survived glaciation due to its subterranean habitat (Clifford and Bergstrom 1976; Holsinger *et al*. 1983). Greater sowbug survey coverage across Alberta could be achieved if studies that involve arthropod diversity surveys (e.g. ABMI) simply reported sowbug absence if none are collected and applied survey methods suitable for recovering larger-bodied ground-dwelling invertebrates (e.g. pitfall traps). When using Tullgren funnel extractions to recover arthropods, sowbugs can be co-collected by placing the sample on top of a flat piece of cheesecloth suspended by a coarse

grid rather than wrapping the sample in a ball of cheesecloth (Van Slyke 2023). Given that introduced sowbugs may not be able to overwinter in cold climates without human-modified habitats (Wright 1997), surveys of relatively undisturbed parts of Alberta are important for determining whether range expansion into these regions has occurred. Testing the cold tolerance of sowbug population in Alberta would determine if overwintering may be possible in these areas, and may also reveal physiological or molecular evidence of cold adaptation. At least two species of sowbug (*Armadillidium nasatum* Budde-Lund and *A. vulgare* (Latreille)) possess ice-binding proteins (Box *et al*. 2022), and the presence of an existing level of cold adaptation raises the question of whether selection for greater tolerance may have occurred in populations of these species in Alberta. Finally, surveys of other potential sites of primary introduction may aid in determining how sowbugs may have entered the province in the first place and whether introduction is ongoing. Such sites would include areas that receive shipments of objects which could provide shelter for sowbugs, including piles of wood in lumber yards or mulch and gravel in landscaping supply centers.

5.3. Additional research opportunities

Several results from this study raised interesting questions about sowbug biology and ecology that were outside the scope of the three data chapters. Firstly, the very low COI diversity of *Porcellio spinicornis* in Canada (Fig. 4.11) raises the question of whether *Wolbachia* bacteria may have played a role in reducing mitochondrial diversity. Selective sweeps and reduction in mitochondrial haplotype diversity associated with infection with a particular *Wolbachia* strain are thought to have occurred in insects (Graham and Wilson 2012; Deng *et al*. 2021). My tests for the presence of *Wolbachia* in sowbugs collected for this study were inconclusive (Chapter 3); the use of different primers or a modified amplification protocol may make it possible to determine

whether more than one strain of *Wolbachia* is present in *Porcellio spinicornis* populations in Alberta and the rest of Canada, and whether those strains are associated with different mitochondrial haplotypes.

Secondly, genetic evidence from *P. spinicornis* populations in Edmonton suggested the possibility that this species is capable of widespread active dispersal (Chapter 4). While sowbugs are often assumed to be poor dispersers (Hornung 2011; Lee *et al*. 2014; Szlavecz *et al*. 2018; Dimitriou *et al*. 2022), preliminary data from lab tests conducted during the duration of this study (HS, unpublished) suggest that *P. spinicornis* is capable of walking at least 100 m in three hours, and *Cylisticus convexus* (De Geer) can travel at least 100 meters in 3.5 hours, which is consistent with the theoretical dispersal capacity of *Armadillidium vulgare* (Furukawa *et al*. 2017). Sowbugs may therefore be surprisingly competent active dispersers. As the active dispersal capacity of sowbugs has implications for the spread of introduced populations, the dispersal capacity of commonly introduced sowbug species (see Jass and Klausmeier 2000) should be assessed in both the lab and in the field to determine how far these species can and do disperse.

Thirdly, the presence of sowbugs in many greenhouses in Alberta, sometimes in large numbers (Chapter 4), raises the question of the impact they may have on seedlings. Sowbugs may occasionally feed on and damage seedlings in greenhouses (Hatch 1947; Messelink and Bloemhard 2007). Their feeding could cause negative economic impact in commercial greenhouses, and could also affect experimental plants in research greenhouses (sowbugs were found both in the University of Alberta Biological Sciences greenhouse and in the Agricultural, Life & Environmental Sciences Teaching Research greenhouses). Controlled studies to assess the impact of sowbugs on seedlings would provide insight into whether some species are more likely

to engage in this behavior than others, and the circumstances under which feeding occurs (e.g. high population density, type of plant).

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Appendix A: Supplementary Materials for Chapter 2

Table A1: List of sowbug specimens for which COI and/or partial 18S sequences were obtained in this study. All resulted from bidirectional sequencing except *Porcellionides pruinosus*, which is a consensus from two separate forward reads. Residual tissues (when available) and/or conspecifics from the same collection site are deposited in the E.H. Strickland Entomological Museum collections (University of Alberta) under the accession numbers listed in the table.

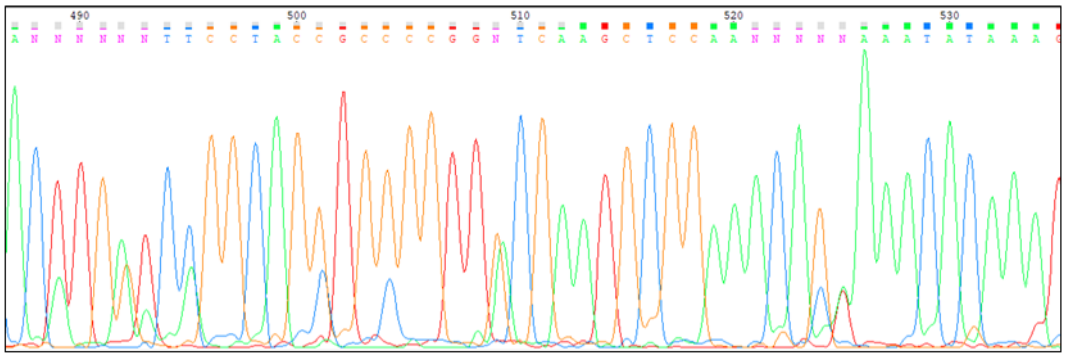
SPECIES	FAMILY	SEQUENCE TYPE(S)	LENGTH (mm) / SEX	LOCALITY	RESEARCH ID	GENBANK ACCESSION NUMBER(S)	STRICKLAND ACCESSION NUMBER
Armadillidium nasatum	Armadillidiidae	COI	11, M	Canada: AB: Edmonton (University of Alberta Botanic Gardens, warm temperate greenhouse)	059AAG	PP995851	UASM407051 Conspecifics: UASM407052 UASM407049
Armadillidium nasatum	Armadillidiidae	COI	10, F	Canada: AB: Westerose (greenhouse)	079AAA	PP995852	UASM407086
Armadillidium nasatum	Armadillidiidae	COI	9.5, M	Canada: AB: Edmonton (greenhouse in NE Edmonton)	086AAF	PP995853	UASM407108
Armadillidium vulgare	Armadillidiidae	COI	8, F	Canada: BC: Parksville (wooded area)	057AAH	PP995854	UASM407038
Armadillidium vulgare	Armadillidiidae	COI	12.5, M	Canada: AB: Coaldale (urban yard)	104AAV	PP995855	UASM407143
Armadillidium vulgare	Armadillidiidae	COI	>8, F	Canada: AB: Lethbridge (urban yard)	105b-1	PP995856	UASM407221 Conspecifics: UASM407365 UASM407367
Armadillidium vulgare	Armadillidiidae	COI	>10, F	Canada: AB: Drumheller (greenhouse)	199AAB	PP995857	UASM407286
Cylisticus convexus	Cylisticidae	COI	11, M	Canada: AB: Sherwood Park (greenhouse)	047AAG	PP995858	UASM407289 Conspecifics: UASM407018 UASM407019 UASM407020 UASM407021
Cylisticus convexus	Cylisticidae	COI	10, M	Canada: AB: Spruce Grove (greenhouse)	082AAA	PP995859	UASM407097 Conspecific: UASM407098
Cylisticus convexus	Cylisticidae	COI	9, M	Canada: AB: Edmonton (University of Alberta Biological Sciences greenhouse)	1331C3	PP995860	UASM407186 Conspecific: UASM407185
Cylisticus convexus	Cylisticidae	COI	>8, F	Canada: AB: Calgary (Edgemont)	150-1	PP995861	UASM407242
Cylisticus convexus	Cylisticidae	COI	10, M	Canada: ON: Port Hope (urban yard)	184B2	PP995862	UASM407258 Conspecifics: UASM407257

							UASM407259
Hyloniscus riparius	Trichoniscidae	COI	4, F	Canada: ON: Port Hope (wooded trail)	185A1	PP995863	UASM407265 Conspecific: UASM407266
Nagurus cristatus	Trachelipodidae	COI (?), 18S	4, F	Canada: AB: Edmonton (University of Alberta Biological Sciences greenhouse)	046005	PP995864 (COI) PQ001582 (partial 18S)	No residual tissue Conspecifics: UASM407002 UASM407003 UASM407004 UASM407005
Nagurus cristatus	Trachelipodidae	COI (?), 18S	4, F	Canada: AB: Edmonton (University of Alberta Biological Sciences greenhouse)	046004	PP995865 (COI) PQ001581 (partial 18S)	UASM407005 Conspecifics: UASM407002 UASM407003 UASM407004
Nagurus cristatus	Trachelipodidae	COI (?), 18S	4, F	Canada: AB: Edmonton (University of Alberta Biological Sciences greenhouse)	046008	PP995867 (COI) PQ001583 (partial 18S)	No residual tissue Conspecifics: UASM407002 UASM407003 UASM407004 UASM407005
Oniscus asellus	Oniscidae	COI	10.5, M	Canada: BC: Prince George (Kiwanis Park)	063AAC	PP995868	UASM407290 Conspecifics: UASM407063 UASM407064
Oniscus asellus	Oniscidae	COI	12, M	Canada: BC: Vancouver (Stanley Park)	1082A3	PP995866	UASM407292 Conspecifics: UASM407362 UASM407144 UASM407363 UASM407145 UASM407364
Philoscia muscorum	Philosciidae	COI	Not recorded, F	Canada: BC: Vancouver Island (Qualicum Beach, yard)	007AAD	PP995869	No residual tissue No conspecifics
Philoscia muscorum	Philosciidae	COI	9.5, F	Canada: BC: Parksville (urban yard)	183B4	PP995870	UASM407252 Conspecific: UASM407284
Philoscia muscorum	Philosciidae	COI	7, M	Canada: ON: Port Hope (wooded trail)	185C1B	PP995871	UASM407261 Conspecifics: UASM407260 UASM407262 UASM407263
Porcellionides pruinosus	Porcellionidae	COI	>7, M	Canada: AB: Drumheller	155001	PP995872	UASM407211
Porcellio dilatatus	Porcellionidae	COI	14, F	Canada: AB: St. Albert (greenhouse)	049ABB	PP995873	UASM407281 Conspecifics: UASM407010 UASM407011 UASM407012 UASM407013

							UASM407293
Porcellio scaber	Porcellionidae	COI	7.5, M	Canada: AB: Edmonton (University of Alberta Botanic Gardens, warm temperate greenhouse)	059AAE	PP995874	Conspecifics: UASM407045 UASM407046 UASM407047 UASM407048
Porcellio scaber	Porcellionidae	COI	12, M	Canada: AB: Edmonton (University of Alberta north campus)	065AAD	PP995875	UASM407294
Porcellio scaber	Porcellionidae	COI	9.5, F	Canada: AB: Edmonton (greenhouse in SE Edmonton)	074AAF	PP995876	UASM407094
Porcellio scaber	Porcellionidae	COI	12, F	Canada: BC: Prince George (urban yard)	080AAA	PP995877	UASM407081
Porcellio scaber	Porcellionidae	COI	12, M	Canada: BC: Bamfield (yard)	106AAA	PP995878	UASM407151 Conspecifics: UASM407152
Porcellio scaber	Porcellionidae	COI	10, M	Canada: BC: Vancouver (Stanley Park)	1084B4	PP995879	UASM407295 Conspecifics: UASM407147 UASM407146
Porcellio scaber	Porcellionidae	COI	9, F	Canada: AB: Drumheller (greenhouse)	199AAA	PP995880	UASM407285
Porcellio spinicornis	Porcellionidae	COI	10, F	Canada: AB: Edmonton (greenhouse in NE Edmonton)	070AAA	PP995881	UASM407075 Conspecifics: UASM407329 UASM407330
Porcellio spinicornis	Porcellionidae	COI	8, F	Canada: AB: Coaldale (urban yard)	104AAH	PP995882	UASM407296 Conspecifics: UASM407138 UASM407139 UASM407356
Porcellio spinicornis	Porcellionidae	COI	>9, F	Canada: AB: Calgary (Haysboro)	149-1	PP995883	UASM407200
Porcellio spinicornis	Porcellionidae	COI	10.5, M	Canada: ON: Port Hope (urban yard)	184A1	PP995884	UASM407253 Conspecifics: UASM407254 UASM407255 UASM407256
Porcellio spinicornis	Porcellionidae	COI	7, M	Canada: ON: Port Hope (wooded trail)	185C1A	PP995885	UASM407264
Porcellio spinicornis	Porcellionidae	COI	>12, F	Canada: SK: Regina (in house in urban area)	191-1	PP995886	UASM407276
Trachelipus rathkii	Trachelipodidae	COI	9, M	Canada: AB: Westerose (greenhouse)	079AAD	PP995887	UASM407084 Conspecifics: UASM407083 UASM407085
Trachelipus rathkii	Trachelipodidae	COI	9.5, M	Canada: BC: Prince George (Kiwanis Park)	081AAD	PP995888	UASM407089 Conspecifics: UASM407087 UASM407088
Trachelipus rathkii	Trachelipodidae	COI	9, M	Canada: AB: Spruce Grove (greenhouse)	082AAD	PP995889	UASM407099 Conspecific: UASM407100
Trachelipus rathkii	Trachelipodidae	COI	9.5, M	Canada: AB: Coaldale (urban yard)	104AAP	PP995890	UASM407141

							Conspecific: UASM407142
Trachelipus rathkii	Trachelipodidae	COI	>10, M	Canada: AB: Calgary (North Glenmore)	148-A	PP995891	UASM407222 Conspecifics: UASM407369 (includes multiple individuals)
Trachelipus rathkii	Trachelipodidae	COI	4, F	Canada: ON: Port Hope (wooded trail)	185A4	PP995892	UASM407268 Conspecific: UASM407269
Trachelipus rathkii	Trachelipodidae	COI	7.5, F	Canada: ON: Port Hope (wooded trail)	185B1	PP995893	UASM407269 Conspecific: UASM407268
Trichoniscus pusillus	Trichoniscidae	COI	3, F	Canada: ON: Port Hope (wooded trail)	185A3	PP995894	UASM407267 Conspecific: UASM407270

Oniscus asellus (063AAC)



Porcellionides pruinosus (155-13)

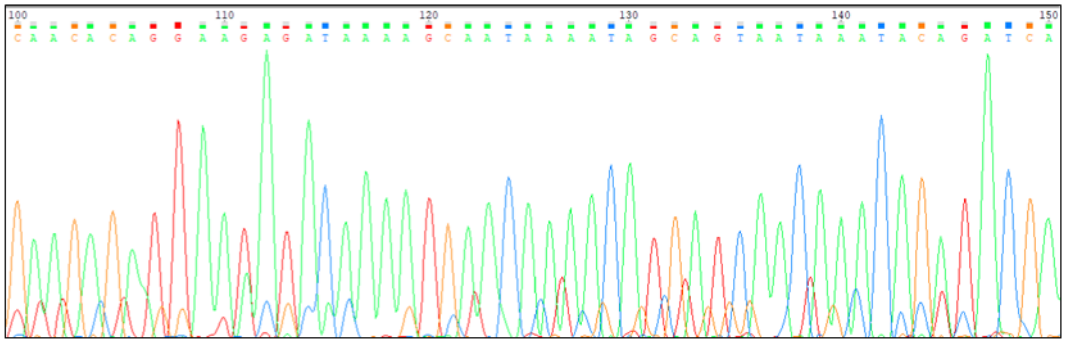


Figure A1: Sequencing chromatograms for *Oniscus asellus* and *Porcellionides pruinosus*. Noise is visible in both chromatograms.

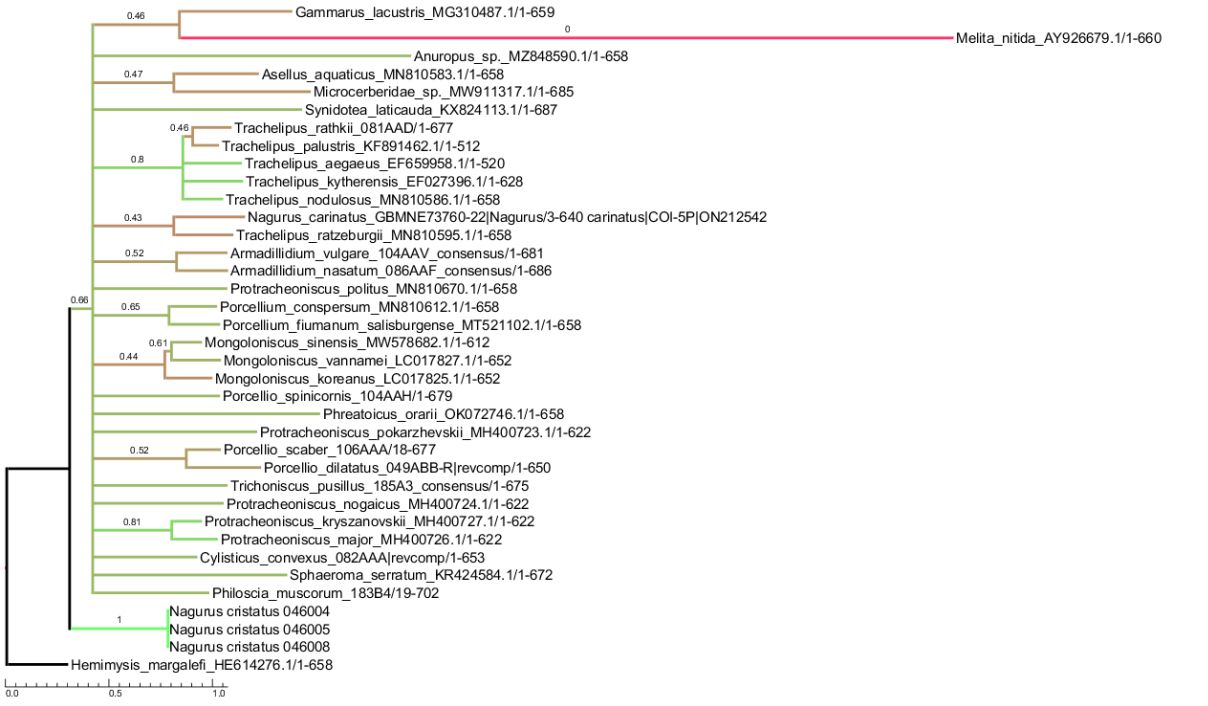


Figure A2: Maximum likelihood phylogeny of peracarid COI sequences made with the GTR+G+I substitution model, including both terrestrial and aquatic isopods. Numbers above the nodes indicate bootstrap support, and lines are colored by bootstrap support for each clade. Nodes with <0.40 (40%) bootstrap support are collapsed. *Nagurus cristatus* is positioned outside a clade containing all other non-mysid Peracarida.

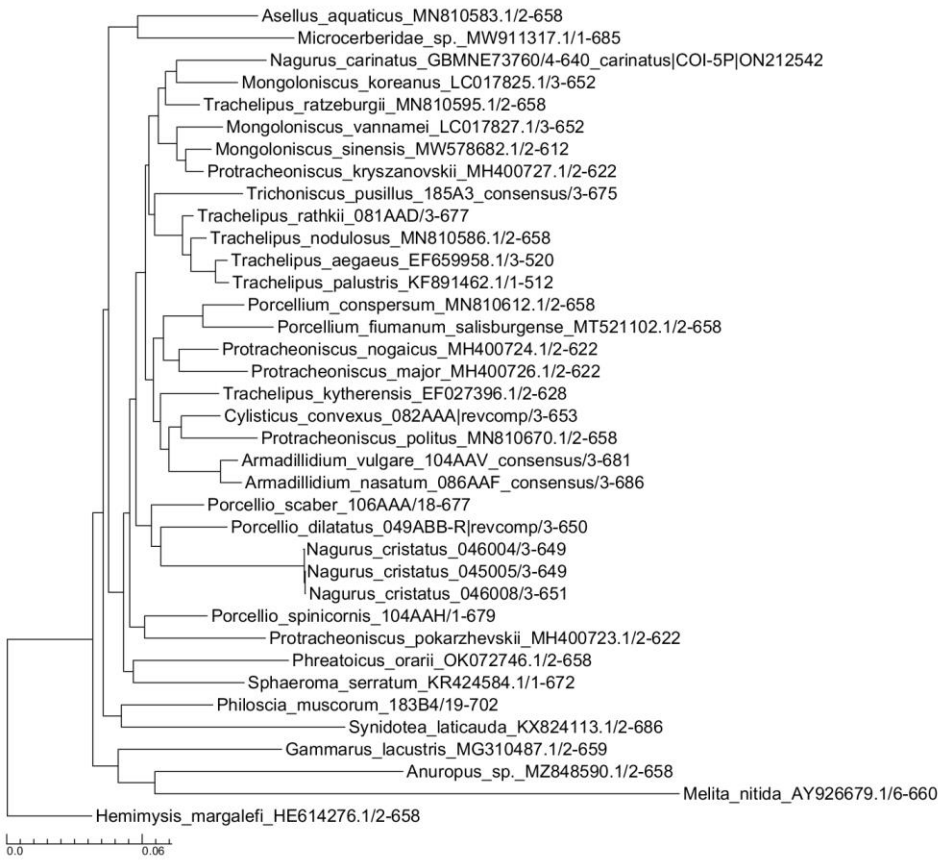


Figure A3: Neighbor-joining tree built by pairwise comparison of amino acid sequences from the COI barcode region of select Peracarida. *Nagurus cristatus* has a moderately long branch compared to other Trachelipodidae (*Trachelipus, Protracheoniscus, Porcellium, Nagurus carinatus*).

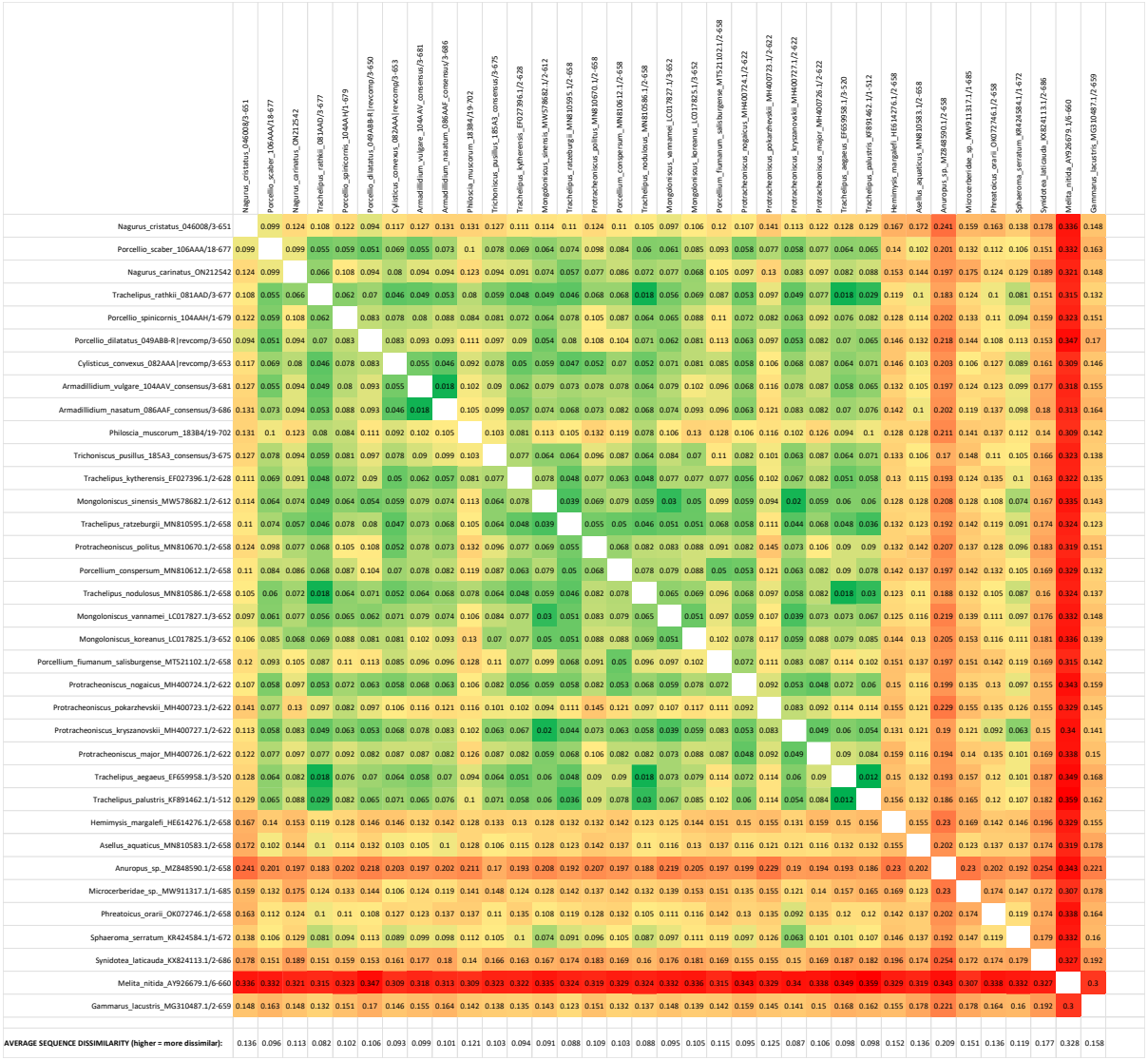


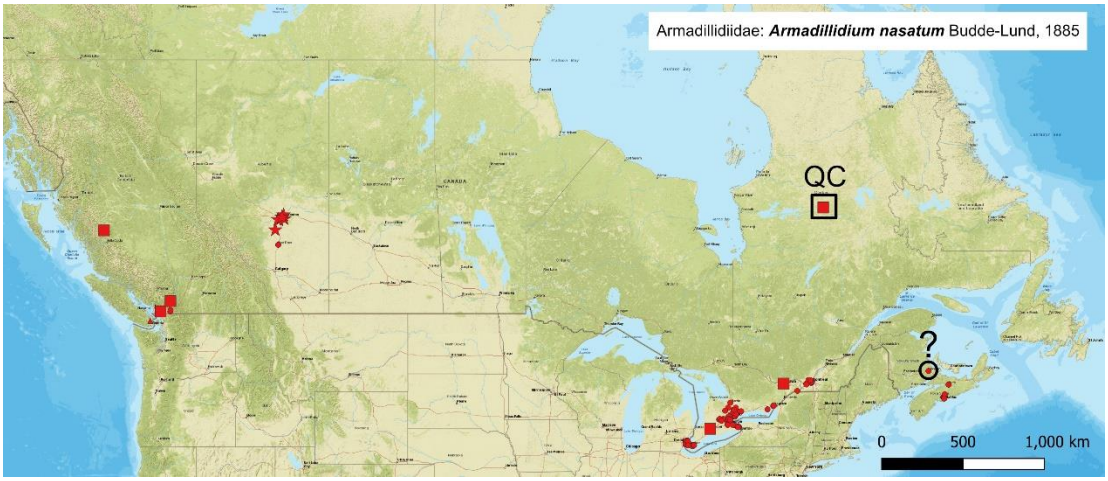
Figure A4: Pairwise comparison matrix of amino acid sequences for the COI barcode region of select Peracarida. Values in the matrix are color-coded based on dissimilarity (dissimilar = red, similar = green). Average sequence dissimilarity (number of amino acid substitutions per site for each pairwise comparison, averaged over multiple comparisons) is listed in the bottom row. Only one *Nagurus cristatus* sequence is included in the matrix, as all three sequences were identical.

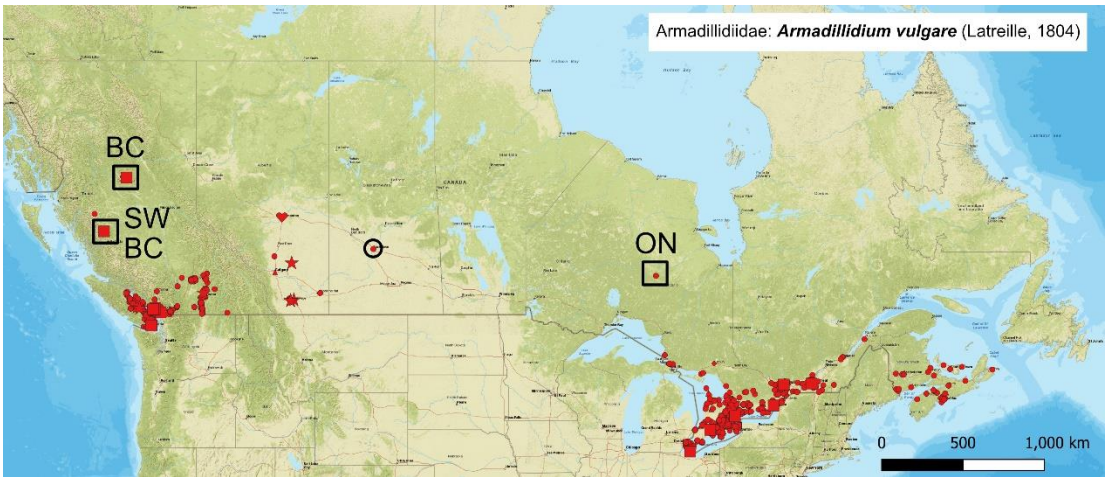


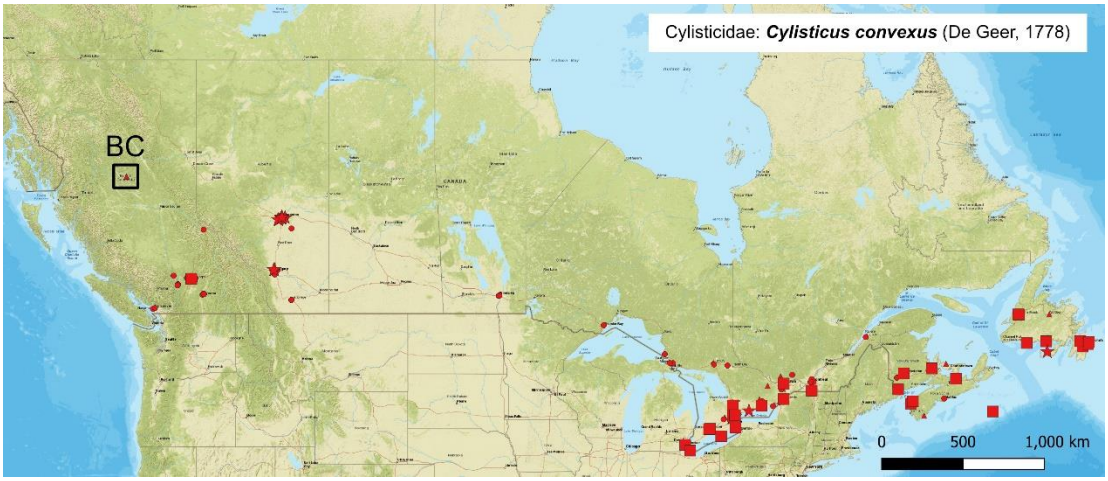
Figure A5: Maximum likelihood phylogeny of sowbug 18S sequences aligned with the L-INS-I algorithm. Sequences are colored by family. Families represented by a single sequence are colored black. *Nagurus cristatus* sequences (Trachelipodidae) are at the top of the phylogeny in a clade containing Scyphacidae, Porcellionidae, and *Levantoniscus*. Numbers above nodes show ultrafast bootstrap support. Nodes with <70% ultrafast bootstrap support are collapsed.

Figure A6 (following pages): Distribution maps of terrestrial isopod species (Isopoda: Oniscidea) found in Canada, sorted alphabetically by family. Zoom to see details (see Fig. 2.5 for a compilation of all maps). Maps show only the Canadian distribution for each species. For distribution in other parts of North America, see Jass and Klausmeier (2000; 2001). Records with the locality listed at province-level are boxed; two records for *Ligia pallasii* that appear to be located in Washington due to coordinate imprecision are also boxed. Doubtful records are indicated with a question mark (see main text). Records that occur apart from other localities in a species' distribution are circled to make them more apparent. Symbols indicate the source of a record: square = previous publication; 5-point star = collections from this study; 4-point star = citizen science initiative from this study; diamond = BugGuide; circle = iNaturalist; triangle = GBIF; heart = E.H. Strickland Entomological Museum.


Alloniscidae: *Alloniscus perconvexus* Dana, 1854
BC
0
500
1,000 km


Armadillidiidae: *Armadillidium nasatum* Budde-Lund, 1885
QC
?
0
500
1,000 km


Armadillidiidae: ***Armadillidium vulgare*** (Latreille, 1804)
BC
SW BC
ON
0
500
1,000 km


Cylisticidae: ***Cylisticus convexus*** (De Geer, 1778)
BC
0
500
1,000 km


Detonidae: ***Armadilloniscus holmesi*** Arcangeli, 1933
BC
0
500
1,000 km


Detonidae: Detonella papillicornis (Richardson, 1904)
0
500
1,000 km

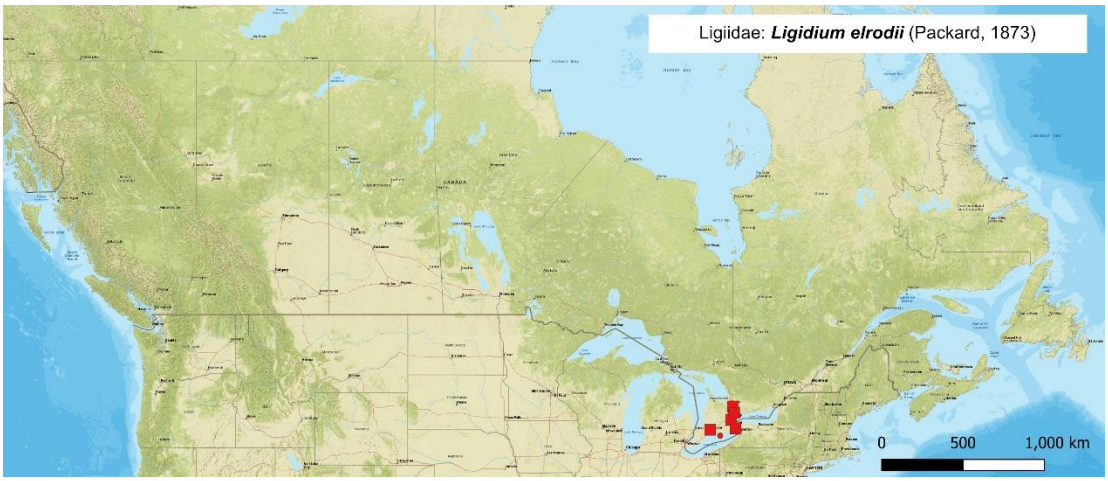

Halophilosciidae: Littorophiloscia richardsonae (Holmes & Gay, 1909)
0
500
1,000 km


Halophilosciidae: Littorophiloscia vittata (Say, 1818)
0
500
1,000 km


Ligiidae: *Ligia occidentalis* (Dana, 1853)
0
500
1,000 km

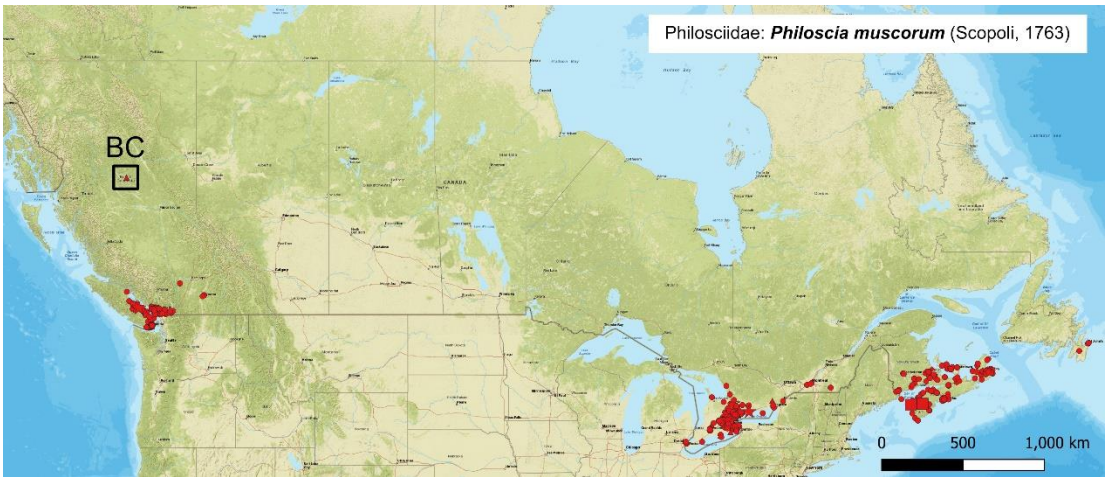

Ligiidae: *Ligia oceanica* (Linnaeus, 1767)
?
0
500
1,000 km

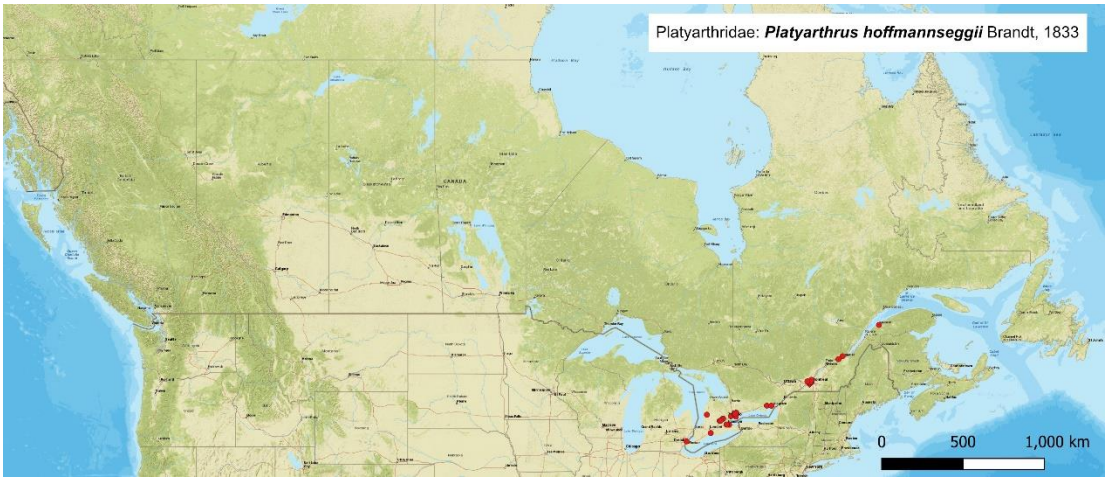

Ligiidae: *Ligia pallasii* Brandt, 1833
BC
0
500
1,000 km


Ligiidae: *Ligidium elrodii* (Packard, 1873)
0
500
1,000 km


Ligiidae: *Ligidium gracile* (Dana, 1854)
BC
0
500
1,000 km

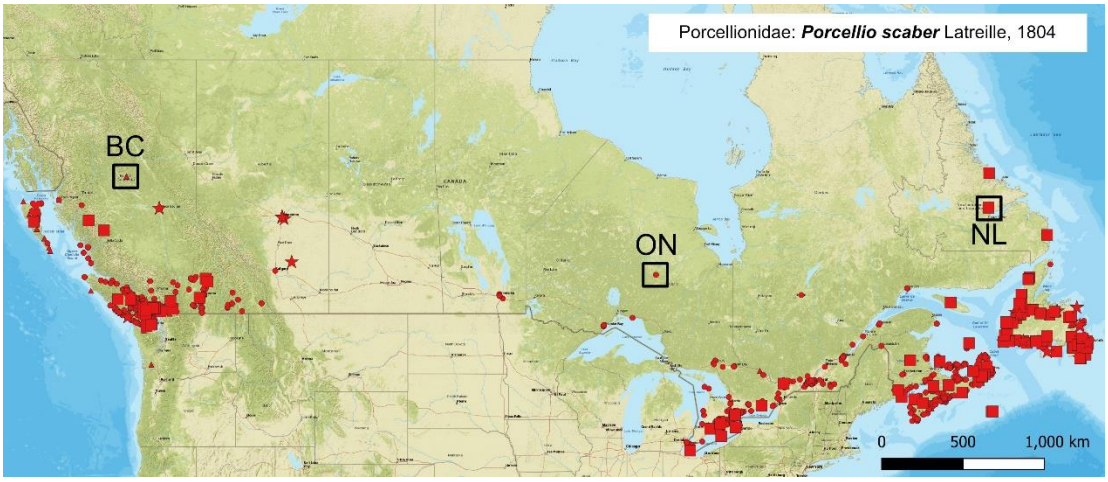

Oniscidae: *Oniscus asellus* Linnaeus, 1758
BC
ON
NL
0
500
1,000 km

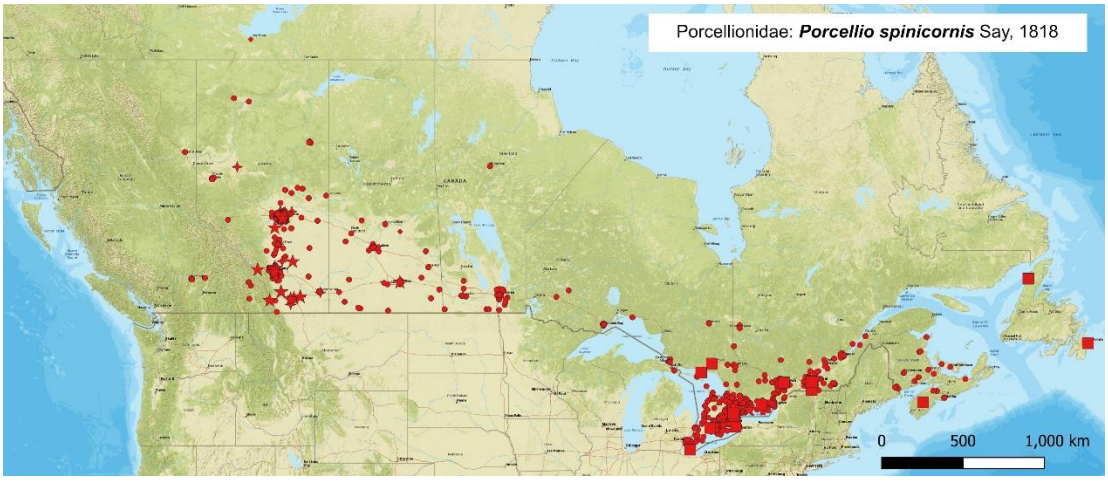

Philosciidae: *Philoscia muscorum* (Scopoli, 1763)
BC
0
500
1,000 km

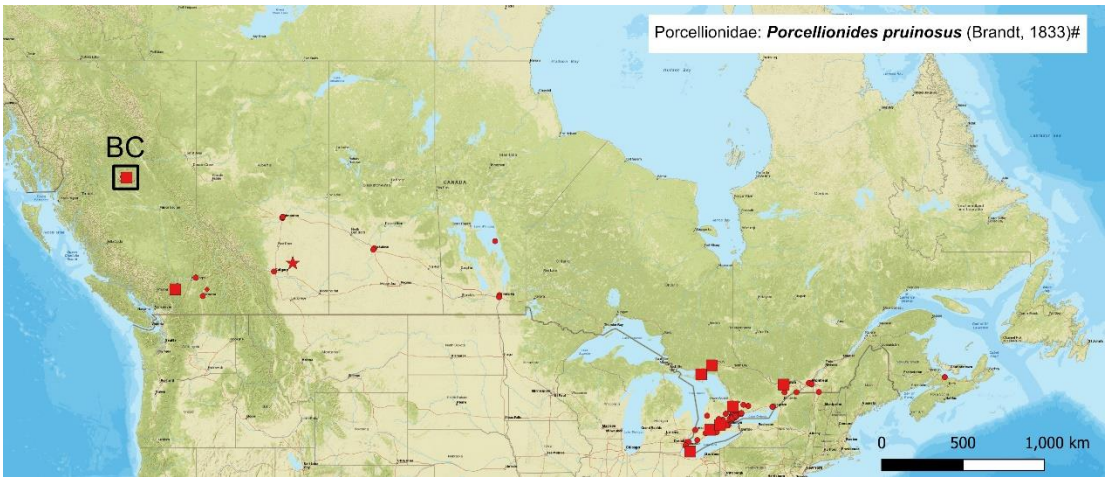

Platyarthridae: *Platyarthrus hoffmannseggii* Brandt, 1833
0
500
1,000 km


Porcellionidae: *Porcellio dilatatus* Brandt, 1831
0
500
1,000 km

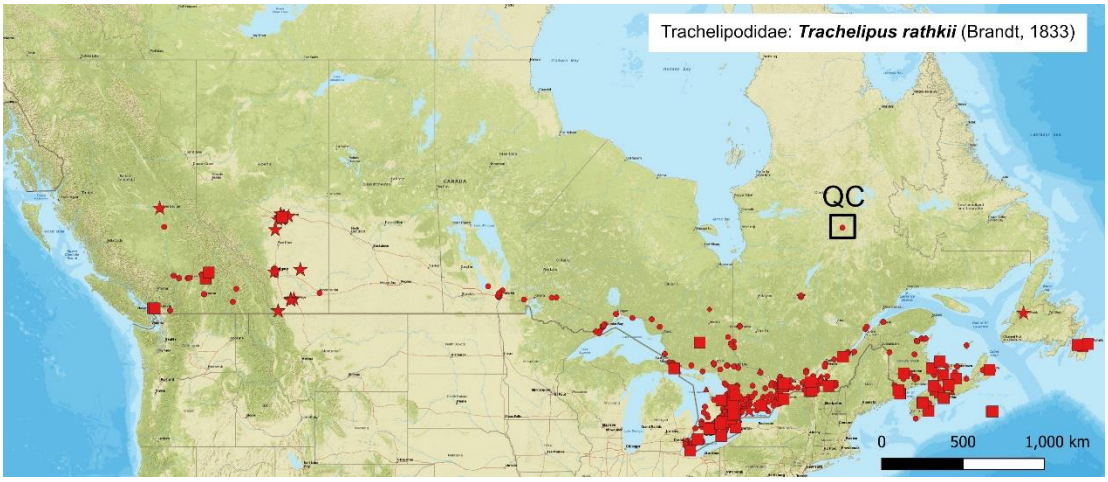

Porcellionidae: *Porcellio laevis* Latreille, 1804
?
0
500
1,000 km

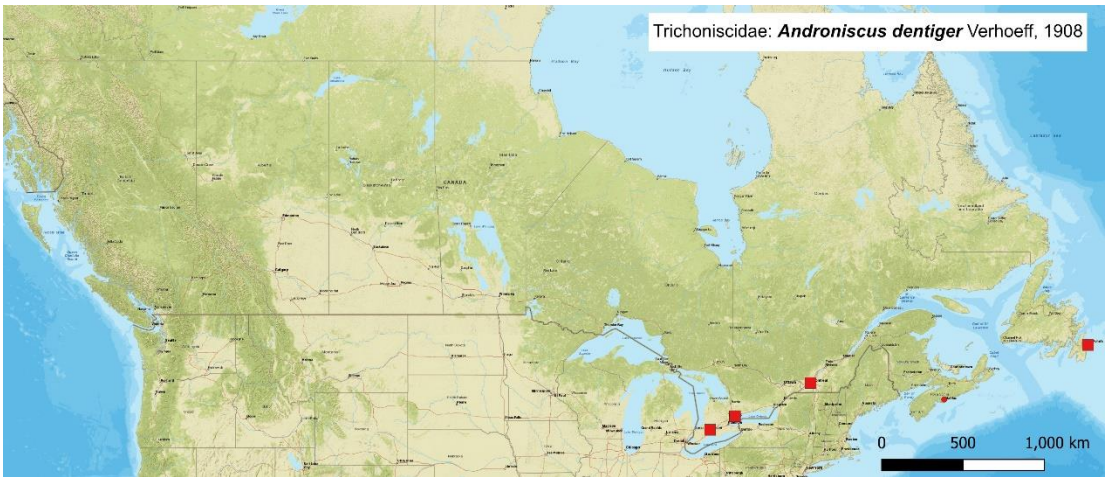

Porcellionidae: *Porcellio scaber* Latreille, 1804
BC
ON
NL
0
500
1,000 km

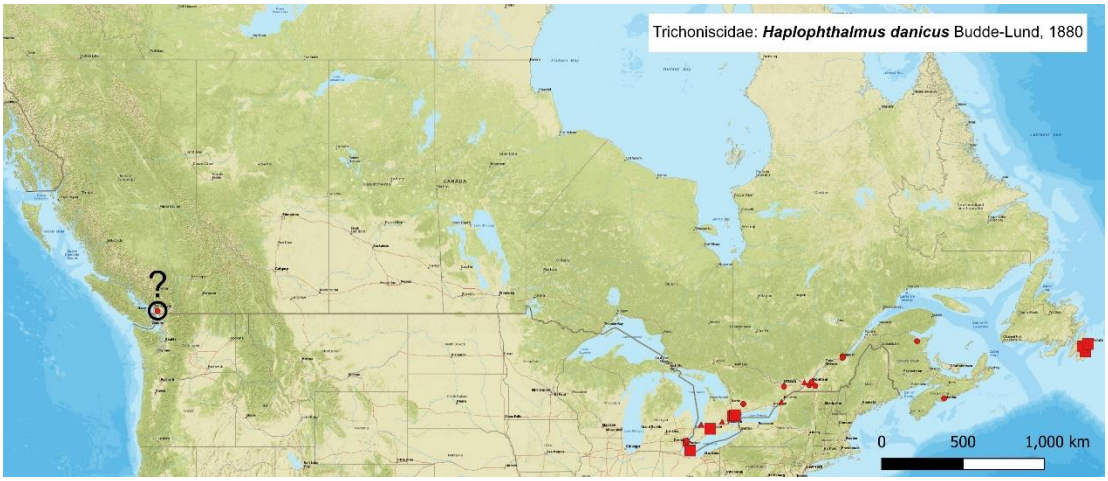

Porcellionidae: *Porcellio spinicornis* Say, 1818
0
500
1,000 km


Porcellionidae: ***Porcellionides pruinosus*** (Brandt, 1833)#
BC
0
500
1,000 km

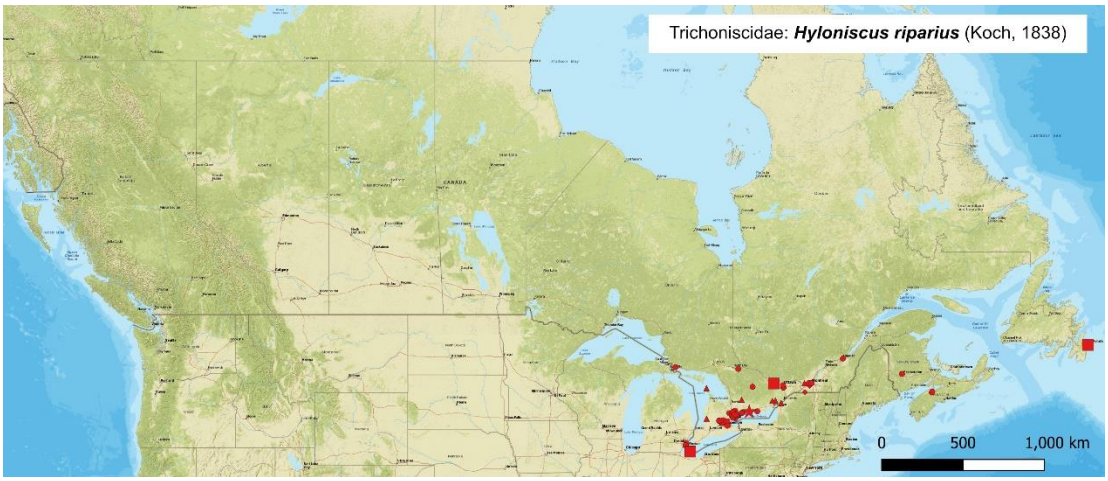

Trachelipodidae: ***Nagurus cristatus*** (Dollfus, 1889)
0
500
1,000 km


Trachelipodidae: ***Trachelipus rathkii*** (Brandt, 1833)
QC
0
500
1,000 km


Trichoniscidae: *Androniscus dentiger* Verhoeff, 1908
0
500
1,000 km

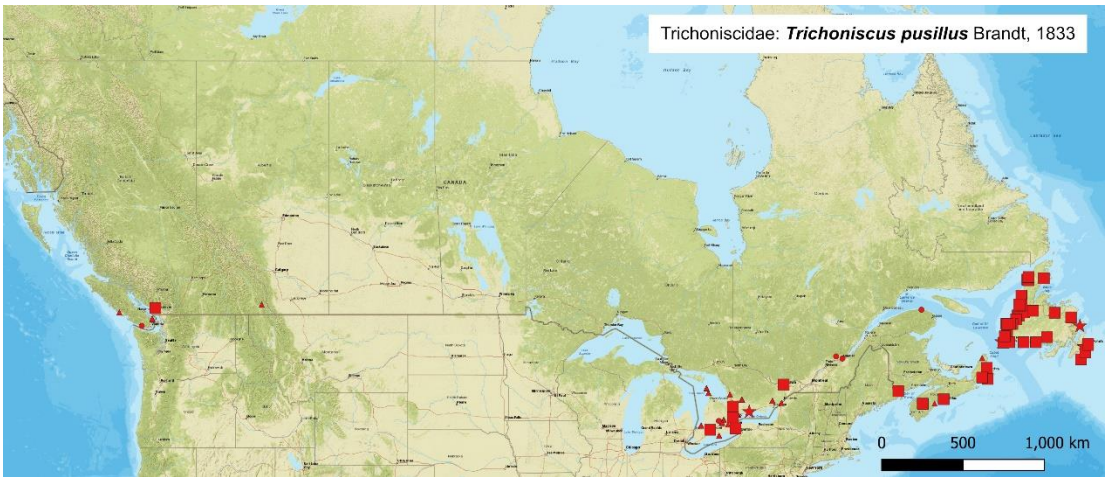

Trichoniscidae: *Haplophthalmus danicus* Budde-Lund, 1880
?
0
500
1,000 km


Trichoniscidae: *Haplophthalmus mengii* (Zaddach, 1844)
?
0
500
1,000 km


Trichoniscidae: *Hyloniscus riparius* (Koch, 1838)
0
500
1,000 km


Trichoniscidae: *Trichoniscoides sarsi* Patience, 1908
NL
0
500
1,000 km


Trichoniscidae: *Trichoniscus provisorius* Racovitza, 1908
0
500
1,000 km


Trichoniscidae: *Trichoniscus pusillus* Brandt, 1833
0
500
1,000 km


Trichoniscidae: *Trichoniscus pygmaeus* Sars, 1898
0
500
1,000 km

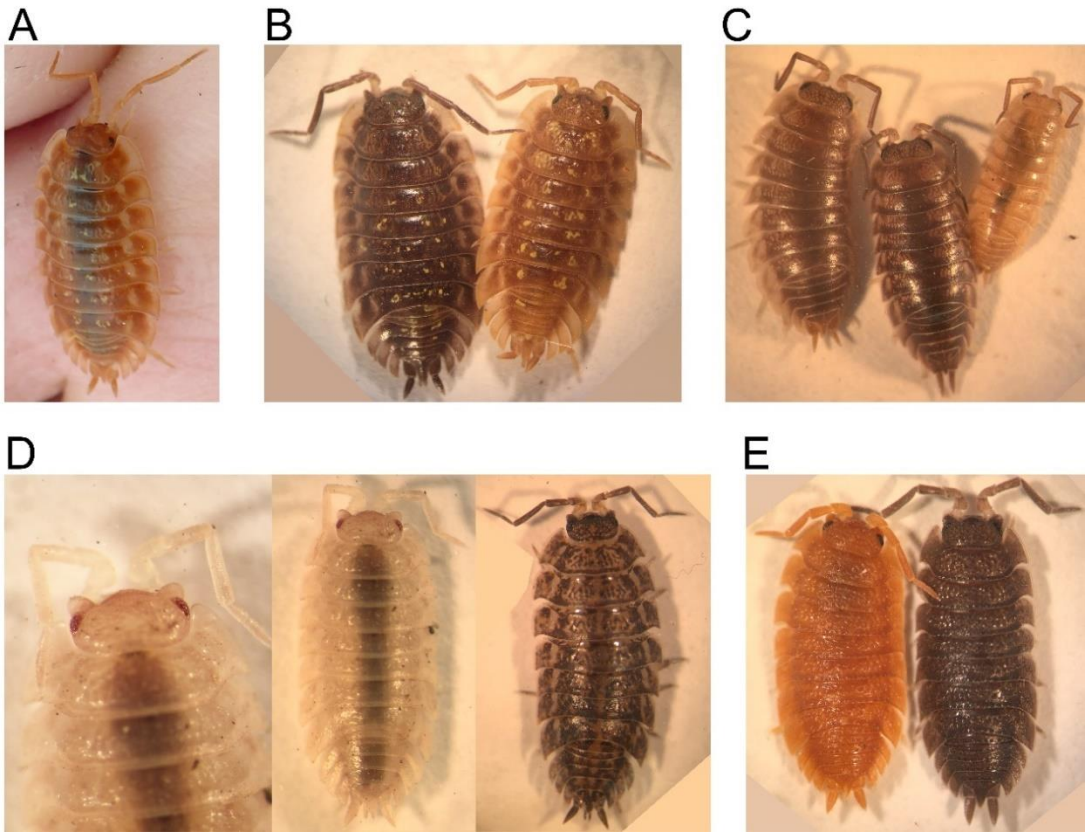
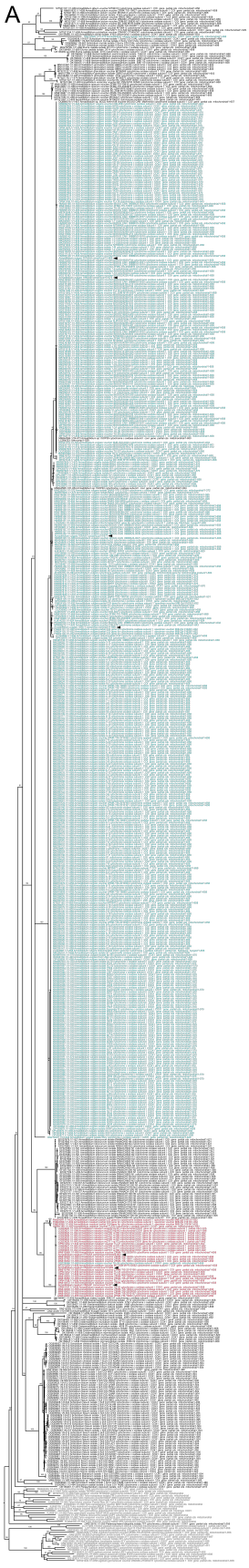
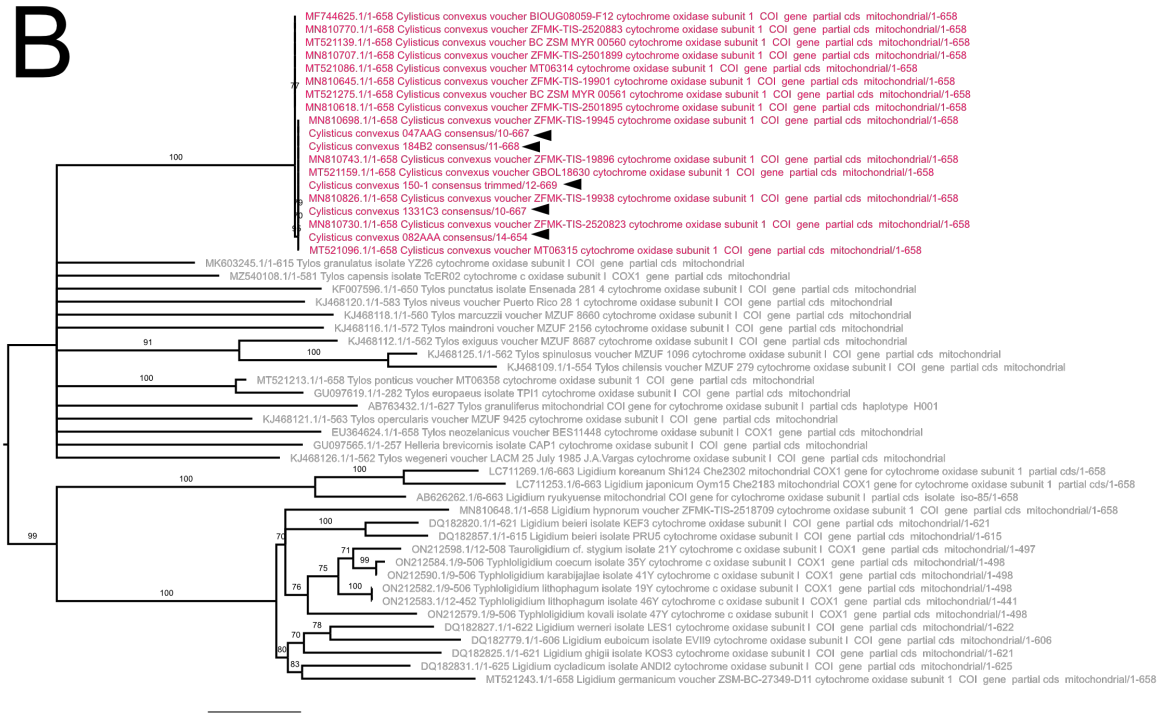


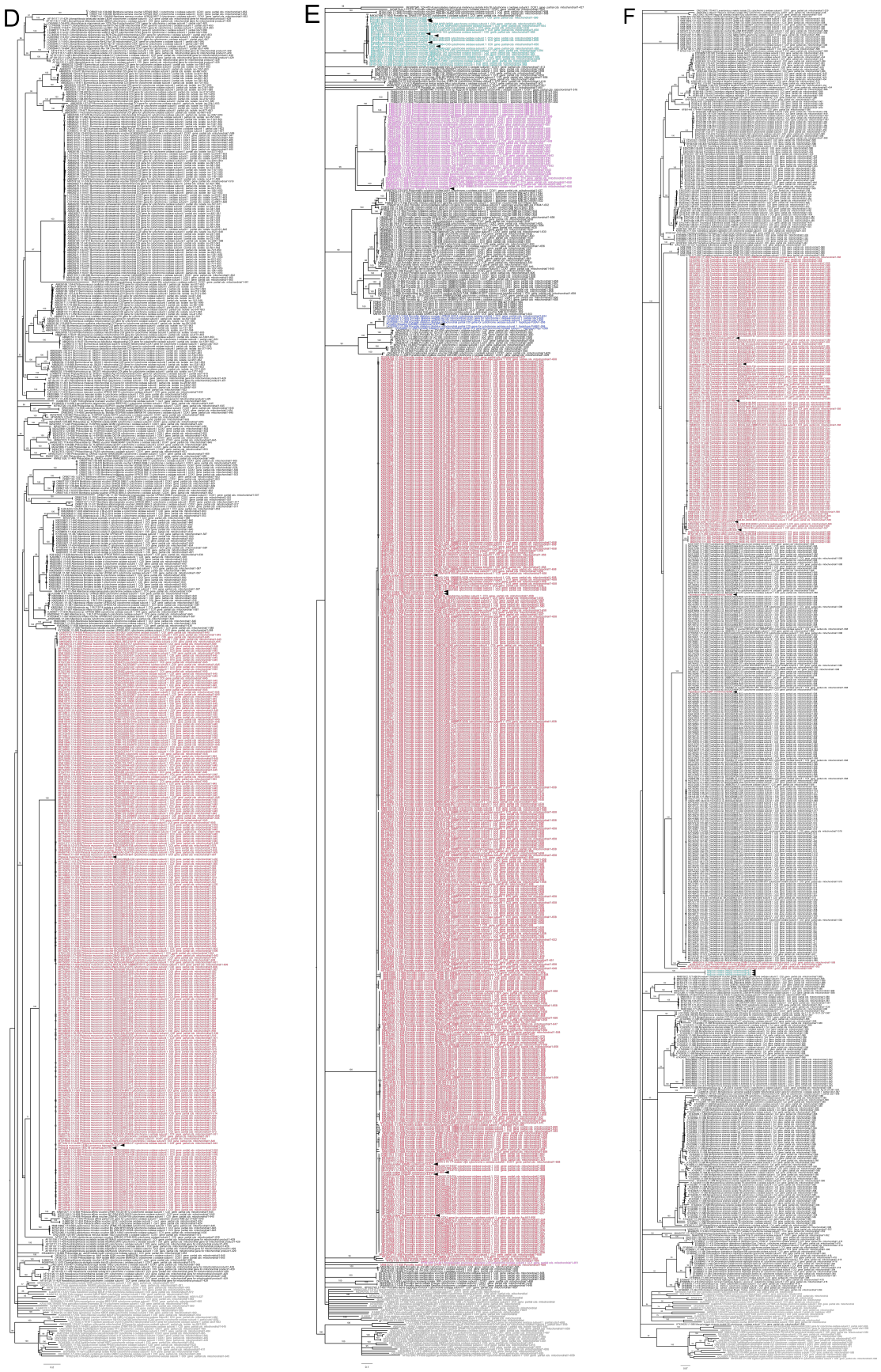
Figure A7: Sowbugs with unusual pigmentation collected from Canada in this study. A: Bright orange *Oniscus asellus* from Prince George, British Columbia; B: Grey *Oniscus asellus* from Vancouver, British Columbia (left) with a dull orange individual from the same population (right); C: Light brown, dark brown, and pale orange *Cylisticus convexus* from the Biological Sciences Greenhouse, University of Alberta; D: Depigmented *Trachelipus rathkii* with red eyes from Edmonton, Alberta, with a pigmented individual from the same population; E: Bright orange *Porcellio scaber* from Bamfield, British Columbia (left) with a grey individual from the same population (right). Images have been edited to remove debris and color balance and brightness have been adjusted to reflect the natural appearance of the sowbugs.

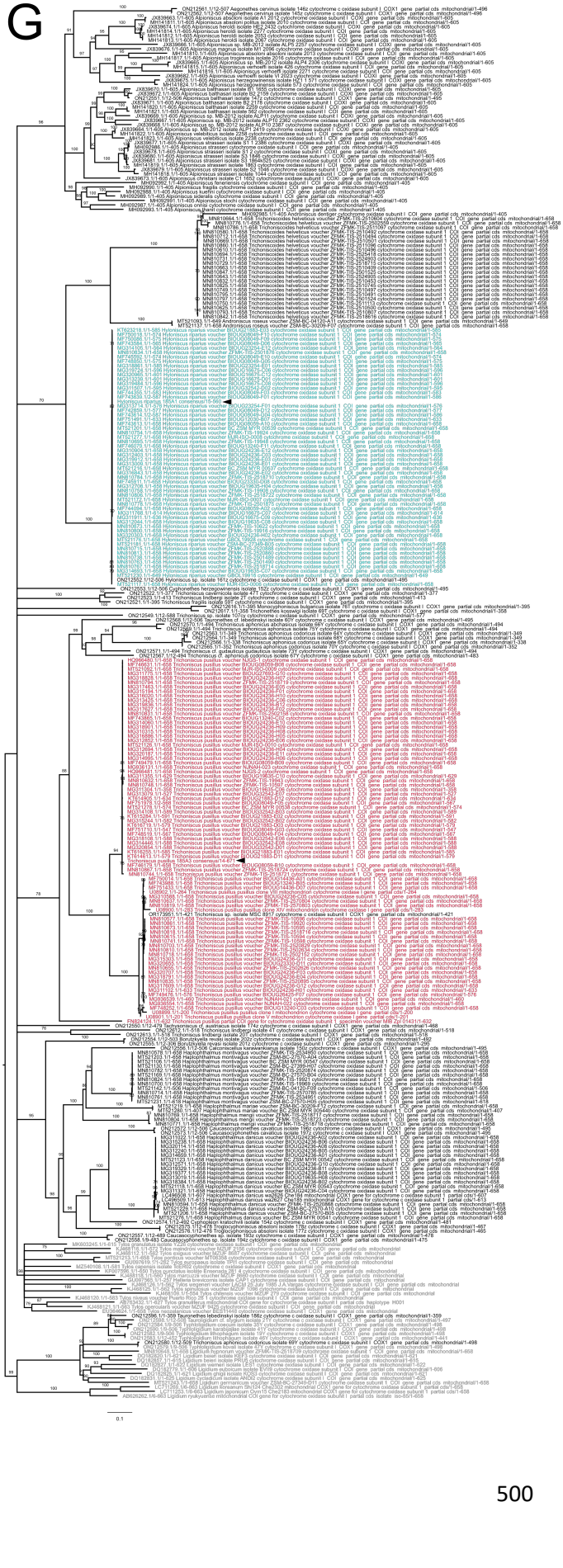
Figure A8 (following pages)**:** Maximum-likelihood phylogenies of seven sowbug families built with COI barcode sequences. See Fig. 2.3a-g for trees with the large clades condensed. Black arrows indicate sequences obtained in this study. Outgroup clades (Tylidae and Ligiidae, excluding *Ligia*) are colored grey; clades belonging to a species that had at least one COI barcode produced in this study are colored by species. Numbers above nodes show ultrafast bootstrap support. Nodes with <70% ultrafast bootstrap support are collapsed. In the phylogeny for Trachelipodidae, *Nagurus cristatus* sequences form a polytomy with Trachelipodidae and Tylidae. Please note that the inclusion of GenBank sequences in each family reflects the GenBank taxonomic classification of these genera, and may not be in accordance with currently-accepted taxonomy. A: Armadillidiidae; B: Cylisticidae; C: Oniscidae; D: Philosciidae; E: Porcellionidae; F: Trachelipodidae; G: Trichoniscidae.


A


B
MF744625.1/1-658 Cylisticus convexus voucher BIOUG08059-F12 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810770.1/1-658 Cylisticus convexus voucher ZFMK-TIS-2520883 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521139.1/1-658 Cylisticus convexus voucher BC ZSM MYR 00560 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810707.1/1-658 Cylisticus convexus voucher ZFMK-TIS-2501899 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521086.1/1-658 Cylisticus convexus voucher MT06314 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810645.1/1-658 Cylisticus convexus voucher ZFMK-TIS-19901 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MT521275.1/1-658 Cylisticus convexus voucher BC ZSM MYR 00561 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810618.1/1-658 Cylisticus convexus voucher ZFMK-TIS-2501895 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
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Cylisticus convexus 047AAG consensus/10-667
Cylisticus convexus 184B2 consensus/11-668
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MT521159.1/1-658 Cylisticus convexus voucher GBOL18630 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
Cylisticus convexus 150-1 consensus trimmed/12-669
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Cylisticus convexus 1331C3 consensus/10-667
MN810730.1/1-658 Cylisticus convexus voucher ZFMK-TIS-2520823 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
Cylisticus convexus 082AAA consensus/14-654
MT521096.1/1-658 Cylisticus convexus voucher MT06315 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MK603245.1/1-615 Tylos granulatus isolate YZ26 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MZ540108.1/1-581 Tylos capensis isolate TcER02 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial
KF007596.1/1-650 Tylos punctatus isolate Ensenada 281 4 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468120.1/1-583 Tylos niveus voucher Puerto Rico 28 1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468118.1/1-560 Tylos marcuzzii voucher MZUF 8660 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468116.1/1-572 Tylos maindroni voucher MZUF 2156 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468112.1/1-562 Tylos exiguus voucher MZUF 8687 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468125.1/1-562 Tylos spinulosus voucher MZUF 1096 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468109.1/1-554 Tylos chilensis voucher MZUF 279 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MT521213.1/1-658 Tylos ponticus voucher MT06358 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial
GU097619.1/1-282 Tylos europaeus isolate TPI1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
AB763432.1/1-627 Tylos granuliferus mitochondrial COI gene for cytochrome oxidase subunit I partial cds haplotype H001
KJ468121.1/1-563 Tylos opercularis voucher MZUF 9425 cytochrome oxidase subunit I COI gene partial cds mitochondrial
EU364624.1/1-658 Tylos neozelanicus voucher BES11448 cytochrome oxidase subunit I COX1 gene partial cds mitochondrial
GU097565.1/1-257 Helleria brevicornis isolate CAP1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468126.1/1-562 Tylos wegeneri voucher LACM 25 July 1985 J.A.Vargas cytochrome oxidase subunit I COI gene partial cds mitochondrial
LC711269.1/6-663 Ligidium koreanum Shi124 Che2302 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
LC711253.1/6-663 Ligidium japonicum Oym15 Che2183 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
AB626262.1/6-663 Ligidium ryukyuense mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate iso-85/1-658
MN810648.1/1-658 Ligidium hypnorum voucher ZFMK-TIS-2518709 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
DQ182820.1/1-621 Ligidium beieri isolate KEF3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182857.1/1-615 Ligidium beieri isolate PRU5 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-615
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ON212584.1/9-506 Typhloligidium coecum isolate 35Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212590.1/9-506 Typhloligidium karabijajlae isolate 41Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212582.1/9-506 Typhloligidium lithophagum isolate 19Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212583.1/12-452 Typhloligidium lithophagum isolate 46Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-441
ON212579.1/9-506 Typhloligidium kovali isolate 47Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
DQ182827.1/1-622 Ligidium werneri isolate LES1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-622
DQ182779.1/1-606 Ligidium eubeicum isolate EVII9 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-606
DQ182825.1/1-621 Ligidium ghigii isolate KOS3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182831.1/1-625 Ligidium cycladicum isolate ANDI2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-625
MT521243.1/1-658 Ligidium germanicum voucher ZSM-BC-27349-D11 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
0.2


C
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MN810582.1/1-658 Oniscus asellus voucher ZFMK-TIS-2510832 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
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MN810719.1/1-658 Oniscus asellus voucher ZFMK-TIS-19934 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
KY554644.1 Oniscus_asellus_isolate_13_cytochrome_oxidase_subunit_I_(COI)_gene,_partial_cds;_mitochondrial
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MT521290.1/1-658 Oniscus asellus voucher MT06438 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810690.1/1-658 Oniscus asellus voucher ZFMK-TIS-2525671 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
MN810777.1/1-658 Oniscus asellus voucher ZFMK-TIS-2525738 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
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Oniscus asellus 1082A3 consensus/11-577
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ON212544.1/9-506 Rodoniscus anophthalmus isolate 203z cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
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KJ668156.1/1-418 Sardoniscus verhoeffi voucher LB122 cytochrome oxidase subunit 1 cox1 gene partial cds mitochondrial/1-418
MK603245.1/1-615 Tylos granulatus isolate YZ26 cytochrome oxidase subunit I COI gene partial cds mitochondrial
MZ540108.1/1-581 Tylos capensis isolate TcER02 cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial
AB763432.1/1-627 Tylos granuliferus mitochondrial COI gene for cytochrome oxidase subunit I partial cds haplotype H001
KJ468121.1/1-563 Tylos opercularis voucher MZUF 9425 cytochrome oxidase subunit I COI gene partial cds mitochondrial
EU364624.1/1-658 Tylos neozelanicus voucher BES11448 cytochrome oxidase subunit I COX1 gene partial cds mitochondrial
MT521213.1/1-658 Tylos ponticus voucher MT06358 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial
GU097619.1/1-282 Tylos europaeus isolate TPI1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468126.1/1-562 Tylos wegeneri voucher LACM 25 July 1985 J.A.Vargas cytochrome oxidase subunit I COI gene partial cds mitochondrial
KF007596.1/1-650 Tylos punctatus isolate Ensenada 281 4 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468120.1/1-583 Tylos niveus voucher Puerto Rico 28 1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468118.1/1-560 Tylos marcuzzii voucher MZUF 8660 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468116.1/1-572 Tylos maindroni voucher MZUF 2156 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468112.1/1-562 Tylos exiguus voucher MZUF 8687 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468125.1/1-562 Tylos spinulosus voucher MZUF 1096 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KJ468109.1/1-554 Tylos chilensis voucher MZUF 279 cytochrome oxidase subunit I COI gene partial cds mitochondrial
GU097565.1/1-257 Helleria brevicornis isolate CAP1 cytochrome oxidase subunit I COI gene partial cds mitochondrial
KU955991.1/1-631 Oniscus asellus isolate 69W1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-631
KU955992.1/1-630 Oniscus asellus isolate 69W2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-630
MT521243.1/1-658 Ligidium germanicum voucher ZSM-BC-27349-D11 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
DQ182831.1/1-625 Ligidium cycladicum isolate ANDI2 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-625
DQ182827.1/1-622 Ligidium werneri isolate LES1 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-622
DQ182779.1/1-606 Ligidium eubeicum isolate EVII9 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-606
DQ182825.1/1-621 Ligidium ghigii isolate KOS3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
MN810648.1/1-658 Ligidium hypnorum voucher ZFMK-TIS-2518709 cytochrome oxidase subunit 1 COI gene partial cds mitochondrial/1-658
DQ182820.1/1-621 Ligidium beieri isolate KEF3 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-621
DQ182857.1/1-615 Ligidium beieri isolate PRU5 cytochrome oxidase subunit I COI gene partial cds mitochondrial/1-615
ON212598.1/12-508 Tauroligidium cf. stygium isolate 21Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-497
ON212584.1/9-506 Typhloligidium coecum isolate 35Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212590.1/9-506 Typhloligidium karabijajlae isolate 41Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212582.1/9-506 Typhloligidium lithophagum isolate 19Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
ON212583.1/12-452 Typhloligidium lithophagum isolate 46Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-441
ON212579.1/9-506 Typhloligidium kovali isolate 47Y cytochrome c oxidase subunit I COX1 gene partial cds mitochondrial/1-498
LC711269.1/6-663 Ligidium koreanum Shi124 Che2302 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
LC711253.1/6-663 Ligidium japonicum Oym15 Che2183 mitochondrial COX1 gene for cytochrome oxidase subunit 1 partial cds/1-658
AB626262.1/6-663 Ligidium ryukyuense mitochondrial COI gene for cytochrome oxidase subunit I partial cds isolate iso-85/1-658
2.0


D
E
F


G

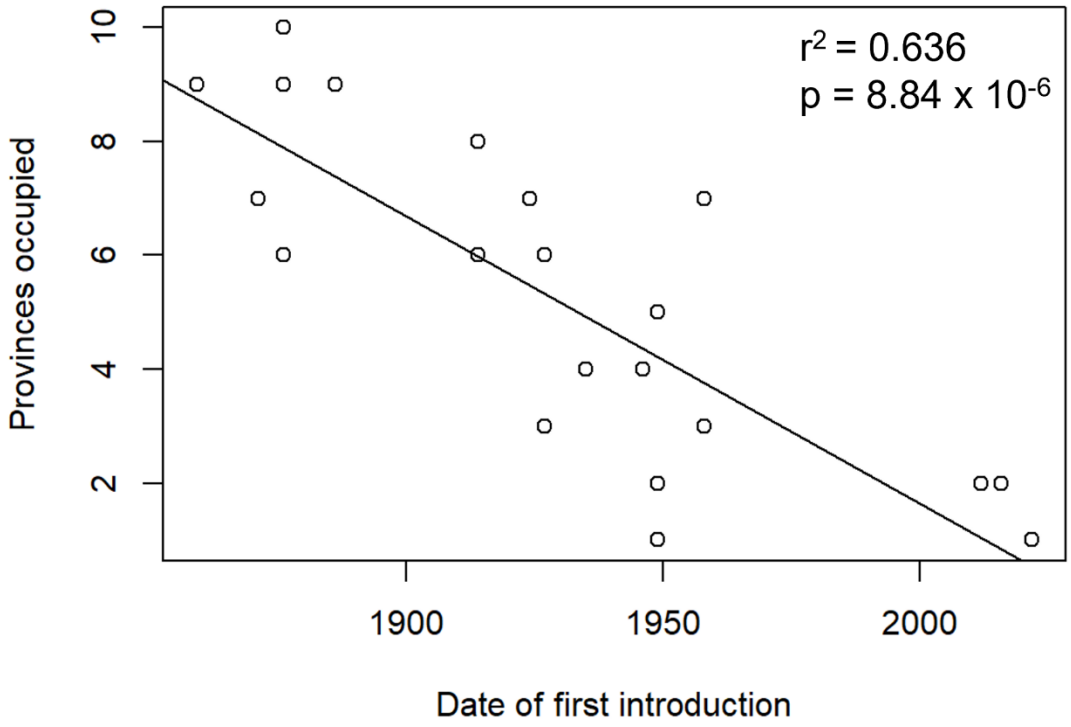


Figure A9: Simple linear regression between the number of provinces occupied and date of first record for all species of introduced sowbugs in Canada. There is a significant negative correlation between the two variables (species with more recent introduction dates tend to occupy fewer provinces).

Appendix B: Supplementary Citations for Chapter 2

BugGuide. 2023d. *Armadillidium nasatum* in Ontario. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=55219&location[]=ON [accessed 10 December 2023].

BugGuide. 2023e. *Armadillidium vulgare* in Alberta. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=94180&location[]=AB [accessed 10 December 2023].

BugGuide. 2023f. *Armadillidium vulgare* in British Columbia. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=94180&location[]=AB [accessed 10 December 2023].

BugGuide. 2023g. *Armadillidium vulgare* in Ontario. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=94180&location[]=ON [accessed 10 December 2023].

BugGuide. 2023h. *Armadillidium vulgare* in Québec. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=94180&location[]=QC [accessed 10 December 2023].

BugGuide. 2023i. *Armadillidium vulgare* in New Brunswick. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=94180&location[]=NB [accessed 10 December 2023].

BugGuide. 2023j. *Cylisticus convexus* in New Brunswick. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=92420&location[]=NB [accessed 10 December 2023].

BugGuide. 2023k. *Cylisticus convexus* in Ontario. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=92420&location[]=ON [accessed 10 December 2023].

BugGuide. 2023l. *Ligia occidentalis* in British Columbia. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=392515&location[]=BC [accessed 10 December 2023].

BugGuide. 2023m. *Ligia pallasii* in British Columbia. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=170135&location[]=BC [accessed 10 December 2023].

BugGuide. 2023n. *Ligidium elrodii* in Ontario. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=1024061&location[]=ON [accessed 10 December 2023].

BugGuide. 2023o. *Oniscus asellus* in British Columbia. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=33847&location[]=BC [accessed 10 December 2023].

BugGuide. 2023p. *Oniscus asellus* in New Brunswick. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=33847&location[]=NB [accessed 10 December 2023].

BugGuide. 2023q. *Oniscus asellus* in Newfoundland and Labrador. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=33847&location[]=NL [accessed 10 December 2023].

BugGuide. 2023r. *Oniscus asellus* in Nova Scotia. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=33847&location[]=NS [accessed 10 December 2023].

BugGuide. 2023s. *Oniscus asellus* in Ontario. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=33847&location[]=ON [accessed 10 December 2023].

BugGuide. 2023t. *Oniscus asellus* in Québec. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=33847&location[]=QC [accessed 10 December 2023].

BugGuide. 2023u. *Philoscia muscorum* in British Columbia. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=55264&location[]=BC [accessed 10 December 2023].

BugGuide. 2023v. *Philoscia muscorum* in New Brunswick. Available from https://bugguide.net/adv_search/bgsearch.php?taxon=55264&location[]=NB [accessed 10 December 2023].

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Appendix C: Supplementary Materials for Chapter 3

Table C1 (following pages): Viruses, bacteria, protists, and fungi associated with terrestrial isopods, sorted by symbiont species. See Table 3.1 for a list of metazoans associated with terrestrial isopods and for the associated references. The bacteria and fungal taxa listed here do not include all the taxa that have been recorded in association with sowbugs. Associations that are supported only by experimental infection are not included, but associations found "accidentally" occurring in lab populations of isopods are included. Taxon names are listed in their most recent form, with alternative name(s) given in the original source(s) listed below the most recent name. Most often these are synonymies, but occasionally are due to misidentifications that were noted and corrected in later literature or to misspellings. Note that the localities listed for the associations are supported by a minimum of one of the listed references, but not necessarily by all of them. References for this table are included at the bottom of the table.

VIRUSES			
Taxonomy (Symbiont)	**Host Species**	**Localities**	**References**
Nucleocytoviricota			
Megaviricetes			
Pimascovirales			
Iridoviridae			
Iridovirus	***Alloniscus balssii* (Verhoeff, 1928)**	Japan	61
This section contains records that mention blue or purple isopods but did not confirm the presence of viral particles.	***Androniscus dentiger* Verhoeff, 1908**	England	75
	***Armadillidium decorum* Brandt, 1833**	Italy	144
	***Armadillidium vulgare* (Latreille, 1804)**	The Netherlands, Japan, Republic of Türkiye, United States, Italy	58, 61, 62, 63, 64, 75, 77, 78, 79, 144, 201
	***Burmoniscus kathmandius* (Schmalfuss, 1983)** = *Burmoniscus kathmandia* (Schmalfuss, 1983)	Japan	61
	***Cylisticus convexus* (De Geer, 1778)**	United States	64
	***Haplophthalmus danicus* Budde-Lund, 1880**	The Netherlands	75
	***Haplophthalmus mengii* (Zaddach, 1844)**	The Netherlands	58, 75
	***Hyloniscus riparius* (Koch, 1838)**	The Netherlands	58, 75
	***Ligidium hypnorum* (Cuvier, 1792)**	The Netherlands, France, Russia, Czech Republic and/or Slovakia	58, 65, 66, 67, 68, 75
	***Ligidium japonicum* Verhoeff, 1918**	Japan	61
	***Ligidium koreanum* Flasarova, 1972**	Japan	61
	***Littorophiloscia nipponensis* Nunomura, 1986**	Japan	61
	***Niambia capensis* (Dollfus, 1895)** = *Mauritaniscus littorinus* (Miller, 1936)	United States	64
	***Oniscus asellus* Linnaeus, 1758**	The Netherlands, England	58, 76
	***Philoscia affinis* Verhoeff, 1908**	Italy	144
	***Philoscia muscorum* (Scopoli, 1763)**	France, England, the Netherlands	69, 70, 71, 75
	***Porcellio dilatatus* Brandt, 1831**	United States	63, 77
	***Porcellio laevis* Latreille, 1804**	United States	64, 80
	***Porcellio scaber* Latreille, 1804**	The Netherlands, Japan, United States	58, 61, 64, 75, 78, 79, 80
	***Porcellio siculoccidentalis* Viglianisi, Lombardo & Caruso, 1992**	Italy	144
	***Porcellio spinicornis* Say, 1818** = *Porcellio pictus* Brandt	The Netherlands	75
	***Porcellionides pruinosus* (Brandt, 1833)**	United States	64
	***Trachelipus rathkii* (Brandt, 1833)** = *Trachelipus rathkei* (Brandt)	The Netherlands, United States	58, 64, 75
	***Trichoniscoides albidus* (Budde-Lund, 1880)**	The Netherlands	58, 75
	***Trichoniscoides helveticus* (Carl, 1908)**	The Netherlands	58, 75
	***Trichoniscus panormidensis* Montesanto, Caruso, & Lombardo, 2011**	Italy	144
	***Trichoniscus pusillus* Brandt, 1833**	Czech Republic and/or Slovakia, the Netherlands, England	71, 72, 73, 74, 75
	***Venezillo obscurus* (Budde-Lund, 1885)**	Japan	61
	Armadillidae	Japan	61

BACTERIA			
Taxonomy (Symbiont)	**Host Species**	**Localities**	**References**
Unranked taxa			
"Spirilaceae"			
	***Oniscus asellus* Linnaeus, 1758**	?	128

"Plactomycetacia"			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Acidobacteriota			
= Acidobacteria	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
Terriglobia			
= Acidobacteriia	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Actinomycetota			
= Actinobacteria	***Ligia pallasii* Brandt, 1833**	United States	56
	***Porcellio scaber* Latreille, 1804**	England, Republic of Slovenia	111, 155
Actinomycetes			
Acidimicrobiia			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Actinomycetales			
	***Porcellio scaber* Latreille, 1804**	England	111
Geodermatophilales			
Geodermatophilaceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Kitasatosporales			
Streptomycetaceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
***Streptomyces humidus* Nakazawa & Shibata, 1956**	***Protracheoniscus politus* (Koch, 1841)** = *Protracheoniscus amoneus* Koch, 1841	?	139
***Streptomyces moderatus* Reusser, 1965**	***Protracheoniscus politus* (Koch, 1841)** = *Protracheoniscus amoneus* Koch, 1841	?	139
***Streptomyces nodosus* Trejo, 1961**	***Protracheoniscus politus* (Koch, 1841)** = *Protracheoniscus amoneus* Koch, 1841	?	139
***Streptomyces pluricolorescens* Okami & Umezawa, 1961**	***Protracheoniscus politus* (Koch, 1841)** = *Protracheoniscus amoneus* Koch, 1841	?	139
***Streptomyces spadicis* Bromer *et al.*, 1969**	***Protracheoniscus politus* (Koch, 1841)** = *Protracheoniscus amoneus* Koch, 1841	?	139
Micrococcales			
Brevibacteriaceae			
***Brevibacterium* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Jonesiaceae			
= Sanguibacteraceae	***Oniscus asellus* Linnaeus, 1758**	England	111
Microbacteriaceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
***Agromyces* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
***Microbacterium* sp.**	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Micrococcaceae			
	***Oniscus asellus* Linnaeus, 1758**	?	128
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
***Arthrobacter* sp.**	***Oniscus asellus* Linnaeus, 1758**	?	128
	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Promicromonosporaceae			
***Cellulosimicrobium* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Micromonosporales			
Micromonosporaceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Mycobacteriales			
Corynebacteriaceae			
	***Oniscus asellus* Linnaeus, 1758**	?	128

***Corynebacterium* sp.**	***Oniscus asellus* Linnaeus, 1758**	England	133
Mycobacteriaceae			
	***Oniscus asellus* Linnaeus, 1758**	?	128
Nocardiaceae			
***Rhodococcus* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Propionibacteriales			
Nocardioidaceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Pseudonocardiales			
Pseudonocardiaceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Rubrobacteria			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Thermoleophilia			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Coriobacteriia			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Bacillota			
Bacilli			
Caryophanales			
Bacillaceae			
***Bacillus cereus* Frankland & Frankland, 1887**	***Armadillidium* sp.**	United States	132
	***Porcellio scaber* Latreille, 1804**	United States	131, 132
***Bacillus* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	130, 155
***Exiguobacterium* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Caryophanaceae			
***Caryophanon* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
***Planomicrobium* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Listeriaceae			
***Listeria* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
***Planococcus* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Paenibacillaceae			
***Paenibacillus* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Staphylococcaceae			
***Staphylococcus succinus* Lambert *et al.*, 1998**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Lactobacillales			
Enterococcaceae			
***Enterococcus faecium* (Orla-Jensen, 1919) Schleifer & Kilpper-Bälz, 1984**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	130
***Enterococcus* sp.** = *Enterococococcus* [sic] sp.	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	130
Clostridia			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Eubacteriales			
Peptococcaceae			
***Desulfotomaculum ruminis* Campbell & Postgate, 1965** = *Desulphotomaculum* [sic] *ruminis*	***Porcellio scaber* Latreille, 1804**	?	135, 136
Erysipelotrichia			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Bacteroidota			
= Bacteriodetes	***Ligia pallasii* Brandt, 1833**	United States	56
	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England, Republic of Slovenia	111, 155

Bacteroidia			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Bacteroidales			
Bacteroidaceae			
***Bacteroides* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	130
Cytophagia			
Cytophagales			
Cytophagaceae			
***Cytophaga* sp.**	***Armadillidium vulgare* (Latreille, 1804)**	England	134
	***Oniscus asellus* Linnaeus, 1758**	England	134
	***Porcellio scaber* Latreille, 1804**	England, Republic of Slovenia	134, 155
Flavobacteriia			
	***Armadillidium vulgare* (Latreille, 1804)**	France	156
Flavobacteriales			
Flavobacteriaceae			
	***Ligia pallasii* Brandt, 1833**	United States	56
	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
	***Porcellio scaber* Latreille, 1804**	England	111
***Flavobacterium* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
	***Trachelipus rathkii* (Brandt, 1833)** = *Tracheoniscus rathkei* (Brandt)	?	138
***Lacinutrix* sp.**	***Ligia pallasii* Brandt, 1833**	United States	56
Sphingobacteriia			
Sphingobacteriales			
Sphingobacteriaceae			
***Sphingobacterium faecium* Takeuchi & Yokota, 1993**	***Oniscus asellus* Linnaeus, 1758**	England	111
***Sphingobacterium kitahiroshimense* Matsuyama *et al.*, 2008**	***Oniscus asellus* Linnaeus, 1758**	England	111
Chlamydiota = Chlamydiae	***Oniscus asellus* Linnaeus, 1758**	England	111
Chlamydiia			
Chlamydiales			
Candidatus Rhabdochlamydiaceae Horn, 2010			
***Candidatus* Rhabdochlamydia porcellionis Kostanjšek *et al.*, 2004** = *Chlamydia isopodii* Shay *et al.*, 1985	***Porcellio scaber* Latreille, 1804**	?	23, 47, 50
Chloroflexota = Chloroflexi	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
Anaerolineae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Chloroflexia			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Dehalococcoidia			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Ktedonobacteria			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Cyanobacteriota = Cyanobacteria	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
Cyanophyceae = Oxyphotobacteria			

	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Candidatus Melainabacteria Soo *et al.*, 2014			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Deinococcota			
= Deinococcus	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
Candidatus Dependentiae Yeoh *et al.*, 2016			
Candidatus Babeliae Yeoh *et al.*, 2016			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Fibrobacterota			
Fibrobacteria			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Fusobacteriota			
= Fusobacteria	***Oniscus asellus* Linnaeus, 1758**	England	111
Gemmatimonadota			
Gemmatimonadetes			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Longimicrobiia			
=Longimicrobia	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Candidatus Gracilibacteria Rinke *et al.*, 2013			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Candidatus Melainabacteria Di Rienzi *et al.*, 2013			
Candidatus Sericytochromatia Soo *et al.*, 2017			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Mycoplasmatota			
= Tenericutes			
Mollicutes			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia, England	111, 130, 136
***Candidatus* Bacilliplasma Kostanjšek *et al.*, 2007**	***Armadillidium vulgare* (Latreille, 1804)**	France	156
	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia, Republic of Austria	147
***Candidatus* Hepatoplasma Wang *et al.*, 2004**	***Alloniscus perconvexus* Dana, 1854**	Canada	54
	***Armadillidium vulgare* (Latreille, 1804)**	Federal Republic of Germany	54
	***Ligia oceanica* (Linnaeus, 1767)**	Federal Republic of Germany	54
	***Oniscus asellus* Linnaeus, 1758**	England, Federal Republic of Germany	54, 111
	***Philoscia muscorum* (Scopoli, 1763)**	Federal Republic of Germany	54
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
	***Porcellio scaber* Latreille, 1804**	England, Federal Republic of Germany	54, 111
	***Trichoniscus pusillus* Brandt, 1833**	Federal Republic of Germany	54
	***Tylos europaeus* Arcangeli, 1938**	Italy	54
***Candidatus* Hepatoplasma crinochetorum Wang *et al.*, 2004**	***Alloniscus perconvexus* Dana, 1854**	Canada	55
	***Armadillidium vulgare* (Latreille, 1804)**	France, Federal Republic of Germany	55, 156
	***Oniscus asellus* Linnaeus, 1758**	France, Federal Republic of Germany	55
	***Philoscia muscorum* (Scopoli, 1763)**	Federal Republic of Germany	55
	***Porcellio scaber* Latreille, 1804**	Canada, Federal Republic of Germany	52, 55
	***Trachelipus rathkii* (Brandt, 1833)**	Federal Republic of Germany	55
Entomoplasmatales			
	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
Nitrospirota			
Nitrospiria			
= Nitrospira	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148

Patescibacteria			
Microgenomatia			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Planctomycetota			
= Planctomycetes	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
Planctomycetia			
Planctomycetales			
Planctomycetaceae	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Phycisphaerae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Pseudomonadota			
Alphaproteobacteria			
	***Armadillidium vulgare* (Latreille, 1804)**	France	156
	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Holosporales			
Candidatus Hepatincolaceae Szokoli *et al.*, 2016			
***Candidatus* Hepatincola Wang *et al.*, 2004**	***Armadillidium vulgare* (Latreille, 1804)**	Federal Republic of Germany	54
	***Oniscus asellus* Linnaeus, 1758**	England, Federal Republic of Germany	54, 111
	***Philoscia muscorum* (Scopoli, 1763)**	Federal Republic of Germany	54
	***Porcellio scaber* Latreille, 1804**	Federal Republic of Germany	54
***Candidatus* Hepatincola porcellionum Wang *et al.*, 2004**	***Armadillidium vulgare* (Latreille, 1804)**	France	156
	***Oniscus asellus* Linnaeus, 1758**	Federal Republic of Germany	55
	***Porcellio scaber* Latreille, 1804**	Canada, Federal Republic of Germany	53, 55
	***Trachelipus rathkii* (Brandt, 1833)**	Federal Republic of Germany	55
Hyphomicrobiales			
Beijerinckiaceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Brucellaceae			
***Brucella anthropi* (Holmes *et al.*, 1988) Hördt *et al.*, 2020**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
= *Ochrobactrum anthropi* Holmes *et al.*, 1988			
Phyllobacteriaceae			
***Mesorhizobium* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Rhizobiaceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
***Rhizobium* sp. / *Agrobacterium* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Xanthobacteraceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Rhodobacterales			
Paracoccaceae			
= Rhodobacteraceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
	***Porcellio scaber* Latreille, 1804**	England	111
***Paracoccus* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	126, 155
Roseobacteraceae			
***Roseobacter* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Rickettsiales			
	***Oniscus asellus* Linnaeus, 1758**	England	111
Ehrlichiaceae			
= Anaplasmataceae	***Oniscus asellus* Linnaeus, 1758**	England	111
***Wolbachia pipientis* Hertig 1936**	***Armadillidium granulatum* Brandt, 1833**	Republic of Tunisia	86

	***Armadillidium pallidum* Verhoeff, 1907** = *Armadillidium pelagicum* Arcangeli, 1957	Republic of Tunisia	86
	***Armadillidium sulcatum* Milne-Edwards, 1840**	Republic of Tunisia	86
	***Armadillidium vulgare* (Latreille, 1804)**	France	156
	***Cubaris murina* Brandt, 1833**	France	86
	***Hemilepistus reaumuri* (Milne Edwards, 1840)**	Republic of Tunisia	86
	***Platyarthrus hoffmannseggii* Brandt, 1833**	France	86
	***Porcellio albinus* Budde-Lund, 1885**	Republic of Tunisia	86
	***Porcellio buddelundi* Simon, 1885**	Republic of Tunisia	86
	***Porcellio lamellatus* Budde-Lund, 1885**	Republic of Tunisia	86
	***Porcellio variabilis* Lucas, 1849**	Republic of Tunisia	86
	***Porcellionides cingendus* (Kinahan, 1857)**	France	86
	***Trachelipus rathkii* (Brandt, 1833)**	France	86
***Wolbachia* sp.**	***Armadillidium vulgare* (Latreille, 1804)**	France	146
	***Porcellio dilatatus* Brandt, 1831**	France, Portuguese Republic	146, 148
Sphingomonadales			
Sphingomonadaceae			
***Sphingomonas* sp.**	***Armadillidium vulgare* (Latreille, 1804)**	France	156
Betaproteobacteria			
Burkholderiales			
Alcaligenaceae			
***Achromobacter* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
***Alcaligenes* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Burkholderiaceae			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
***Ralstonia pickettii* (Ralston *et al.*, 1973) Yabuuchi *et al.*, 1996**	***Ligia occidentalis* (Dana, 1853)**	United States	56
	***Ligia pallasii* Brandt, 1833**	United States	56
Comamonadaceae			
	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
***Delftia acidovorans* (den Dooren de Jong, 1926) Wen *et al.*, 1999**	***Oniscus asellus* Linnaeus, 1758**	England	111
Neisseriales			
Chromobacteriaceae			
***Chromobacterium violaceum* Bergonzini 1880** = *Chrmombacterium* [sic] *violaceum*	***Oniscus asellus* Linnaeus, 1758**	?	128
Neisseriaceae			
***Neisseria* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	130
Deltaproteobacteria			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Gammaproteobacteria			
	***Armadillidium vulgare* (Latreille, 1804)**	France	156
	***Ligia pallasii* Brandt, 1833**	United States	56
	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Aeromonadales			
Aeromonadaceae			
***Aeromonas* sp.**	***Porcellio scaber* Latreille, 1804**	?	127
Alteromonadales			
Shewanellaceae			
	***Porcellio scaber* Latreille, 1804**	England	111
***Shewanella* sp.**	***Armadillidium vulgare* (Latreille, 1804)**	France	156
= *Shevanella* [sic] sp.	***Porcellio scaber* Latreille, 1804**	?	126
Enterobacterales			
Enterobacteriaceae			

	***Oniscus asellus* Linnaeus, 1758**	?	128
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
***Citrobacter freundii* (Braak, 1928) Werkman & Gillen, 1932**	***Oniscus asellus* Linnaeus, 1758**	?	127
	***Porcellio scaber* Latreille, 1804**	?	127
***Enterobacter agglomerans* (Beijerinck, 1888) Ewing & Fife, 1972**	***Oniscus asellus* Linnaeus, 1758**	?	137
***Enterobacter intermedius* Izard *et al.*, 1980**	***Porcellio scaber* Latreille, 1804**	?	127
***Klebsiella pneumoniae* (Schroeter, 1886) Trevisan, 1887**	***Porcellio scaber* Latreille, 1804**	?	127
	***Oniscus asellus* Linnaeus, 1758**	England	133
	***Porcellio scaber* Latreille, 1804**	?	127
***Klebsiella* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
***Kluyvera* sp.**	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
***Plesiomonas* sp.**	***Oniscus asellus* Linnaeus, 1758**	?	137
Legionellales			
Coxiellaceae			
	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
***Rickettsiella grylli* (ex Vago & Martoja, 1963) Weiss *et al.*, 1984**	***Armadillidium vulgare* (Latreille, 1804)**	United States, France	145, 156
	***Porcellio dilatatus* Brandt, 1831**	United States	145
	***Porcellio scaber* Latreille, 1804**	England	22
***Rickettsiella popilliae* (Dutky & Gooden, 1952) Philip, 1956**	***Armadillidium vulgare* (Latreille, 1804)**	France	48, 110, 156
= *Rickettsiella armadillidii* Frutos *et al.*, 1994	***Helleria brevicornis* Ebner, 1868**	France	48
***Candidatus* Rickettsiella isopodorum Kleespies *et al.*, 2014**	***Philoscia muscorum* (Scopoli, 1763)**	Spain	48
	***Armadillidium vulgare* (Latreille, 1804)**	United States	49
***Rickettsiella* sp.**	***Porcellio scaber* Latreille, 1804**	Federal Republic of Germany	49
	***Armadillidium nasatum* Budde-Lund, 1885**	?	158
	***Armadillidium granulatum* Brandt, 1833**	?	158
	***Armadillidium vulgare* (Latreille, 1804)**	?	158
	***Atlantoscia floridana* (Van Name, 1940)**	?	157
	***Eluma caelata* (Miers, 1877)**	?	158
	= *Eluma purpurascens* Budde-Lund, 1885		
	***Oniscus asellus* Linnaeus, 1758**	England	111, 158
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
	***Porcellio gallicus* Dollfus, 1904**	?	158
	***Porcellio laevis* Latreille, 1804**	?	158
	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	51
Lysobacterales			
Lysobacteraceae			
***Stenotrophomonas pavanii* Ramos *et al.*, 2011**	***Oniscus asellus* Linnaeus, 1758**	England	111
***Stenotrophomonas rhizophila* Wolf *et al.*, 2002**	***Oniscus asellus* Linnaeus, 1758**	England	111
***Xanthomonas maltophilia* (Hugh, 1981) Swings *et al.*, 1983**	***Oniscus asellus* Linnaeus, 1758**	England	111
= *Stenotrophomonas maltophilia* (Hugh, 1981) Palleroni & Bradbury, 1993			
***Xanthomonas* sp. / *Pseudoxanthomonas* sp.**	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Oceanospirillales			
Halomonadaceae			
***Cobetia* sp.**	***Ligia pallasii* Brandt, 1833**	United States	56
***Halomonas* sp.**	***Armadillidium vulgare* (Latreille, 1804)**	France	156
	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
Pseudomonadales			
Moraxellaceae			

***Acinetobacter calcoaceticus* (Beijerinck, 1911) Baumann *et al.*, 1968**	***Oniscus asellus* Linnaeus, 1758**	?	128
Pseudomonadaceae			
	***Oniscus asellus* Linnaeus, 1758**	?	128
***Azomonas agilis* (Beijerinck, 1901) Winogradsky, 1938**	***Oniscus asellus* Linnaeus, 1758**	United States	129
= *Azotobacter agilis* Beijerinck, 1901			
***Pseudomonas fluorescens* Migula, 1895**	***Oniscus asellus* Linnaeus, 1758**	Republic of Slovenia, England	111, 137
***Pseudomonas fragi* (Eichholz, 1902) Gruber, 1905**	***Oniscus asellus* Linnaeus, 1758**	England	111
***Pseudomonas helmanticensis* Ramírez-Bahena *et al.*, 2014**	***Oniscus asellus* Linnaeus, 1758**	England	111
***Pseudomonas koreensis* Kwon *et al.*, 2003**	***Oniscus asellus* Linnaeus, 1758**	England	111
***Pseudomonas marginalis* (Brown, 1918) Stevens, 1925**	***Oniscus asellus* Linnaeus, 1758**	England	111, See Fraune and Zimmer 2008
***Pseudomonas* sp.**	***Armadillidium vulgare* (Latreille, 1804)**	France	156
	***Ligia oceanica* (Linnaeus, 1767)**	Federal Republic of Germany	55
	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia, England	111, 130, See Fraune and Zimmer 2008
	***Trachelipus rathkii* (Brandt, 1833)**	?	138
	= *Tracheoniscus rathkei* (Brandt)		
	***Trichoniscus pusillus* Brandt, 1833**	?	See Fraune and Zimmer 2008
Vibrionales			
Vibrionaceae			
***Vibrio penaeicida* Ishimaru *et al.*, 1995**	***Ligia occidentalis* (Dana, 1853)**	United States	56
	***Ligia pallasii* Brandt, 1833**	United States	56
***Vibrio rumoiensis* Yumoto *et al.*, 1999**	***Ligia pallasii* Brandt, 1833**	United States	56
= *Vibrio rumoence* [sic]	***Porcellio scaber* Latreille, 1804**	Republic of Slovenia	155
***Vibrio* sp.**	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England, Republic of Slovenia	111, 155
Candidatus Saccharibacteria Albertsen *et al.*, 2013			
Candidatus Saccharimonadia Lemos *et al.*, 2019			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Candidatus Tectomicrobia Wilson *et al.*, 2014			
Candidatus Entotheonellia			
	***Porcellio dilatatus* Brandt, 1831**	Portuguese Republic	148
Verrucomicrobiota			
= Verrucomicrobia	***Ligia pallasii* Brandt, 1833**	United States	56
	***Porcellio scaber* Latreille, 1804**	England	111
	***Oniscus asellus* Linnaeus, 1758**	England	111

PROTISTS

Taxonomy (Symbiont)	Host Species	Localities	References
"Amoeboid protist"			
***Discella ligidii* Nemec, 1895**	***Ligidium hypnorum* (Cuvier, 1792)**	Czech Republic and/or Slovakia	164
	= *Ligidium agile* (Persoon, 1793)		
Apicomplexa			
Conoidasida			
(Coccidiasina)			
	***Oniscus asellus* Linnaeus, 1758**	Europe	38
	***Philoscia muscorum* (Scopoli, 1763)**	Europe	38
	***Porcellio scaber* Latreille, 1804**	Europe	38
Eugregarinorida			
	***Armadillidium vulgare* (Latreille, 1804)**	Spain	88

	***Chaetophiloscia elongata* (Dollfus)**	France	69
Ciliophora			
Ciliatea			
Cyrtophorida			
Chilododontidae			
***Chilodonella longidens* (Nemec, 1895)**	***Ligidium hypnorum* (Cuvier, 1792)**	Czech Republic and/or Slovakia, France, Europe	164, 165
= *Chilodon longidens* Nemec, 1895			
***Chilodonella porcellionis* Doigel & Furssenko, 1921**	***Oniscus asellus* Linnaeus, 1758**	Europe	165
	***Porcellio scaber* Latreille, 1804**	Europe	165
	***Porcellio* sp.**	Russia	162
	***Trachelipus rathkii* (Brandt, 1833)**	Europe	165
	= *Tracheoniscus rathkei* (Brandt)		
***Chilodonella* sp.**	***Ligia italica* Fabricius, 1798**	?	166
Trochiliidae			
***Dysterioides sessilia* Matthes, 1950**	***Oniscus asellus* Linnaeus, 1758**	Europe	165
	***Porcellio scaber* Latreille, 1804**	Europe	165
	***Trachelipus rathkii* (Brandt, 1833)**	Europe	165
	= *Tracheoniscus rathkei* (Brandt)		
Oligohymenophorea			
Sessilida			
Operculariidae			
***Ballodora dimorpha* Dogiel & Furssenko, 1921**	***Androniscus dentiger* Verhoeff, 1908**	France	163
	***Armadillidium vulgare* (Latreille, 1804)**	France	163
	***Cylisticus convexus* (De Geer, 1778)**	France, Europe	163, 165
	***Oniscus asellus* Linnaeus, 1758**	France, Scotland, Europe	161, 163, 165
	***Porcellio scaber* Latreille, 1804**	France, Ukraine, Europe	163, 165, 194
	***Porcellio* sp.**	Russia	162
	***Protracheoniscus politus* (Koch, 1841)**	Europe	165
	***Trachelipus rathkii* (Brandt, 1833)**	Europe	165
	= *Tracheoniscus rathkei* (Brandt)		
***Ballodora marceli* Remy, 1928**	***Androniscus dentiger* Verhoeff, 1908**	France, Europe	161, 165
	***Hyloniscus riparius* (Koch, 1838)**	Europe	165
	***Trichoniscus provisorius* Racovitza, 1908**	France, Europe	163, 165
	= *Trichoniscus pusillus provisorius* Racovitza, 1908		
	***Trichoniscus* sp.**	Europe	165
***Opercularia epistyliformis* Nemec, 1895**	***Ligidium hypnorum* (Cuvier, 1792)**	Czech Republic and/or Slovakia, France, Europe	161, 164, 165
= *Epistylis epistyliformis*			
***Opercularia ligiae* Matthes, 1955**	***Ligia italica* Fabricius, 1798**	Ukraine	166, 194
***Opercularia stammeri* Matthes, 1950**	***Oniscus asellus* Linnaeus, 1758**	Germany	165
Vaginicolidae			
***Pyxicola ligiae* Cuenot, 1891**	***Ligia oceanica* (Linnaeus, 1767)**	France, Europe	161, 163, 165, 189
= *Pixicola* [sic] *ligiae*			
= *Cothurnia ligiae* Cuenot, 1891			
Vorticellidae			
***Carchesium voigti* Matthes**	***Ligia oceanica* (Linnaeus, 1767)**	Europe	165
Mesomycetozoea			
***Eccrinopsis ligidii* Maessen, 1955** nom. dub.	***Ligidium hypnorum* (Cuvier, 1792)**	?	116
***Nodocrinella hylonisci* Scheer, 1977** nom. nud.	***Hyloniscus riparius* (Koch, 1838)**	?	117
Eccrinales			
Eccrinaceae			
***Eccrinoides helleriae* Manier ex Lichtwardt, 1984**	***Helleria brevicornis* Ebner, 1868**	France	123
***Eccrinoides monticolae* (Poisson, 1931) Manier, 1970**	***Porcellio monticola* Lereboullet, 1853**	France	114, 124
Parataeniellaceae			

***Parataeniella armadillidii* Lichtwardt & Chen, 1964**	***Armadillidium nasatum* Budde-Lund, 1885**	United States	112, 142
	***Armadillidium vulgare* (Latreille, 1804)**	United States, Japan	112, 125, 142
	***Armadillidium* sp.**	United States, Argentine Republic, Spain	143
***Parataeniella dilatata* Poisson, 1929**	***Androniscus dentiger* Verhoeff, 1908**	France	122
= *Parataeniella binucleata* Poisson, 1929	= *Trichoniscus dentiger* (Verheff, 1908)		
= *Parataeniella intermedia* Poisson, 1929	***Androniscus roseus* (Koch, 1838)**	Federal Republic of Germany	118
	= *Trichoniscus roseus* (Koch, 1838)		
	***Armadillo officinalis* Duméril, 1816**	Federal Republic of Germany, France	118, 122
	***Armadillo* sp.**	Spain	121
	***Porcellio duboscqui* Paulian de Felice, 1941**	France	122
	Poission (1929) describes the host as similar to *P. laevis* but expresses uncertainty about the identification and ultimately lists the host as *Porcellio* sp., noting Vandel's opinion that it would be difficult to identify the species given the complexity of the genus. Several decades later, Vandel lists the host for this association as *P. duboscqui* (Vandel 1962). The host for this association is sometimes listed as *P. laevis* (Lichtwardt 1986).		
	***Porcellio laevis* Latreille, 1804**	Federal Republic of Germany	118
	***Porcellio lamellatus* Budde-Lund, 1885**	Federal Republic of Germany	118
	***Porcellio* sp.**	Spain, United States	121, 143
	***Protracheoniscus fossuliger* (Verhoeff, 1901)**	Federal Republic of Germany	118
	= *Protracheoniscus occidentalis* Vandel, 1939		
***Parataeniella flavospora* Chien & Hsieh, 2001**	***Armadillidium vulgare* (Latreille, 1804)**	Taiwan	119
	***Porcellio scaber* Latreille, 1804**	Taiwan	119
***Parataeniella latrobi* Williams & Lichtwardt, 1990**	***Porcellio scaber* Latreille, 1804**	Commonwealth of Australia	120
***Parataeniella mercieri* (Poisson, 1928) Poisson, 1929**	***Oniscus asellus* Linnaeus, 1758**	France, Federal Republic of Germany	118, 122
	***Trachelipus rathkii* (Brandt, 1833)**	Federal Republic of Germany	118
	= *Tracheoniscus rathkii* Brandt		
***Parataeniella scotonisci* Manier ex Manier, 1970**	***Scotoniscus macromelos* Racovitza, 1908**	France	150
	= *Scotoniscus marcomelos* [sic]		
***Parataeniella* sp.**	***Armadillidium* sp.**	United States	143
	***Oniscus asellus* Linnaeus, 1758**	United States	87
	***Porcellio scaber* Latreille, 1804**	United States	87
***Parataeniella* sp. / *Eccrinoides* sp.**	***Oniscus asellus* Linnaeus, 1758**	United States	87
	***Porcellio scaber* Latreille, 1804**	United States	87
Palavasciaceae			
***Palavascia philosciae* Tuzet & Manier ex Manier & Lichtwardt, 1964**	***Halophiloscia couchi* (Kinahan, 1858)**	France	160, 192
	= *Philoscia couchi* Kinahan, 1858		

FUNGI

Taxonomy (Symbiont)	Host Species	Localities	References
Kickxellomycota			
Asellariales			
Asellariaceae			
***Asellaria armadillidii* Tuzet & Manier ex Manier, 1968**	***Armadillidium assimile* Budde-Lund, 1885**	?	175
	***Armadillidium nasatum* Budde-Lund, 1885**	?	114
	***Armadillidium simoni* Dollfus, 1887**	France	113

	***Armadillidium vulgare* (Latreille, 1804)**	Taiwan, Japan, United States	114, 119, 125, 142
	***Porcellio* sp.**	?	114
	***Protracheoniscus fossuliger* (Verhoeff, 1901)** = *Protracheoniscus occidentalis* Vandel, 1939	?	114
***Asellaria dactylopus* Valle & Cafaro, 2008**	***Venezillo* sp.**	Puerto Rico	149
***Asellaria jatibonicua* Valle & Cafaro, 2008**	***Littorophiloscia culebrae* (Moore, 1901)**	Puerto Rico	149
***Asellaria ligiae* Tuzet & Manier ex Manier, 1968**	***Ligia exotica* Roux, 1828**	Taiwan, Japan, United States	119, 151, 154
	***Ligia italica* Fabricius, 1798**	Spain	115, 121
	Ligia mediterranea nom. dub.	France	152
	***Ligia* sp.**	Bosnia and Herzegovina, Republic of Croatia, Montenegro, Republic of North Macedonia, Republic of Serbia, and/or Republic of Slovenia, Hawaii, United States	114, 153
***Asellaria saezii* Valle, 2006**	***Trichoniscus pusillus* Brandt, 1833**	Spain	115
Ascomycota / Basidiomycota (?)			
	***Haplophthalmus danicus* Budde-Lund, 1880**	The Netherlands	58
	***Oniscus asellus* Linnaeus, 1758**	The Netherlands	58
	***Porcellio scaber* Latreille, 1804**	The Netherlands	58
***Kebertia oniscidarum* Boissevain, 1919**	***Oniscus asellus* Linnaeus, 1758** = *Oniscus murarius* Cuvier, 1792	The Netherlands	191
	***Porcellio* sp.**	The Netherlands	191
Ascomycota			
Dothideomycetes			
Cladosporiales			
Cladosporiaceae = Davidiellaceae	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
***Cladosporium cladosporioides* (Fresenius) de Vries, 1952**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
***Cladosporium herbarum* (Persoon) Link, 1816**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140
Dothideales			
Dothioraceae	***Oniscus asellus* Linnaeus, 1758**	England	111
Saccotheciaceae			
***Aureobasidium* sp.**	***Porcellio scaber* Latreille, 1804**	England	111
Pleosporales			
Didymosphaeriaceae = Montagnulaceae	***Porcellio scaber* Latreille, 1804**	England	111
Massarinaceae	***Oniscus asellus* Linnaeus, 1758**	England	111
Phaeosphaeriaceae	***Oniscus asellus* Linnaeus, 1758**	England	111
Pleosporaceae			
***Alternaria alternata* (Fries) Keissler, 1912**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
Eurotiomycetes			
Chaetothyriales			
Herpotrichiellaceae	***Oniscus asellus* Linnaeus, 1758**	England	111
Eurotiales			
Aspergillaceae			
***Aspergillus candidus* Link, 1809**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140
***Aspergillus flavus* Link, 1809**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
***Aspergillus nidulans* (Eidam) Winter, 1884**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140

***Aspergillus niger* Tieghem, 1867**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
***Penicillium citrinum* Thom, 1910**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
***Penicillium chrysogenum* Thom, 1910**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
Thermoascaceae			
***Paecilomyces variotii* Bainier, 1907**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140
= *Paecilomyces verioti* [sic]			
Trichocomaceae			
	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
***Talaromyces funiculosus* (Thom) Samson *et al.*, 2011**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
= *Penicillium funiculosum* Thom, 1910			
Laboulbeniomycetes			
Laboulbeniales			
= Laboulbeniaceen [sic]	***Trachelipus arcuatus* (Budde-Lund, 1885)**	Federal Republic of Germany	188
	= *Porcellio arcuatus* Budde-Lund, 1885		
	***Trichoniscoides albidus* (Budde-Lund, 1880)**	Federal Republic of Germany	188
	= *Trichoniscus albidus* Budde-Lund, 1880		
Lecanoromycetes			
Lecanorales			
Parmeliaceae			
	***Porcellio scaber* Latreille, 1804**	England	111
Leotiomycetes			
Helotiales			
Sclerotiniaceae			
***Botrytis* sp.**	***Porcellio scaber* Latreille, 1804**	England	111
Saccharomycetes			
Saccharomycetales			
***Candida* sp.**	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
***Cyberlindnera* sp.**	***Porcellio scaber* Latreille, 1804**	England	111
Debaryomycetaceae			
***Debaryomyces* sp.**	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
***Debaryomyces mycophilus* Thanh *et al*., 2002**	***Armadillidium vulgare* (Latreille, 1804)**	Ukraine	199
Wickerhamomycetaceae			
***Wickerhamomyces* sp.**	***Oniscus asellus* Linnaeus, 1758**	England	111
Sordariomycetes			
	***Oniscus asellus* Linnaeus, 1758**	England	111
Hypocreales			
Bionectriaceae			
***Clonostachys rosea f. catenulata* (Gilman & Abbott) Schroers, 2001**	***Porcellio scaber* Latreille, 1804**	United States	179
Cordycipitaceae			
	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
***Lecanicillium psalliotae* (Treschew) Zare & Gams, 2001**	***Armadillidium vulgare* (Latreille, 1804)**	United States	195
= *Lecanicillium saksenae* (Kushwaha) Kurihara & Sukarno, 2009	***Porcellio laevis* Latreille, 1804**	United States	195
	***Porcellio scaber* Latreille, 1804**	United States	195
Hypocreaceae			
***Trichoderma harzianum* Rifai, 1969**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141

***Trichoderma viride* Persoon, 1794**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
***Trichoderma* sp.**	***Oniscus asellus* Linnaeus, 1758**	England	111
Nectriaceae			
	***Oniscus asellus* Linnaeus, 1758**	England	111
	***Porcellio scaber* Latreille, 1804**	England	111
***Fusarium oxysporum* Schlechtendal, 1824**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
***Fusarium verticillioides* (Saccardo) Nirenberg, 1976** = *Fusarium moniliforme* Sheldon, 1904	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
Sordariales			
Chaetomiaceae			
***Trichocladium griseum* (Traaen) Wei Wang & Houbraken, 2018** = *Humicola grisea* Traaen, 1914	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140
Xylariales			
Apiosporaceae			
	***Oniscus asellus* Linnaeus, 1758**	England	111
Basidiomycota			
Tremellomycetes			
	***Oniscus asellus* Linnaeus, 1758**	England	111
Filobasidiales			
Filobasidiaceae			
	***Oniscus asellus* Linnaeus, 1758**	England	111
Tremellales			
= Trichosporonales	***Porcellio scaber* Latreille, 1804**	England	111
Trichosporonaceae			
	***Porcellio scaber* Latreille, 1804**	England	111
Mucoromycota			
Mucoromycetes			
Mucorales			
Backusellaceae			
***Backusella chlamydospora* Lee & Nguyen, 2021**	***Porcellio scaber* Latreille, 1804**	Republic of Korea	196
Mucoraceae			
***Mucor hiemalis* Wehmer, 1903**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
***Mucor racemosus* Bulliard, 1791**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140, 141
***Rhizopus stolonifer* (Ehrenberg) Vuillemin, 1902**	***Burmoniscus kempi* Collinge, 1916**	Republic of India	140

Table C2 (following pages): Viruses, bacteria, fungi, and protists associated with terrestrial isopods, sorted by isopod host family and species. See Table 3.2 for a list of metazoan symbionts sorted by isopod host family and species, and Table 3.1 for the list of references. The bacteria and fungal taxa listed here do not include all the taxa that have been recorded in association with sowbugs. Associations that are supported only by experimental infection are not included, but associations found "accidentally" occurring in lab populations of isopods are included. Taxon names are listed in their most recent form, with alternative name(s) given in the original source(s) listed below the most recent name. Most often these are synonymies, but occasionally are due to misidentifications that were noted and corrected in later literature or to misspellings. Note that the localities listed for the associations are supported by a minimum of one of the listed references, but not necessarily by all of them.

Taxonomy (Host)	Symbiont family	Symbiont species	Localities	References
Alloniscidae				
***Alloniscus balssii* (Verhoeff, 1928)**	Iridoviridae	***Iridovirus***	Japan	61
***Alloniscus perconvexus* Dana, 1854**	N/A (Mollicutes)	***Candidatus* Hepatoplasma Wang *et al.*, 2004**	Canada	54
		***Candidatus* Hepatoplasma crinochetorum Wang *et al.*, 2004**	Canada	55
Agnaridae				
***Hemilepistus reaumuri* (Milne Edwards, 1840)**	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	Republic of Tunisia	86
***Protracheoniscus fossuliger* (Verhoeff, 1901)** = *Protracheoniscus occidentalis* Vandel, 1939	Parataeniellaceae	***Parataeniella dilatata Poisson,* 1929** = *Parataeniella binucleata* Poisson, 1929 = *Parataeniella intermedia* Poisson, 1929	Federal Republic of Germany	118
	Asellariaceae	***Asellaria armadillidii* Tuzet & Manier ex Manier, 1968**	?	114
***Protracheoniscus politus* (Koch, 1841)** = *Protracheoniscus amoneus* Koch, 1841	Streptomycetaceae	***Streptomyces humidus* Nakazawa & Shibata, 1956**	?	139
		***Streptomyces moderatus* Reusser, 1965**	?	139
		***Streptomyces nodosus* Trejo, 1961**	?	139
		***Streptomyces pluricolorescens* Okami & Umezawa, 1961**	?	139
		***Streptomyces spadicis* Bromer *et al.*, 1969**	?	139
	Opercullariidae	***Ballodora dimorpha* Dogiel & Furssenko, 1921**	Europe	165
Armadillidae				
	Iridoviridae	***Iridovirus***	Japan	61
***Armadillo officinalis* Duméril, 1816**	Parataeniellaceae	***Parataeniella dilatata Poisson,* 1929** = *Parataeniella binucleata* Poisson, 1929 = *Parataeniella intermedia* Poisson, 1929	Federal Republic of Germany, France	118, 122
***Armadillo* sp.**	Parataeniellaceae	***Parataeniella dilatata Poisson,* 1929** = *Parataeniella binucleata* Poisson, 1929 = *Parataeniella intermedia* Poisson, 1929	Spain	121
***Cubaris murina* Brandt, 1833**	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	France	86
***Venezillo obscurus* (Budde-Lund, 1885)**	Iridoviridae	***Iridovirus***	Japan	61
***Venezillo* sp.**	Asellariaceae	***Asellaria dactylopus* Valle & Cafaro, 2008**	Puerto Rico	149
Armadillidiidae				
***Armadillidium assimile* Budde-Lund, 1885**	Asellariaceae	***Asellaria armadillidii* Tuzet & Manier ex Manier, 1968**	?	175
***Armadillidium decorum* Brandt, 1833**	Iridoviridae	***Iridovirus***	Italy	144
***Armadillidium granulatum* Brandt, 1833**	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	Republic of Tunisia	86
	Coxiellaceae	***Rickettsiella* sp.**	?	158
***Armadillidium nasatum* Budde-Lund, 1885**	Coxiellaceae	***Rickettsiella* sp.**	?	158
	Parataeniellaceae	***Parataeniella armadillidii* Lichtwardt & Chen, 1964**	United States	112, 142
	Asellariaceae	***Asellaria armadillidii* Tuzet & Manier ex Manier, 1968**	?	114
***Armadillidium pallidum* Verhoeff, 1907** = *Armadillidium pelagicum* Arcangeli, 1957	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	Republic of Tunisia	86
***Armadillidium simoni* Dollfus, 1887**	Asellariaceae	***Asellaria armadillidii* Tuzet & Manier ex Manier, 1968**	France	113
***Armadillidium sulcatum* Milne-Edwards, 1840**	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	Republic of Tunisia	86
***Armadillidium vulgare* (Latreille, 1804)** = *Armadillidium pillularis* = *Armadillidium vulgaris* [sic]	Iridoviridae	***Iridovirus***	The Netherlands, Japan, Republic of Türkiye, United States, Italy	58, 61, 62, 63, 64, 75, 77, 78, 79, 144, 201
	Cytophagaceae	***Cytophaga* sp.**	England	134
	N/A (Flavobacteriia)	Flavobacteriia	France	156
	N/A (Mollicutes)	***Candidatus* Bacilliplasma Kostanjšek *et al.*, 2007**	France	156
		***Candidatus* Hepatoplasma Wang *et al.*, 2004**	Federal Republic of Germany	54
		***Candidatus* Hepatoplasma crinochetorum Wang *et al.*, 2004**	France, Federal Republic of Germany	55, 156
	N/A (Alphaproteobacteria)	Alphaproteobacteria	France	156
	Candidatus Hepatincolaceae Szokoli *et al.*, 2016	***Candidatus* Hepatincola Wang *et al.*, 2004**	Federal Republic of Germany	54

		***Candidatus* Hepatincola porcellionum Wang *et al.*, 2004**	France	156
	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	France	156
		***Wolbachia* sp.**	France	146
	Sphingomonadaceae	***Sphingomonas* sp.**	France	156
	N/A (Gammaproteobacteria)	Gammaproteobacteria	France	156
	Shewanellaceae	***Shewanella* sp.** = *Shevanella* [sic] sp.	France	156
	Coxiellaceae	***Rickettsiella grylli* (ex Vago & Martoja, 1963) Weiss *et al.*, 1984**	United States, France	145, 156
		***Rickettsiella popilliae* (Dutky & Gooden, 1952) Philip, 1956** = *Rickettsiella armadillidii* Frutos *et al.*, 1994	France	48, 110, 156
		***Candidatus* Rickettsiella isopodorum Kleespies *et al.*, 2014**	United States	49
		***Rickettsiella* sp.**	?	158
	Halomonadaceae	***Halomonas* sp.**	France	156
	Pseudomonadaceae	***Pseudomonas* sp.**	France	156
	N/A (Eugregarinorida)	Eugregarinorida	Spain	88
	Operculariidae	***Ballodora dimorpha* Dogiel & Furssenko, 1921**	France	163
	Parataeniellaceae	***Parataeniella armadillidii* Lichtwardt & Chen, 1964**	United States, Japan	112, 125, 142
		***Parataeniella flavospora* Chien & Hsieh, 2001**	Taiwan	119
	Asellariaceae	***Asellaria armadillidii* Tuzet & Manier ex Manier, 1968**	Taiwan, Japan, United States	114, 119, 125, 142
	Debaryomycetaceae	***Debaryomyces mycophilus* Thanh *et al*., 2002**	Ukraine	199
	Cordycipitaceae	***Lecanicillium psalliotae* (Treschew) Zare & Gams, 2001** = *Lecanicillium saksenae* (Kushwaha) Kurihara & Sukarno, 2009	United States	195
***Armadillidium* sp.**	Bacillaceae	***Bacillus cereus* Frankland & Frankland, 1887**	United States	132
	Parataeniellaceae	***Parataeniella armadillidii* Lichtwardt & Chen, 1964**	United States, Argentine Republic, Spain	143
		***Parataeniella* sp.**	United States	143
***Eluma caelata* (Miers, 1877)** = *Eluma purpurascens* Budde-Lund, 1885	Coxiellaceae	***Rickettsiella* sp.**	?	158
Cylisticidae				
***Cylisticus convexus* (De Geer, 1778)** = *Cilisticus* [sic] *convexus*	Iridoviridae	***Iridovirus***	United States	64
	Operculariidae	***Ballodora dimorpha* Dogiel & Furssenko, 1921**	France, Europe	163, 165
Halophilosciidae				
***Halophiloscia couchi* (Kinahan, 1858)** = *Philoscia couchi* Kinahan, 1858	Palavasciaceae	***Palavascia philosciae* Tuzet & Manier ex Manier & Lichtwardt, 1964**	France	160, 192
***Littorophiloscia culebrae* (Moore, 1901)**	Asellariaceae	***Asellaria jatibonicua* Valle & Cafaro, 2008**	Puerto Rico	149
***Littorophiloscia nipponensis* Nunomura, 1986**	Iridoviridae	***Iridovirus***	Japan	61
Ligiidae				
***Ligia exotica* Roux, 1828**	Asellariaceae	***Asellaria ligiae* Tuzet & Manier ex Manier, 1968**	Taiwan, Japan, United States	119, 151, 154
***Ligia italica* Fabricius, 1798**	Chilododontidae	***Chilodonella* sp.**	?	166
	Opercularidae	***Opercularia ligiae* Matthes, 1955**	Ukraine	166, 194
	Asellariaceae	***Asellaria ligiae* Tuzet & Manier ex Manier, 1968**	Spain	115, 121
***Ligia mediterranea* nom. dub.**	Asellariaceae	***Asellaria ligiae* Tuzet & Manier ex Manier, 1968**	France	152
***Ligia occidentalis* (Dana, 1853)**	Burkholderiaceae	***Ralstonia pickettii* (Ralston *et al.*, 1973) Yabuuchi *et al.*, 1996**	United States	56
	Vibrionaceae	***Vibrio penaeicida* Ishimaru *et al.*, 1995**	United States	56
***Ligia oceanica* (Linnaeus, 1767)**	N/A (Mollicutes)	***Candidatus* Hepatoplasma Wang *et al.*, 2004**	Federal Republic of Germany	54
	Pseudomonadaceae	***Pseudomonas* sp.**	Federal Republic of Germany	55
	Vaginicolidae	***Pyxicola ligiae* Cuenot, 1891** = *Pixicola* [sic] *ligiae* = *Cothurnia ligiae* Cuenot, 1891	France, Europe	161, 163, 165, 189
	Vorticellidae	***Carchesium voigti* Matthes**	Europe	165
***Ligia pallasii* Brandt, 1833**	N/A (Actinomycetota)	Actinomycetota = Actinobacteria	United States	56

	N/A (Bacteroidota)	Bacteroidota = Bacteriodetes	United States	56
	Flavobacteriaceae	Flavobacteriaceae	United States	56
		***Lacinutrix* sp.**	United States	56
	Burkholderiaceae	***Ralstonia pickettii* (Ralston *et al.*, 1973) Yabuuchi *et al.*, 1996**	United States	56
	N/A (Gammaproteobacteria)	Gammaproteobacteria	United States	56
	Halomonadaceae	***Cobetia* sp.**	United States	56
	Vibrionaceae	***Vibrio penaeicida* Ishimaru *et al.*, 1995**	United States	56
		***Vibrio rumoiensis* Yumoto *et al.*, 1999** = *Vibrio rumoence* [sic]	United States	56
	N/A (Verrucomicrobiota)	Verrucomicrobiota = Verrucomicrobia	United States	56
***Ligia* sp.**	Asellariaceae	***Asellaria ligiae* Tuzet & Manier ex Manier, 1968**	Bosnia and Herzegovina, Republic of Croatia, Montenegro, Republic of North Macedonia, Republic of Serbia, and/or Republic of Slovenia, Hawaii, United States	114, 153
***Ligidium hypnorum* (Cuvier, 1792)** = *Ligidium agile* (Persoon, 1793)	Iridoviridae	***Iridovirus***	The Netherlands, France, Russia, Czech Republic and/or Slovakia	58, 65, 66, 67, 68, 75
	N/A ("Amoeboid protist")	***Discella ligidii* Nemec, 1895**	Czech Republic and/or Slovakia	164
	Chilododontidae	***Chilodonella longidens* (Nemec, 1895)** = *Chilodon longidens* Nemec, 1895	Czech Republic and/or Slovakia, France, Europe	164, 165
	Operculariidae	***Opercularia epistyliformis* Nemec, 1865** = *Epistylis epistyliformis*	Czech Republic and/or Slovakia, France, Europe	161, 164, 165
	N/A ("Mesomycetozoea")	***Eccrinopsis ligidii* Maessen, 1955** nom. dub.	?	116
	Philodinidae	***Mniobia branchicola* (Nemec, 1895)** = *Macrotrachela branchicola* Harring, 1913 = *Callidina branchicola* Nemec, 1895	France, Czech Republic and/or Slovakia, Europe	161, 164, 165
***Ligidium japonicum* Verhoeff, 1918**	Iridoviridae	***Iridovirus***	Japan	61
***Ligidium koreanum* Flasarova, 1972**	Iridoviridae	***Iridovirus***	Japan	61
***Ligidium* sp.**	Philodinidae	***Mniobia branchicola* (Nemec, 1895)** = *Macrotrachela branchicola* Harring, 1913 = *Callidina branchicola* Nemec, 1895	?	178
Oniscidae				
***Oniscus asellus* Linnaeus, 1758** = *Oniscus murarius* Cuvier, 1792	Iridoviridae	***Iridovirus***	The Netherlands, England	58, 76
	N/A (Acidobacteriota)	Acidobacteriota = Acidobacteria	England	111
	"Spirilaceae"	"Spirilaceae"	?	128
	Jonesiaceae	Jonesiaceae = Sanguibacteraceae	England	111
	Microbacteriaceae	***Microbacterium* sp.**	England	111
	Micrococcaceae	Micrococcaceae	?	128
		***Arthrobacter* sp.**	?	128
	Corynebacteriaceae	Corynebacteriaceae	?	128
		***Corynebacterium* sp.**	England	133
	Mycobacteriaceae	Mycobacteriaceae	?	128
	N/A (Bacteroidota)	Bacteroidota = Bacteriodetes	England	111
	Cytophagaceae	***Cytophaga* sp.**	England	134
	Flavobacteriaceae	Flavobacteriaceae	England	111
	Sphingobacteriaceae	***Sphingobacterium faecium* Takeuchi & Yokota, 1993**	England	111
		***Sphingobacterium kitahiroshimense* Matsuyama *et al.*, 2008**	England	111
	N/A (Chlamydiota)	Chlamydiota	England	111

	= Chlamydiae		
N/A (Chloroflexota)	Chloroflexota = Chloroflexi	England	111
N/A (Cyanobacteriota)	Cyanobacteriota = Cyanobacteria	England	111
N/A (Deinococcota)	Deinococcota = Deinococcus	England	111
N/A (Fusobacteriota)	Fusobacteriota = Fusobacteria	England	111
N/A (Mollicutes)	***Candidatus* Bacilliplasma Kostanjšek *et al.*, 2007**	England	111
	***Candidatus* Hepatoplasma Wang *et al.*, 2004**	England, Federal Republic of Germany	54, 111
	***Candidatus* Hepatoplasma crinochetorum Wang *et al.*, 2004**	France, Federal Republic of Germany	55
N/A (Entomoplasmatales)	Entomoplasmatales	England	111
N/A (Planctomycetota)	Planctomycetota = Planctomycetes	England	111
Candidatus Hepatincolaceae Szokoli *et al.*, 2016	***Candidatus* Hepatincola Wang *et al.*, 2004**	England, Federal Republic of Germany	54, 111
	***Candidatus* Hepatincola porcellionum Wang *et al.*, 2004**	Federal Republic of Germany	55
N/A (Rickettsiales)	Rickettsiales	England	111
Ehrlichiaceae	Ehrlichiaceae = Anaplasmataceae	England	111
Comamonadaceae	***Delftia acidovorans* (den Dooren de Jong, 1926) Wen *et al.*, 1999**	England	111
Chromobacteriaceae	***Chromobacterium violaceum* Bergonzini 1880** = *Chrmombacterium* [sic] *violaceum*	?	128
Enterobacteriaceae	Enterobacteriaceae	?	128
	***Citrobacter freundii* (Braak, 1928) Werkman & Gillen, 1932**	?	127
	***Enterobacter agglomerans* (Beijerinck, 1888) Ewing & Fife, 1972**	?	137
	***Klebsiella pneumoniae* (Schroeter, 1886) Trevisan, 1887**	England	133
	***Kluyvera* sp.**	England	111
	***Plesiomonas* sp.**	?	137
Coxiellaceae	Coxiellaceae	England	111
	***Rickettsiella* sp.**	England	111, 158
Lysobacteraceae	***Stenotrophomonas pavanii* Ramos *et al.*, 2011**	England	111
	***Stenotrophomonas rhizophila* Wolf *et al.*, 2002**	England	111
	***Xanthomonas maltophilia* (Hugh, 1981) Swings *et al.*, 1983** = *Stenotrophomonas maltophilia* (Hugh, 1981) Palleroni & Bradbury, 1993	England	111
Moraxellaceae	***Acinetobacter calcoaceticus* (Beijerinck, 1911) Baumann *et al.*, 1968**	?	128
Pseudomonadaceae	Pseudomonadaceae	?	128
	***Azomonas agilis* (Beijerinck, 1901) Winogradsky, 1938** = *Azotobacter agilis* Beijerinck, 1901	United States	129
	***Pseudomonas fluorescens* Migula, 1895**	Republic of Slovenia, England	111, 137
	***Pseudomonas fragi* (Eichholz, 1902) Gruber, 1905**	England	111
	***Pseudomonas helmanticensis* Ramírez-Bahena *et al.*, 2014**	England	111
	***Pseudomonas koreensis* Kwon *et al.*, 2003**	England	111
	***Pseudomonas marginalis* (Brown, 1918) Stevens, 1925**	England	111, See Fraune and Zimmer 2008
	***Pseudomonas* sp.**	England	111
Vibrionaceae	***Vibrio* sp.**	England	111
N/A (Verrucomicrobiota)	Verrucomicrobiota = Verrucomicrobia	England	111

	N/A (Coccidiasina)	Coccidiasina	Europe	38
	Chilododontidae	***Chilodonella porcellionis* Doigel & Furssenko, 1921**	Europe	165
	Trochiliidae	***Dysterioides sessilia* Matthes, 1950**	Europe	165
	Operculariidae	***Ballodora dimorpha* Dogiel & Furssenko, 1921**	France, Scotland, Europe	161, 163, 165
		***Opercularia stammeri* Matthes, 1950**	Germany	165
	Parataeniellaceae	***Parataeniella mercieri* (Poisson, 1928) Poisson, 1929**	France, Federal Republic of Germany	118, 122
		***Parataeniella* sp.**	United States	87
		***Parataeniella* sp. / *Eccrinoides* sp.**	United States	87
	N/A (Ascomycota / Basidiomycota (?)	Ascomycota / Basidiomycota (?)	The Netherlands	58
		***Kebertia oniscidarum* Boissevain, 1919**	The Netherlands	191
	Cladosporiaceae	Cladosporiaceae = Davidiellaceae	England	111
	Dothioraceae	Dothioraceae	England	111
	Massarinaceae	Massarinaceae	England	111
	Phaeosphaeriaceae	Phaeosphaeriaceae	England	111
	Herpotrichiellaceae	Herpotrichiellaceae	England	111
	Trichocomaceae	Trichocomaceae	England	111
	N/A (Saccharomycetales)	***Candida* sp.**	England	111
	Debaryomycetaceae	***Debaryomyces* sp.**	England	111
	Wickerhamomycetaceae	***Wickerhamomyces* sp.**	England	111
	N/A (Sordariomycetes)	Sordariomycetes	England	111
	Cordycipitaceae	Cordycipitaceae	England	111
	Hypocreaceae	***Trichoderma* sp.**	England	111
	Nectriaceae	Nectriaceae	England	111
	Apiosporaceae	Apiosporaceae	England	111
	N/A (Tremellomycetes)	Tremellomycetes	England	111
	Filobasidiaceae	Filobasidiaceae	England	111
Philosciidae				
***Atlantoscia floridana* (Van Name, 1940)**	Coxiellaceae	***Rickettsiella* sp.**	?	157
***Burmoniscus kathmandius* (Schmalfuss, 1983)** = *Burmoniscus kathmandia* (Schmalfuss, 1983)	Iridoviridae	***Iridovirus***	Japan	61
***Burmoniscus kempi* Collinge, 1916**	Cladosporiaceae	***Cladosporium cladosporioides* (Fresenius) de Vries, 1952**	Republic of India	140, 141
		***Cladosporium herbarum* (Persoon) Link, 1816**	Republic of India	140
	Pleosporaceae	***Alternaria alternata* (Fries) Keissler, 1912**	Republic of India	140, 141
	Aspergillaceae	***Aspergillus flavus* Link, 1809**	Republic of India	140, 141
		***Aspergillus nidulans* (Eidam) Winter, 1884**	Republic of India	140
		***Aspergillus niger* Tieghem, 1867**	Republic of India	140, 141
		***Aspergillus candidus* Link, 1809**	Republic of India	140
		***Penicillium citrinum* Thom, 1910**	Republic of India	140, 141
		***Penicillium chrysogenum* Thom, 1910**	Republic of India	140, 141
	Thermoascaceae	***Paecilomyces variotii* Bainier, 1907** = *Paecilomyces verioti* [sic]	Republic of India	140
	Trichocomaceae	***Talaromyces funiculosus* (Thom) Samson *et al.*, 2011** = *Penicillium funiculosum* Thom, 1910	Republic of India	140, 141
	Hypocreaceae	***Trichoderma harzianum* Rifai, 1969**	Republic of India	140, 141
		***Trichoderma viride* Persoon, 1794**	Republic of India	140, 141
	Nectriaceae	***Fusarium oxysporum* Schlechtendal, 1824**	Republic of India	140, 141
		***Fusarium verticillioides* (Saccardo) Nirenberg, 1976** = *Fusarium moniliforme* Sheldon, 1904	Republic of India	140, 141
	Chaetomiaceae	***Trichocladium griseum* (Traaen) Wei Wang & Houbraken, 2018** = *Humicola grisea* Traaen, 1914	Republic of India	140

	Mucoraceae	***Mucor hiemalis* Wehmer, 1903**	Republic of India	140, 141
		***Mucor racemosus* Bulliard, 1791**	Republic of India	140, 141
		***Rhizopus stolonifer* (Ehrenberg) Vuillemin, 1902**	Republic of India	140
***Chaetophiloscia elongata* (Dollfus)**	N/A (Eugregarinorida)	Eugregarinorida	France	69
***Philoscia affinis* Verhoeff, 1908**	Iridoviridae	***Iridovirus***	Italy	144
***Philoscia muscorum* (Scopoli, 1763)**	Iridoviridae	***Iridovirus***	France, England, the Netherlands	69, 70, 71, 75
	N/A (Mollicutes)	***Candidatus* Hepatoplasma Wang *et al.*, 2004**	Federal Republic of Germany	54
		***Candidatus* Hepatoplasma crinochetorum Wang *et al.*, 2004**	Federal Republic of Germany	55
	Candidatus Hepatincolaceae Szokoli *et al.*, 2016	***Candidatus* Hepatincola Wang *et al.*, 2004**	Federal Republic of Germany	54
	Coxiellaceae	***Rickettsiella popilliae* (Dutky & Gooden, 1952) Philip, 1956**	Spain	48
	N/A (Coccidiasina)	Coccidiasina	Europe	38
Platyarthridae				
***Niambia capensis* (Dollfus, 1895)** = *Mauritaniscus littorinus* (Miller, 1936)	Iridoviridae	***Iridovirus***	United States	64
***Platyarthrus hoffmannseggii* Brandt, 1833**	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	France	86
Porcellionidae				
***Porcellio albinus* Budde-Lund, 1885**	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	Republic of Tunisia	86
***Porcellio buddelundi* Simon, 1885**	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	Republic of Tunisia	86
***Porcellio dilatatus* Brandt, 1831**	Iridoviridae	***Iridovirus***	United States	63, 77
	N/A ("Plactomycetacia")	"Plactomycetacia"	Portuguese Republic	148
	N/A (Terriglobia)	Terriglobia = Acidobacteriia	Portuguese Republic	148
	N/A (Acidimicrobiia)	Acidimicrobiia	Portuguese Republic	148
	Geodermatophilaceae	Geodermatophilaceae	Portuguese Republic	148
	Streptomycetaceae	Streptomycetaceae	Portuguese Republic	148
	Microbacteriaceae	Microbacteriaceae	Portuguese Republic	148
	Micrococcaceae	Micrococcaceae	Portuguese Republic	148
	Micromonosporaceae	Micromonosporaceae	Portuguese Republic	148
	Nocardioidaceae	Nocardioidaceae	Portuguese Republic	148
	Pseudonocardiaceae	Pseudonocardiaceae	Portuguese Republic	148
	N/A (Rubrobacteria)	Rubrobacteria	Portuguese Republic	148
	N/A (Thermoleophilia)	Thermoleophilia	Portuguese Republic	148
	N/A (Coriobacteriia)	Coriobacteriia	Portuguese Republic	148
	N/A (Clostridia)	Clostridia	Portuguese Republic	148
	N/A (Erysipelotrichia)	Erysipelotrichia	Portuguese Republic	148
	N/A (Bacteroidia)	Bacteroidia	Portuguese Republic	148
	Flavobacteriaceae	Flavobacteriaceae	Portuguese Republic	148
	Anaerolineae	Anaerolineae	Portuguese Republic	148
	N/A (Chloroflexia)	Chloroflexia	Portuguese Republic	148
	N/A (Dehalococcoidia)	Dehalococcoidia	Portuguese Republic	148
	N/A (Ktedonobacteria)	Ktedonobacteria	Portuguese Republic	148
	Cyanophyceae	Cyanophyceae = Oxyphotobacteria	Portuguese Republic	148
		Candidatus Melainabacteria Soo *et al.*, 2014	Portuguese Republic	148
	N/A (*Candidatus* Babeliae Yeoh *et al.*, 2016)	*Candidatus* Babeliae Yeoh *et al.*, 2016	Portuguese Republic	148
	N/A (Fibrobacteria)	Fibrobacteria	Portuguese Republic	148
	N/A (Gemmatimonadetes)	Gemmatimonadetes	Portuguese Republic	148
	N/A (Longimicrobiia)	Longimicrobiia =Longimicrobia	Portuguese Republic	148
	N/A (*Candidatus* Gracilibacteria Rinke *et al.*, 2013)	*Candidatus* Gracilibacteria Rinke *et al.*, 2013	Portuguese Republic	148

	N/A (*Candidatus* Sericytochromatia Soo *et al.*, 2017)	*Candidatus* Sericytochromatia Soo *et al.*, 2017	Portuguese Republic	148
	N/A (Mollicutes)	Mollicutes	Portuguese Republic	148
		***Candidatus* Hepatoplasma Wang *et al.*, 2004**	Portuguese Republic	148
	N/A (Nitrospiria)	Nitrospiria = Nitrospira	Portuguese Republic	148
	N/A (Microgenomatia)	Microgenomatia	Portuguese Republic	148
	Phycisphaerae	Phycisphaerae	Portuguese Republic	148
	Beijerinckiaceae	Beijerinckiaceae	Portuguese Republic	148
	Rhizobiaceae	Rhizobiaceae	Portuguese Republic	148
	Xanthobacteraceae	Xanthobacteraceae	Portuguese Republic	148
	Paracoccaceae	Paracoccaceae = Rhodobacteraceae	Portuguese Republic	148
	Ehrlichiaceae	***Wolbachia* sp.**	France, Portuguese Republic	146, 148
	Burkholderiaceae	Burkholderiaceae	Portuguese Republic	148
	N/A (Deltaproteobacteria)	Deltaproteobacteria	Portuguese Republic	148
	Enterobacteriaceae	Enterobacteriaceae	Portuguese Republic	148
	Coxiellaceae	***Rickettsiella grylli* (ex Vago & Martoja, 1963) Weiss *et al.*, 1984**	United States	145
		***Rickettsiella* sp.**	Portuguese Republic	148
	N/A (*Candidatus* Saccharimonadia Lemos *et al.*, 2019)	*Candidatus* Saccharimonadia Lemos *et al.*, 2019	Portuguese Republic	148
	N/A (*Candidatus* Entotheonellia)	*Candidatus* Entotheonellia	Portuguese Republic	148
***Porcellio duboscqui* Paulian de Felice, 1941** Poission (1929) describes the host as similar to *P. laevis* but expresses uncertainty about the identification and ultimately lists the host as *Porcellio* sp., noting Vandel's opinion that it would be difficult to identify the species given the complexity of the genus. Several decades later, Vandel lists the host for this association as *P. duboscqui* (Vandel 1962). The host for this association is sometimes listed as *P. laevis* (Lichtwardt 1986).	Parataeniellaceae	***Parataeniella dilatata Poisson,* 1929** = *Parataeniella binucleata* Poisson, 1929 = *Parataeniella intermedia* Poisson, 1929	France	122
***Porcellio gallicus* Dollfus, 1904**	Coxiellaceae	***Rickettsiella* sp.**	?	158
***Porcellio laevis* Latreille, 1804**	Iridoviridae	***Iridovirus***	United States	64, 80
	Coxiellaceae	***Rickettsiella* sp.**	?	158
	Parataeniellaceae	***Parataeniella dilatata Poisson,* 1929** = *Parataeniella binucleata* Poisson, 1929 = *Parataeniella intermedia* Poisson, 1929	Federal Republic of Germany	118
	Cordycipitaceae	***Lecanicillium psalliotae* (Treschew) Zare & Gams, 2001** = *Lecanicillium saksenae* (Kushwaha) Kurihara & Sukarno, 2009	United States	195
***Porcellio lamellatus* Budde-Lund, 1885**	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	Republic of Tunisia	86
	Parataeniellaceae	***Parataeniella dilatata Poisson,* 1929** = *Parataeniella binucleata* Poisson, 1929 = *Parataeniella intermedia* Poisson, 1929	Federal Republic of Germany	118
***Porcellio monticola* Lereboullet, 1853**	Eccrinaceae	***Eccrinoides monticolae* (Poisson, 1931) Manier, 1970**	France	114, 124
***Porcellio scaber* Latreille, 1804**	Iridoviridae	***Iridovirus***	The Netherlands, Japan, United States	58, 61, 64, 75, 78, 79, 80
	N/A (Actinomycetota)	Actinomycetota = Actinobacteria	England, Republic of Slovenia	111, 155
	N/A (Acidobacteriota)	Acidobacteriota	England	111

	= Acidobacteria		
N/A (Actinomycetales)	Actinomycetales	England	111
Brevibacteriaceae	***Brevibacterium* sp.**	Republic of Slovenia	155
Microbacteriaceae	***Agromyces* sp.**	Republic of Slovenia	155
	***Microbacterium* sp.**	Republic of Slovenia	155
Micrococcaceae	***Arthrobacter* sp.**	Republic of Slovenia	155
Promicromonosporaceae	***Cellulosimicrobium* sp.**	Republic of Slovenia	155
Nocardiaceae	***Rhodococcus* sp.**	Republic of Slovenia	155
Bacillaceae	***Bacillus cereus* Frankland & Frankland, 1887**	United States	131, 132
	***Bacillus* sp.**	Republic of Slovenia	130, 155
	***Exiguobacterium* sp.**	Republic of Slovenia	155
Caryophanaceae	***Caryophanon* sp.**	Republic of Slovenia	155
	***Planomicrobium* sp.**	Republic of Slovenia	155
Listeriaceae	***Listeria* sp.**	Republic of Slovenia	155
	***Planococcus* sp.**	Republic of Slovenia	155
	***Paenibacillus* sp.**	Republic of Slovenia	155
Staphylococcaceae	***Staphylococcus succinus* Lambert *et al.*, 1998**	Republic of Slovenia	155
Enterococcaceae	***Enterococcus faecium* (Orla-Jensen, 1919) Schleifer & Kilpper-Bälz, 1984**	Republic of Slovenia	130
	***Enterococcus* sp.**	Republic of Slovenia	130
	= *Enterococococcus* [sic] sp.		
Peptococcaceae	***Desulfotomaculum ruminis* Campbell & Postgate, 1965**	?	135, 136
	= *Desulphotomaculum* [sic] *ruminis*		
N/A (Bacteroidota)	Bacteroidota	England, Republic of Slovenia	111, 155
	= Bacteriodetes		
	***Bacteroides* sp.**	Republic of Slovenia	130
Cytophagaceae	***Cytophaga* sp.**	England, Republic of Slovenia	134, 155
Flavobacteriaceae	Flavobacteriaceae	England	111
	***Flavobacterium* sp.**	Republic of Slovenia	155
Candidatus Rhabdochlamydiaceae Horn, 2010	***Candidatus* Rhabdochlamydia porcellionis Kostanjšek *et al.*, 2004**	?	23, 47, 50
	= *Chlamydia isopodii* Shay *et al.*, 1985		
N/A (Chloroflexota)	Chloroflexota	England	111
	= Chloroflexi		
N/A (Cyanobacteriota)	Cyanobacteriota	England	111
	= Cyanobacteria		
N/A (Deinococcota)	Deinococcota	England	111
	= Deinococcus		
N/A (Mollicutes)	Mollicutes	Republic of Slovenia, England	111, 130, 136
	***Candidatus* Bacilliplasma Kostanjšek *et al.*, 2007**	Republic of Slovenia, Republic of Austria	147
	***Candidatus* Hepatoplasma Wang *et al.*, 2004**	England, Federal Republic of Germany	54, 111
	***Candidatus* Hepatoplasma crinochetorum Wang *et al.*, 2004**	Canada, Federal Republic of Germany	52, 55
N/A (Entomoplasmatales)	Entomoplasmatales	England	111
N/A (Planctomycetota)	Planctomycetota	England	111
	= Planctomycetes		
Planctomycetaceae	Planctomycetaceae	Republic of Slovenia	155
N/A (Alphaproteobacteria)	Alphaproteobacteria	Republic of Slovenia	155
Candidatus Hepatincolaceae Szokoli *et al.*, 2016	***Candidatus* Hepatincola Wang *et al.*, 2004**	Federal Republic of Germany	54
	***Candidatus* Hepatincola porcellionum Wang *et al.*, 2004**	Canada, Federal Republic of Germany	53, 55
Brucellaceae	***Brucella anthropi* (Holmes *et al.*, 1988) Hördt *et al.*, 2020**	Republic of Slovenia	155
	= *Ochrobactrum anthropi* Holmes *et al.*, 1988		
Phyllobacteriaceae	***Mesorhizobium* sp.**	Republic of Slovenia	155

Rhizobiaceae	***Rhizobium* sp. / *Agrobacterium* sp.**	Republic of Slovenia	155
Paracoccaceae	Paracoccaceae = Rhodobacteraceae	England	111
	***Paracoccus* sp.**	Republic of Slovenia	126, 155
Roseobacteraceae	***Roseobacter* sp.**	Republic of Slovenia	155
Alcaligenaceae	***Achromobacter* sp.**	Republic of Slovenia	155
	***Alcaligenes* sp.**	Republic of Slovenia	155
Comamonadaceae	Comamonadaceae	Republic of Slovenia	155
Neisseriaceae	***Neisseria* sp.**	Republic of Slovenia	130
N/A (Gammaproteobacteria)	Gammaproteobacteria	Republic of Slovenia	155
Aeromonadaceae	***Aeromonas* sp.**	?	127
Shewanellaceae	Shewanellaceae	England	111
Enterobacteriaceae	***Shewanella* sp.** = *Shevanella* [sic] sp.	?	126
	***Citrobacter freundii* (Braak, 1928) Werkman & Gillen, 1932**	?	127
	***Enterobacter agglomerans* (Beijerinck, 1888) Ewing & Fife, 1972**	?	127
	***Enterobacter intermedius* Izard *et al.*, 1980**	?	127
	***Klebsiella pneumoniae* (Schroeter, 1886) Trevisan, 1887**	?	127
	***Klebsiella* sp.**	Republic of Slovenia	155
	***Kluyvera* sp.**	England	111
Coxiellaceae	Coxiellaceae	England	111
	***Rickettsiella grylli* (ex Vago & Martoja, 1963) Weiss *et al.*, 1984**	England	22
	***Candidatus* Rickettsiella isopodorum Kleespies *et al.*, 2014**	Federal Republic of Germany	49
	***Rickettsiella* sp.**	Republic of Slovenia	51
Lysobacteraceae	***Xanthomonas* sp. / *Pseudoxanthomonas* sp.**	Republic of Slovenia	155
Halomonadaceae	***Halomonas* sp.**	Republic of Slovenia	155
Pseudomonadaceae	***Pseudomonas* sp.**	Republic of Slovenia, England	111, 130, See Fraune and Zimmer 2008
Vibrionaceae	***Vibrio rumoiensis* Yumoto *et al.*, 1999** = *Vibrio rumoence* [sic]	Republic of Slovenia	155
	***Vibrio* sp.**	England, Republic of Slovenia	111, 155
N/A (Verrucomicrobiota)	Verrucomicrobiota = Verrucomicrobia	England	111
N/A (Coccidiasina)	Coccidiasina	Europe	38
Chilododontidae	***Chilodonella porcellionis* Doigel & Furssenko, 1921**	Europe	165
Trochiliidae	***Dysterioides sessilia* Matthes, 1950**	Europe	165
Operculariidae	***Ballodora dimorpha* Dogiel & Furssenko, 1921**	France, Ukraine, Europe	163, 165, 194
Parataeniellaceae	***Parataeniella flavospora* Chien & Hsieh, 2001**	Taiwan	119
	***Parataeniella latrobi* Williams & Lichtwardt, 1990**	Commonwealth of Australia	120
	***Parataeniella* sp.**	United States	87
	***Parataeniella* sp. / *Eccrinoides* sp.**	United States	87
N/A (Ascomycota / Basidiomycota (?))	Ascomycota / Basidiomycota (?)	The Netherlands	58
Cladosporiaceae	Cladosporiaceae = Davidiellaceae	England	111
Saccotheciaceae	***Aureobasidium* sp.**	England	111
Didymosphaeriaceae	Didymosphaeriaceae = Montagnulaceae	England	111
Trichocomaceae	Trichocomaceae	England	111
Parmeliaceae	Parmeliaceae	England	111
Sclerotiniaceae	***Botrytis* sp.**	England	111
N/A (Saccharomycetales)	***Candida* sp.**	England	111
	***Cyberlindnera* sp.**	England	111

	Debaryomycetaceae	***Debaryomyces* sp.**	England	111
	Bionectriaceae	***Clonostachys rosea f. catenulata* (Gilman & Abbott) Schroers, 2001**	United States	179
	Cordycipitaceae	Cordycipitaceae	England	111
		***Lecanicillium psalliotae* (Treschew) Zare & Gams, 2001** = *Lecanicillium saksenae* (Kushwaha) Kurihara & Sukarno, 2009	United States	195
	Nectriaceae	Nectriaceae	England	111
	N/A (Tremellales)	Tremellales = Trichosporonales	England	111
	Trichosporonaceae	Trichosporonaceae	England	111
	Backusellaceae	***Backusella chlamydospora* Lee & Nguyen, 2021**	Republic of Korea	196
***Porcellio siculoccidentalis* Viglianisi, Lombardo & Caruso, 1992**	Iridoviridae	***Iridovirus***	Italy	144
***Porcellio spinicornis* Say, 1818** = *Porcellio pictus* Brandt	Iridoviridae	***Iridovirus***	The Netherlands	75
***Porcellio variabilis* Lucas, 1849**	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	Republic of Tunisia	86
***Porcellio* sp.**	Chilododontidae	***Chilodonella porcellionis* Doigel & Furssenko, 1921**	Russia	162
	Operculariidae	***Ballodora dimorpha* Dogiel & Furssenko, 1921**	Russia	162
	Parataeniellaceae	***Parataeniella dilatata Poisson,* 1929** = *Parataeniella binucleata* Poisson, 1929 = *Parataeniella intermedia* Poisson, 1929	Spain, United States	121, 143
	Asellariaceae	***Asellaria armadillidii* Tuzet & Manier ex Manier, 1968**	?	114
	N/A (Ascomycota / Basidiomycota (?)	***Kebertia oniscidarum* Boissevain, 1919**	The Netherlands	191
***Porcellionides cingendus* (Kinahan, 1857)**	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	Republic of Tunisia	86
***Porcellionides pruinosus* (Brandt, 1833)**	Iridoviridae	***Iridovirus***	United States	64
Trachelipodidae				
***Trachelipus arcuatus* (Budde-Lund, 1885)** = *Porcellio arcuatus* Budde-Lund, 1885	N/A (Laboulbeniales)	Laboulbeniales = Laboulbeniaceen [sic]	Federal Republic of Germany	188
***Trachelipus rathkii* (Brandt, 1833)** = *Trachelipus rathkei* (Brandt)	Iridoviridae	***Iridovirus***	The Netherlands, United States	58, 64, 75
= *Tracheoniscus rathkei* (Brandt)	Flavobacteriaceae	***Flavobacterium* sp.**	?	138
	N/A (Mollicutes)	***Candidatus* Hepatoplasma crinochetorum Wang *et al*., 2004**	Federal Republic of Germany	55
	Candidatus Hepatincolaceae Szokoli *et al*., 2016	***Candidatus* Hepatincola porcellionum Wang *et al*., 2004**	Federal Republic of Germany	55
	Ehrlichiaceae	***Wolbachia pipientis* Hertig 1936**	France	86
	Pseudomonadaceae	***Pseudomonas* sp.**	?	138
	Chilododontidae	***Chilodonella porcellionis* Doigel & Furssenko, 1921**	Europe	165
	Trochiliidae	***Dysterioides sessilia* Matthes, 1950**	Europe	165
	Opercularidae	***Ballodora dimorpha* Dogiel & Furssenko, 1921**	Europe	165
	Parataeniellaceae	***Parataeniella mercieri* (Poisson, 1928) Poisson, 1929**	Federal Republic of Germany	118
Trichoniscidae				
***Androniscus dentiger* Verhoeff, 1908**	Iridoviridae	***Iridovirus***	England	75
= *Trichoniscus dentiger* (Verheff, 1908)	Opercularidae	***Ballodora dimorpha* Dogiel & Furssenko, 1921**	France	163
		***Ballodora marceli* Remy, 1928**	France, Europe	161, 165
	Parataeniellaceae	***Parataeniella dilatata* Poisson, 1929** = *Parataeniella binucleata* Poisson, 1929 = *Parataeniella intermedia* Poisson, 1929	France	122
***Androniscus roseus* (Koch, 1838)** = *Trichoniscus roseus* (Koch, 1838)	Parataeniellaceae	***Parataeniella dilatata* Poisson, 1929** = *Parataeniella binucleata* Poisson, 1929 = *Parataeniella intermedia* Poisson, 1929	Federal Republic of Germany	118
***Haplophthalmus danicus* Budde-Lund, 1880**	Iridoviridae	***Iridovirus***	The Netherlands	75
	N/A (Ascomycota / Basidiomycota (?)	Ascomycota / Basidiomycota (?)	The Netherlands	58
***Haplophthalmus mengii* (Zaddach, 1844)**	Iridoviridae	***Iridovirus***	The Netherlands	58, 75
***Hyloniscus riparius* (Koch, 1838)**	Iridoviridae	***Iridovirus***	The Netherlands	58, 75

	Operculariidae	***Ballodora marceli* Remy, 1928**	Europe	165
	N/A ("Mesomycetozoea")	***Nodocrinella hylonisci* Scheer , 1977** nom. nud.	?	117
***Scotoniscus macromelos* Racovitza, 1908** = *Scotoniscus marcomelos* [sic]	Parataeniellaceae	***Parataeniella scotonisci* Manier ex Manier, 1970**	France	150
***Trichoniscoides albidus* (Budde-Lund, 1880)** = *Trichoniscus albidus* Budde-Lund, 1880	Iridoviridae	***Iridovirus***	The Netherlands	58, 75
	N/A (Laboulbeniales)	Laboulbeniales = Laboulbeniaceen [sic]	Federal Republic of Germany	188
***Trichoniscoides helveticus* (Carl, 1908)**	Iridoviridae	***Iridovirus***	The Netherlands	58, 75
***Trichoniscus panormidensis* Montesanto, Caruso, & Lombardo, 2011**	Iridoviridae	***Iridovirus***	Italy	144
***Trichoniscus provisorius* Racovitza, 1908** = *Trichoniscus pusillus provisorius* Racovitza, 1908	Operculariidae	***Ballodora marceli* Remy, 1928**	France, Europe	163, 165
***Trichoniscus pusillus* Brandt, 1833**	Iridoviridae	***Iridovirus***	Czech Republic and/or Slovakia, the Netherlands, England	71, 72, 73, 74, 75
	N/A (Mollicutes)	***Candidatus* Hepatoplasma Wang *et al.*, 2004**	Federal Republic of Germany	54
	Pseudomonadaceae	***Pseudomonas* sp.**	?	See Fraune and Zimmer 2008
	Asellariaceae	***Asellaria saezii* Valle, 2006**	Spain	115
***Trichoniscus* sp.**	Opercularidae	***Ballodora marceli* Remy, 1928**	Europe	165
Tylidae				
***Helleria brevicornis* Ebner, 1868**	Coxiellaceae	***Rickettsiella popilliae* (Dutky & Gooden, 1952) Philip, 1956** = *Rickettsiella armadillidii* Frutos *et al.*, 1994	France	48
	Eccrinaceae	***Eccrinoides helleriae* Manier ex Lichtwardt, 1984**	France	123
***Tylos europaeus* Arcangeli, 1938**	N/A (Mollicutes)	***Candidatus* Hepatoplasma Wang *et al.*, 2004**	Italy	54

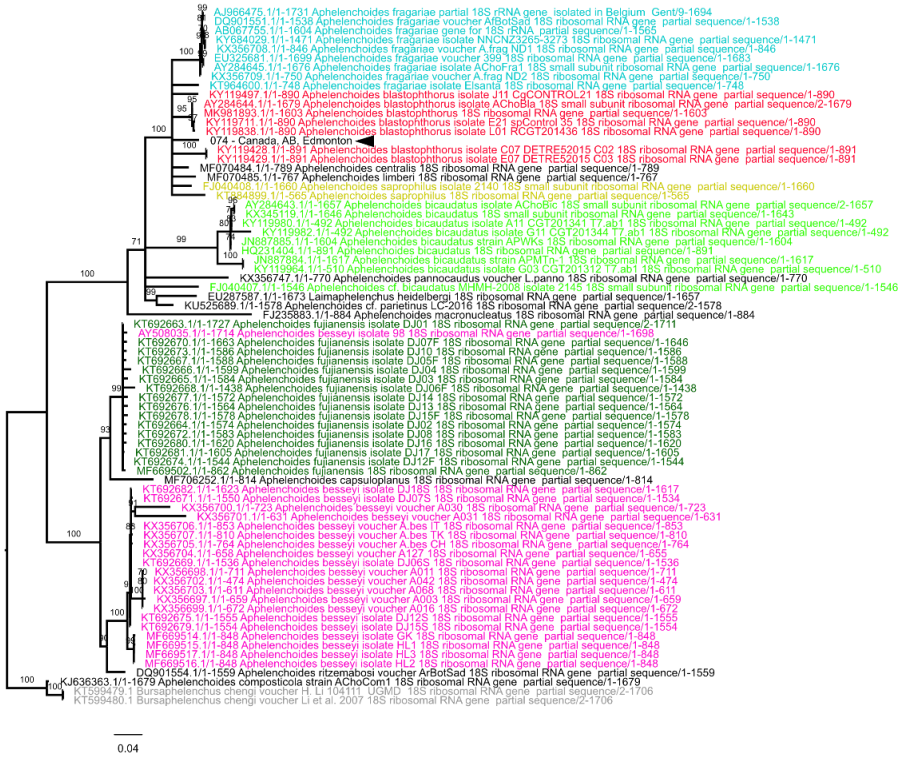


Figure C1: Maximum likelihood phylogeny of *Aphelenchoides* partial 18S sequences excluding unidentified *Aphelenchoides* environmental samples. Species represented by multiple sequences are assigned a unique color; outgroup sequences are grey. The sequence from this study is indicated with a black arrow. Numbers above the nodes indicate ultrafast bootstrap support; clades with <70% support are collapsed. Please note that the names of the sequences obtained from GenBank reflect the names given when the sequences were deposited, and may not be in accordance with currently-accepted taxonomy.

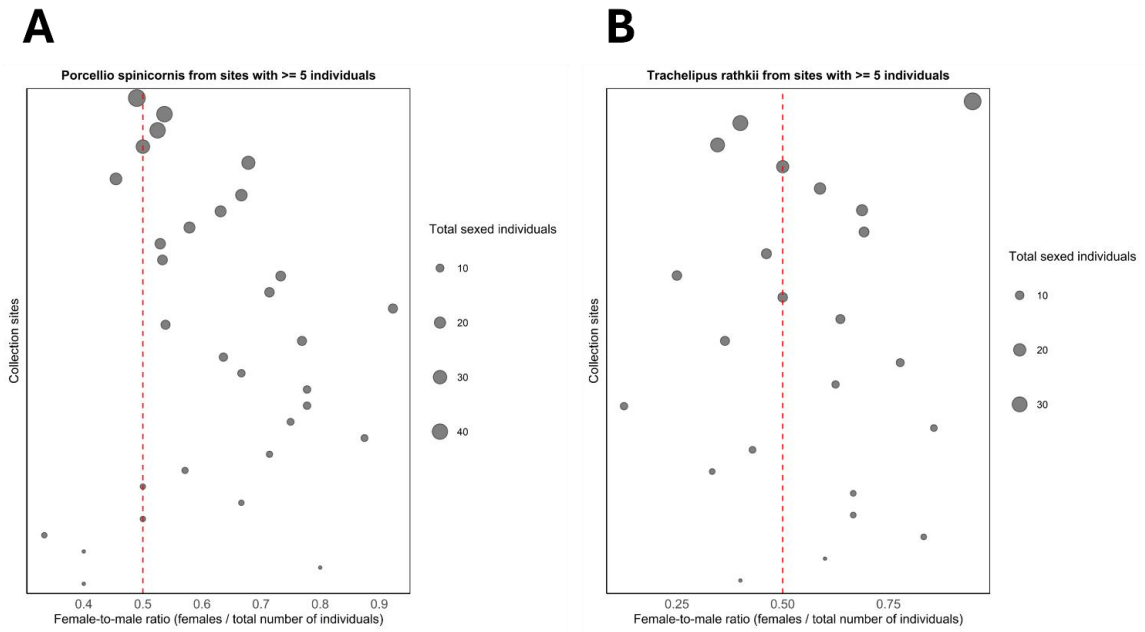


Figure C2: Sex ratios for populations of (A) *Porcellio spinicornis* and (B) *Trachelipus rathkii* in Alberta, Canada. Each point represents a population from a different collection event; sex ratios are shown only for collections of at least five individuals.

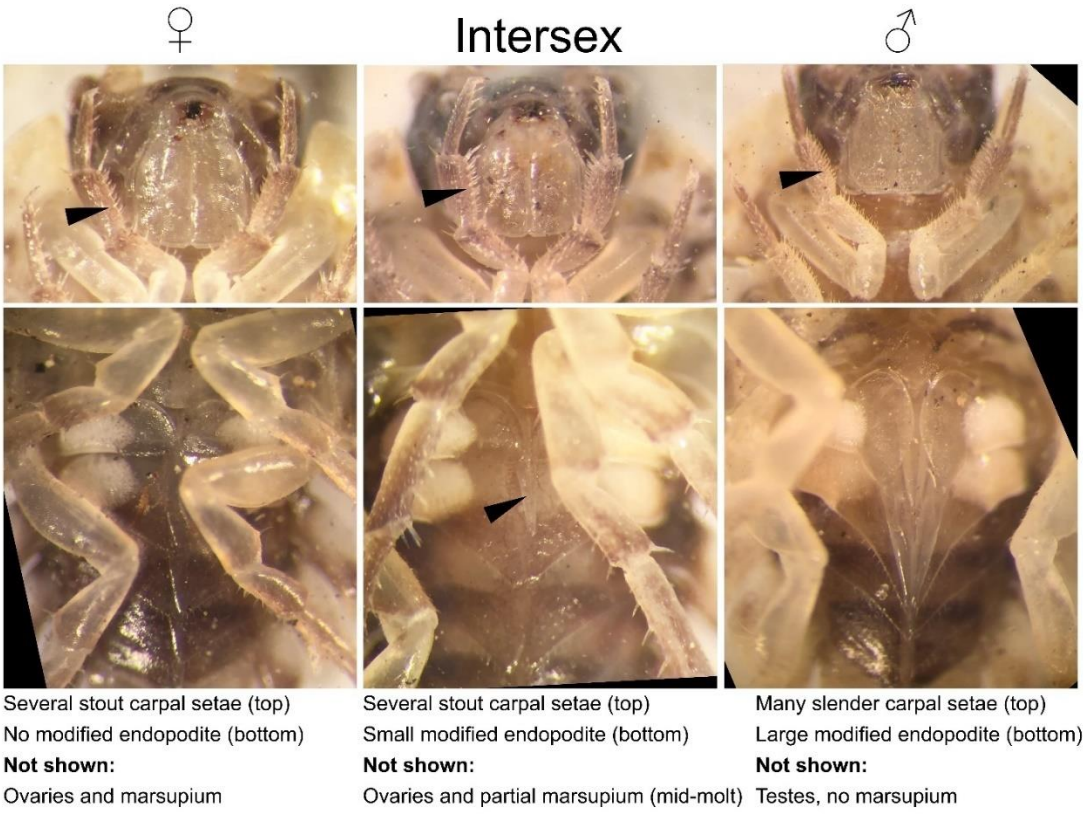


Figure C3: Comparison of sexually dimorphic traits in female, intersex, and male *Porcellio spinicornis* from Alberta, Canada.

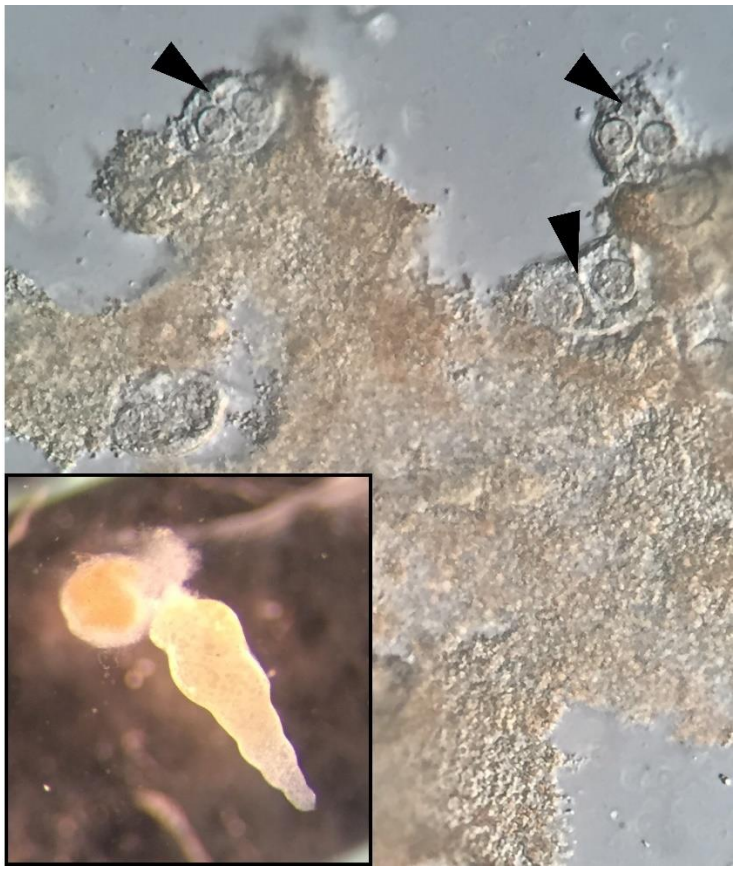


Figure C4: Structures resembling a yeast ascus (Ascomycota) from a female *Porcellio scaber* from Alberta, Canada. These structures were embedded in a tissue growth resembling hepatopancreatic tissue (inset) that was associated with one of the ovaries. Arrows indicate the ascus-like structures embedded in the tissue.

Appendix D: Supplementary Materials for Chapter 4



Figure D1: Comparison of K=2 plots produced by (A) STRUCTURE and (B) ADMIXTURE. Samples are not sorted by cluster assignment in these plots. This analysis was conducted on a preliminary dataset that included a sample (indicated with an arrow) that was later removed from the final dataset (see main text).

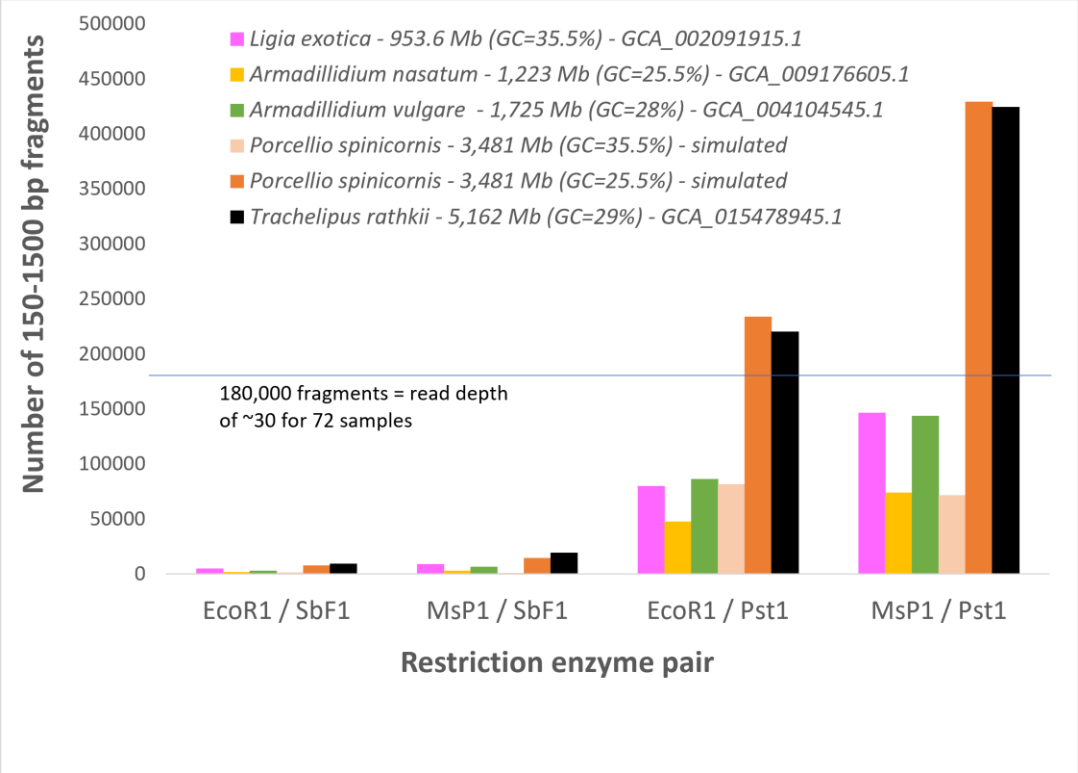


Figure D2: Number of fragments (ddRADseq loci) produced from simulated digests of sowbug genomes with different combinations of restriction enzymes. *Porcellio spinicornis* genomes are simulated; GenBank numbers for all other genomes are listed.

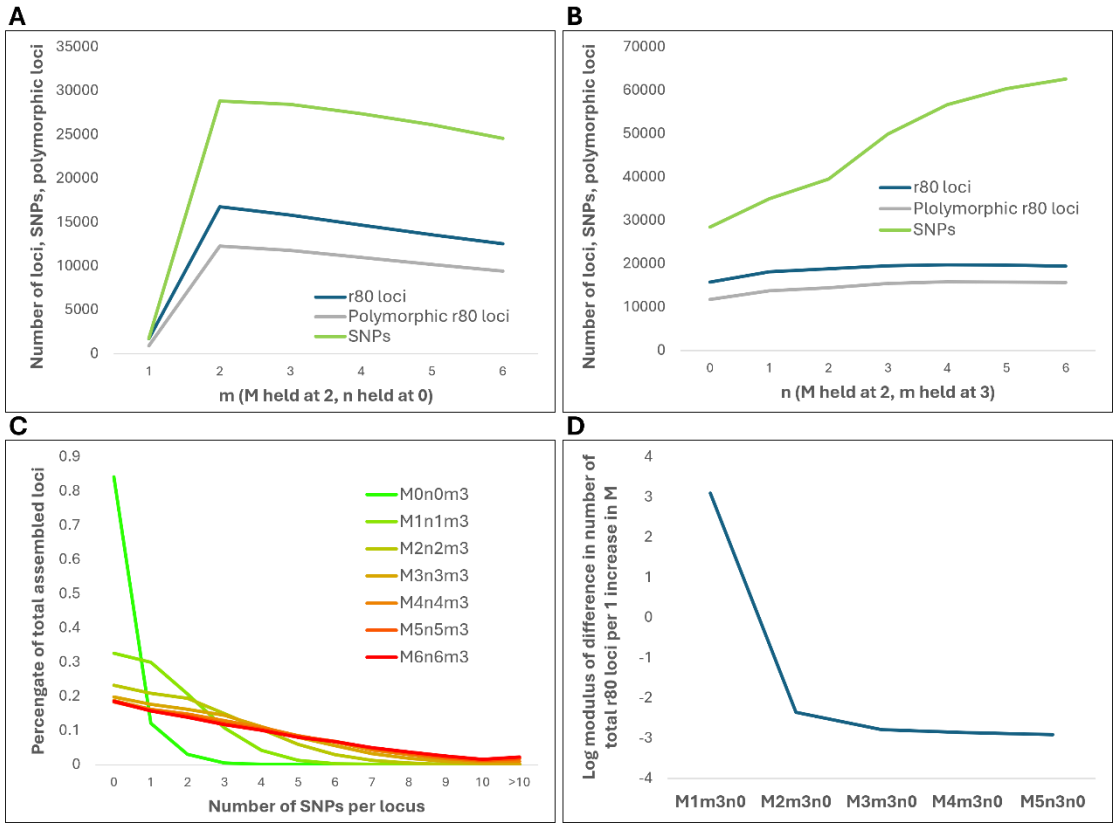


Figure D3: Plots associated with choosing Stacks parameters M, m, and n, which control de novo formation of alleles and loci from RADseq data (Paris *et al*. 2017). "r80 loci" are loci that appear in at least 80% of the dataset. **A:** total polymorphic r80 loci reaches a plateau when m > 1. **B**: total r80 loci reaches a plateau when n = 3. **C:** Change in percentage of total assembled loci with each number of SNPs reaches a plateau when M=3, n=3, and m=3. **D:** M=3, m=3, n=0 has the lowest log modulus of the number of new r80 loci (compared to the number obtained for the previous value of M).

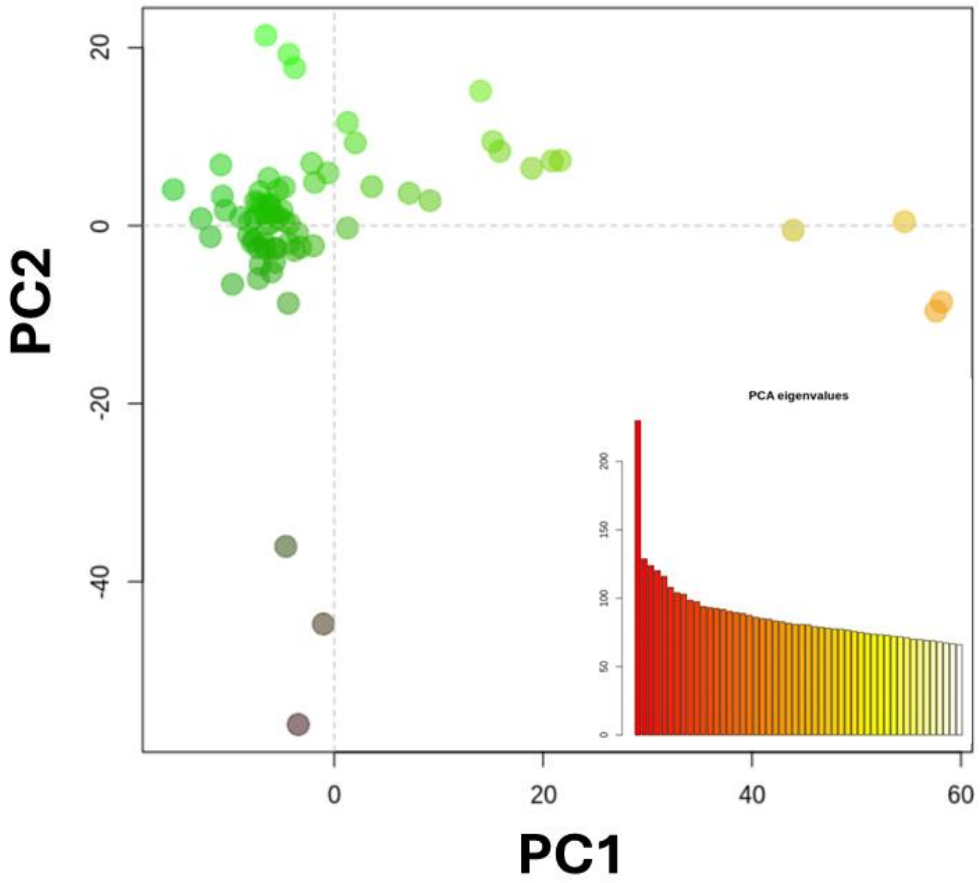


Figure D4: PCA plot produced with 39,978 SNPs from 71 *Porcellio spinicornis* from Alberta. Individuals are colored by the values of the first three principal components. The three main clusters corresponding to three samples from greenhouse site 3 (bottom left, brown), four samples from northern Calgary (right, yellow), and the remaining samples (upper left, green). Inset shows the eigenvalues for the first 50 principal components.

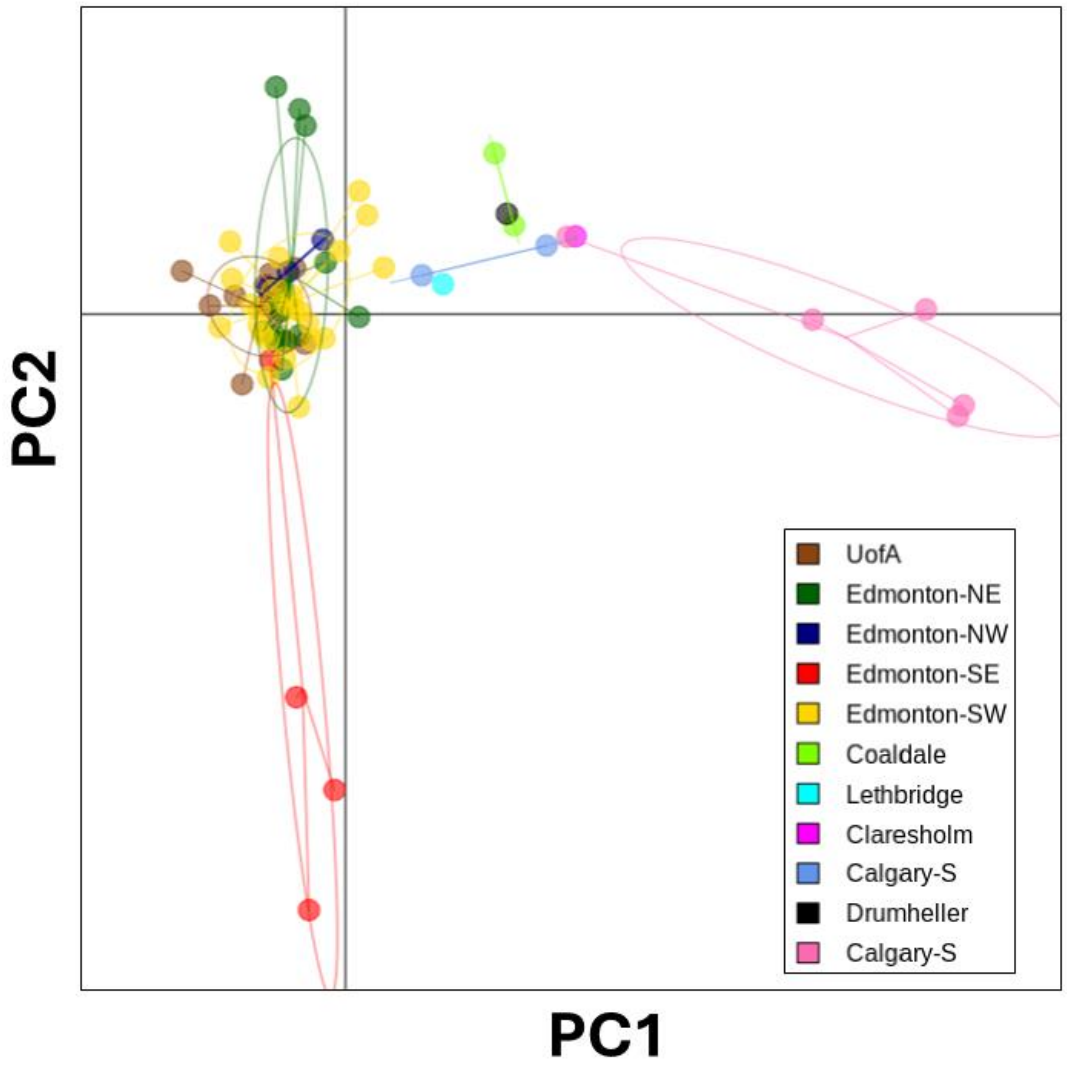


Figure D5: PCA plot produced with 39,978 SNPs from 71 *Porcellio spinicornis* from Alberta, colored by locality. UofA = University of Alberta, NE = northeast, NW = northwest, SE = southeast, SW = southwest, S = south, N = north.

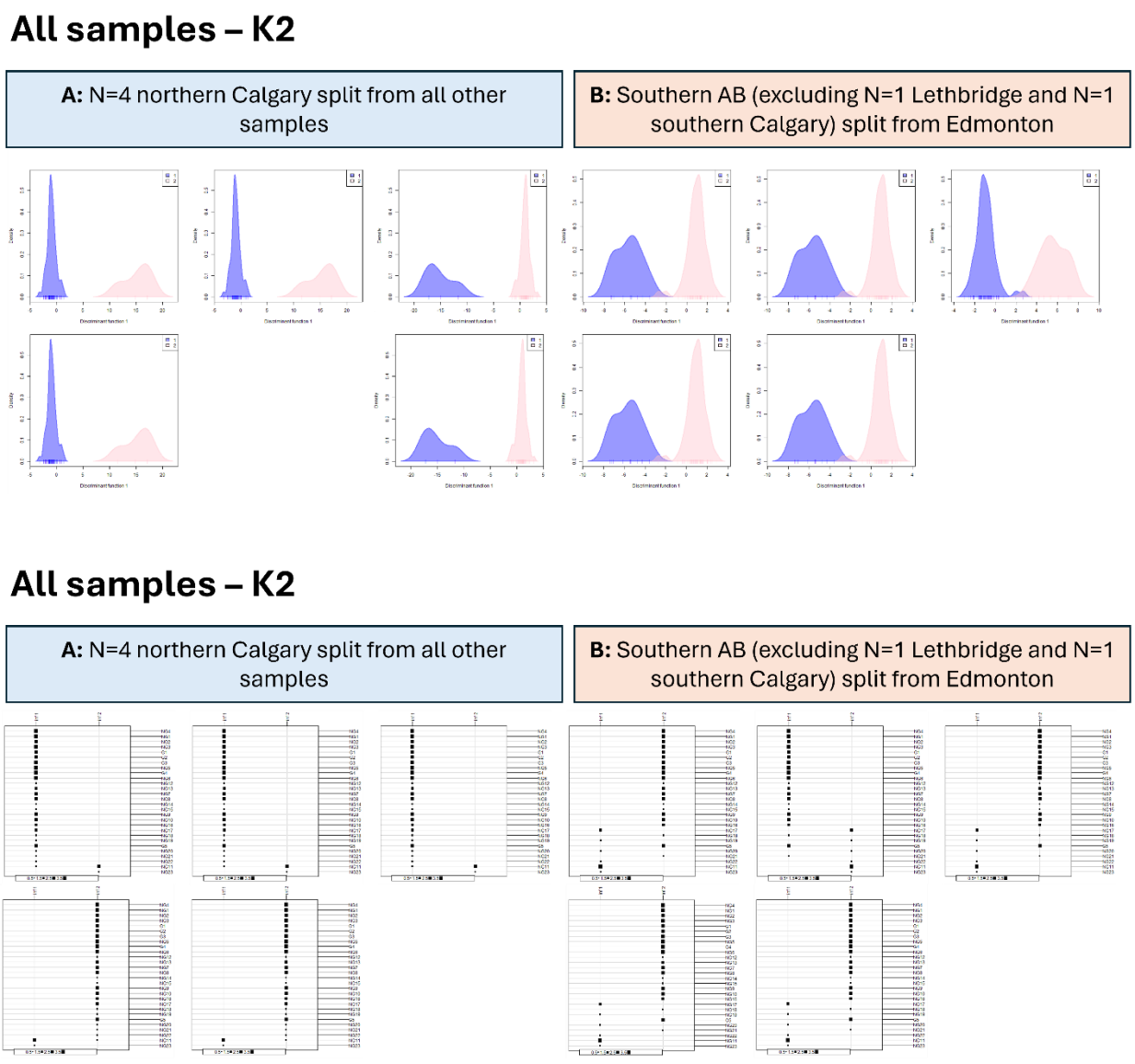


Figure D6: DAPC discriminant functions and K-means clustering plots for 71 *Porcellio spinicornis* from Alberta when K=2. Analyses were repeated 10 times; replicates are sorted into groups that yielded similar results.

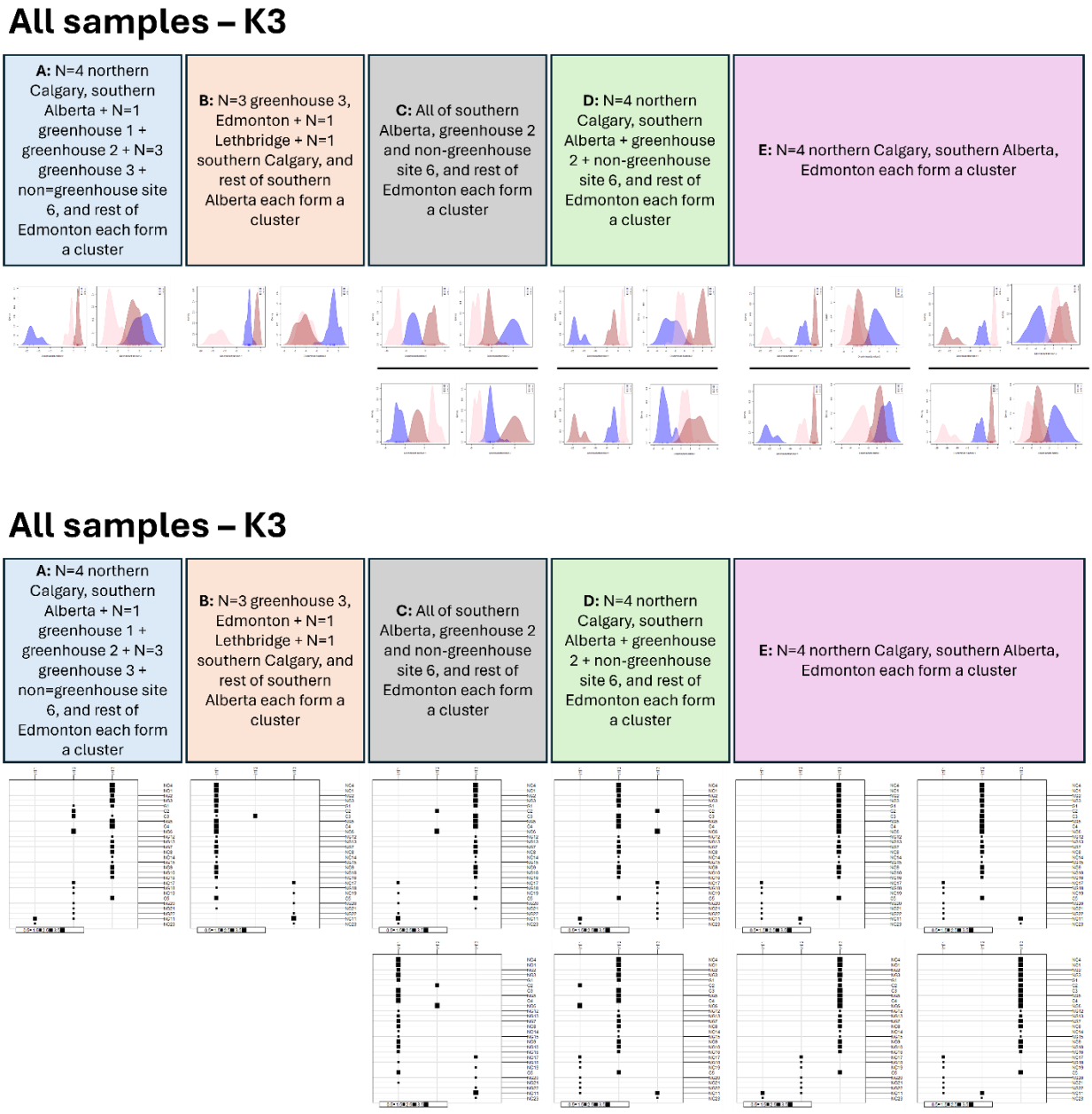
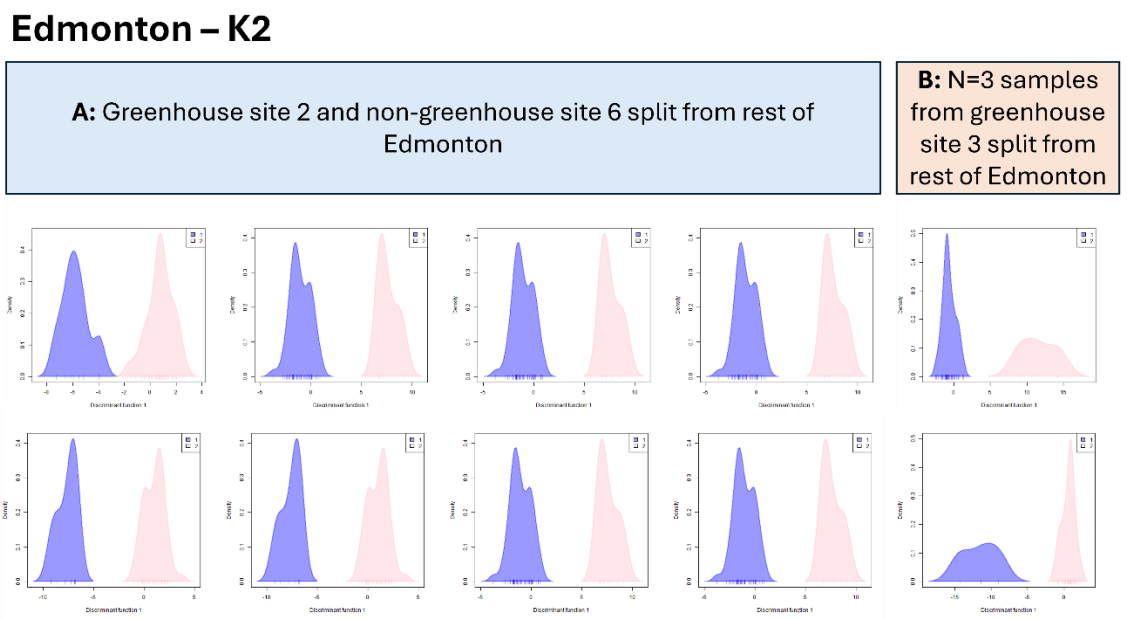


Figure D7: DAPC discriminant functions and K-means clustering plots for 71 *Porcellio spinicornis* from Alberta when K=3. Analyses were repeated 10 times; replicates are sorted into groups that yielded similar results.



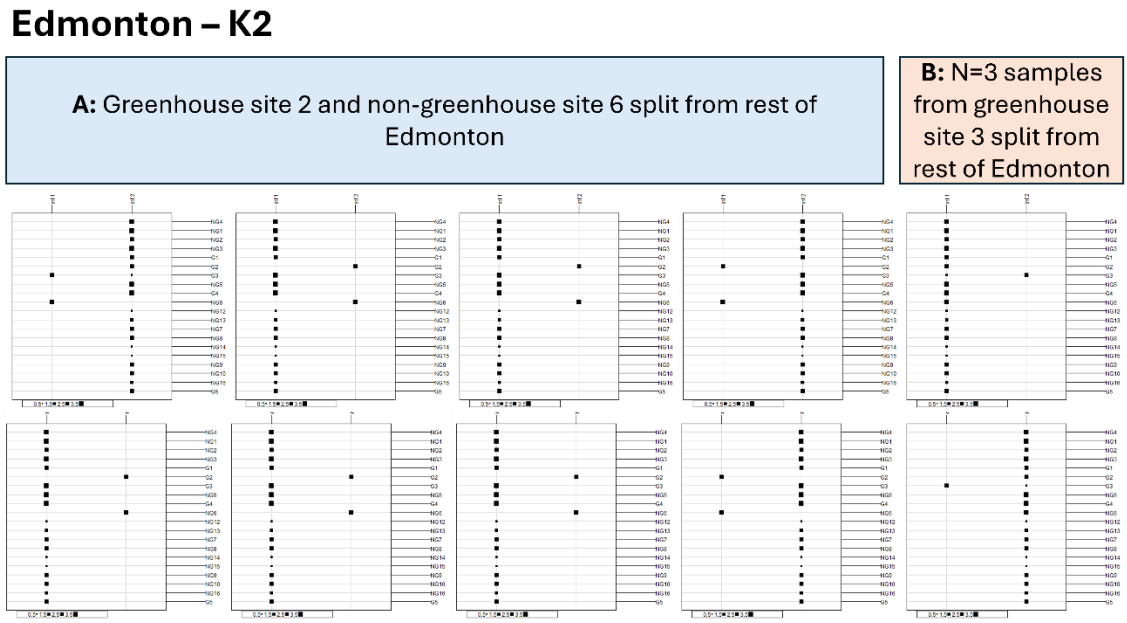


Figure D8: DAPC discriminant functions and K-means clustering results for 59 *Porcellio spinicornis* from Edmonton when K=2. Analyses were repeated 10 times; replicates are sorted into groups that yielded similar results.

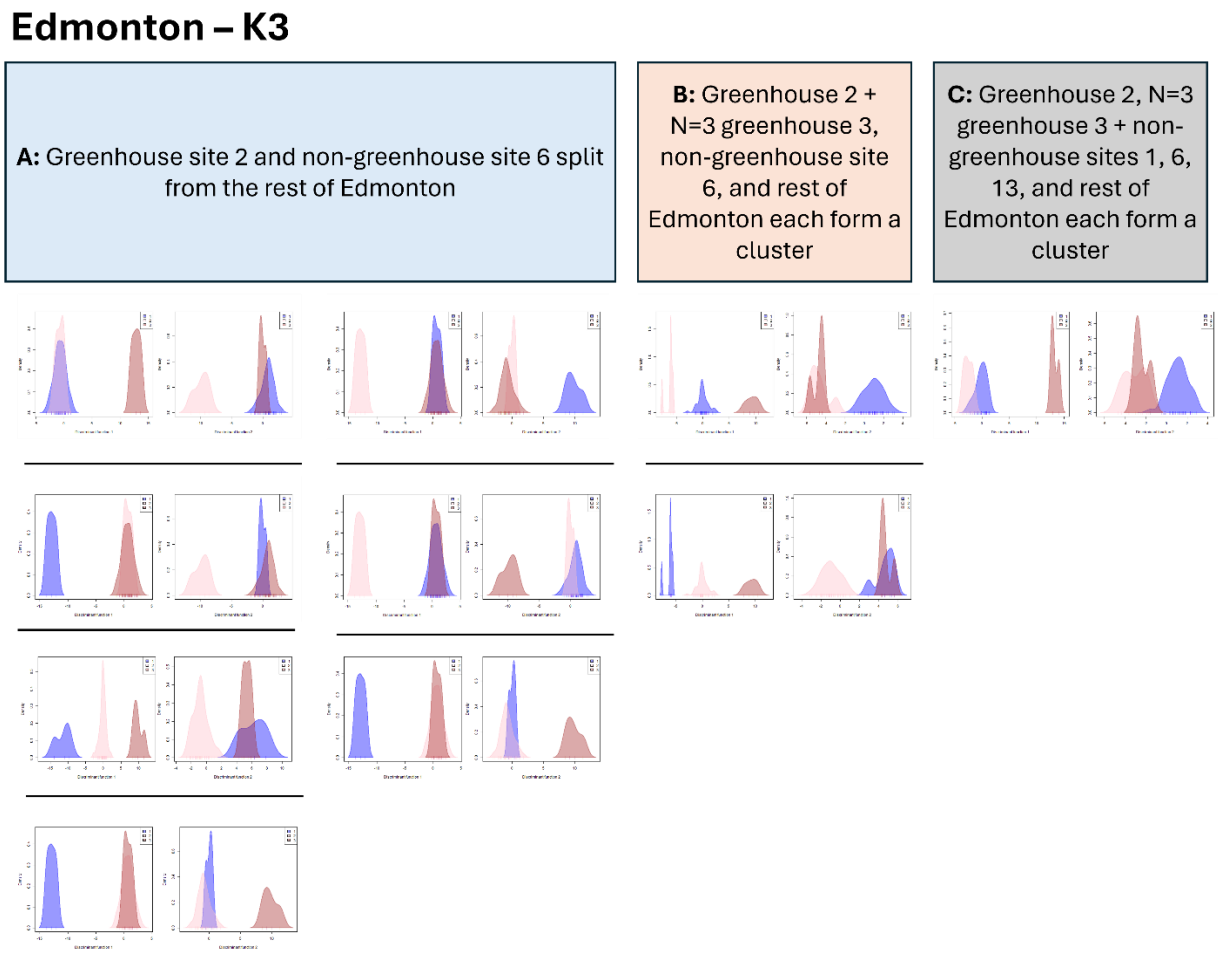


Figure D9 (continued on following page): DAPC discriminant functions and K-means clustering results for 59 *Porcellio spinicornis* from Edmonton when K=3. Analyses were repeated 10 times; replicates are sorted into groups that yielded similar results.

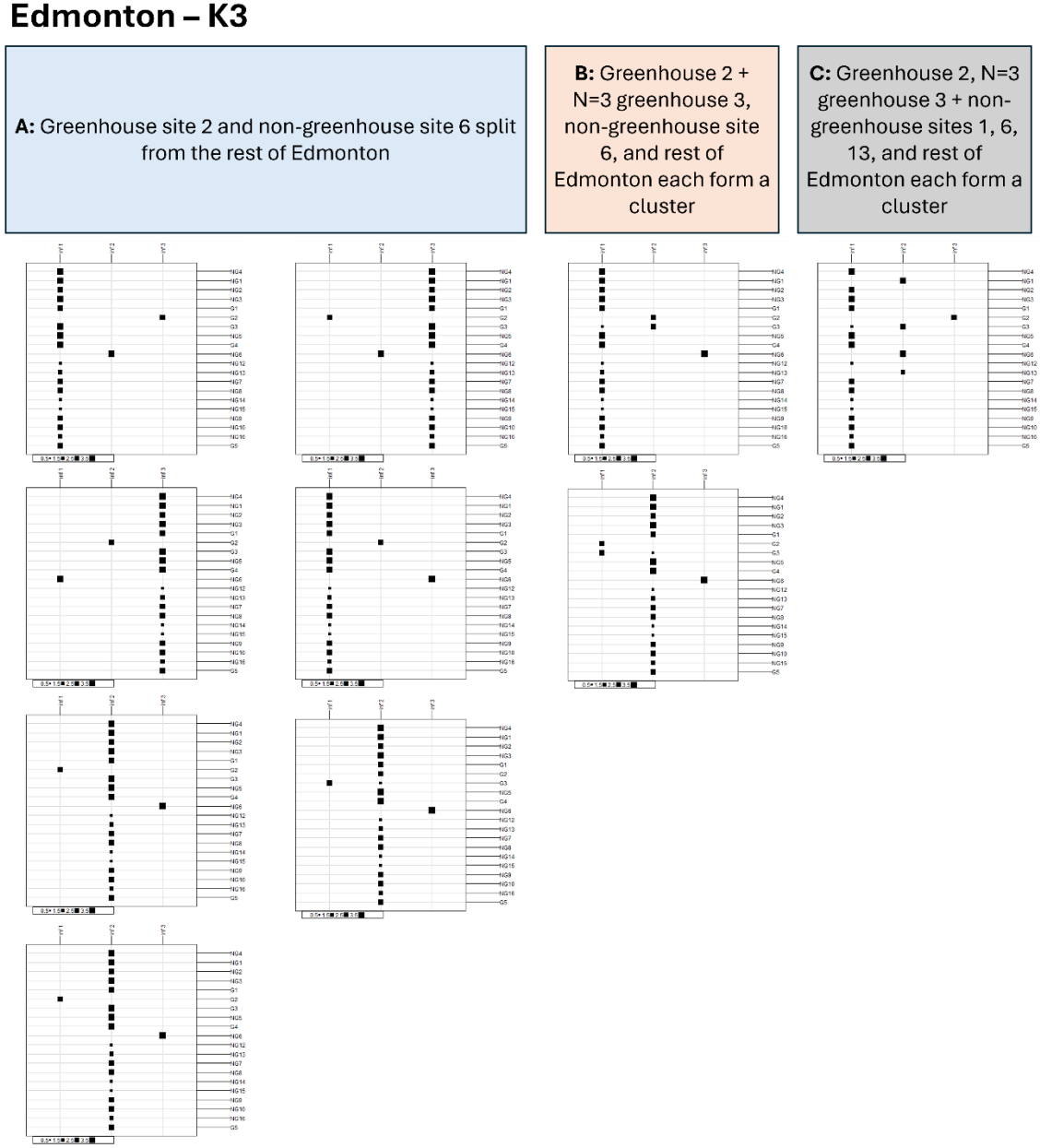


Figure D9 (continued from previous page): DAPC discriminant functions and K-means clustering results for 59 *Porcellio spinicornis* from Edmonton when K=3. Analyses were repeated 10 times; replicates are sorted into groups that yielded similar results.

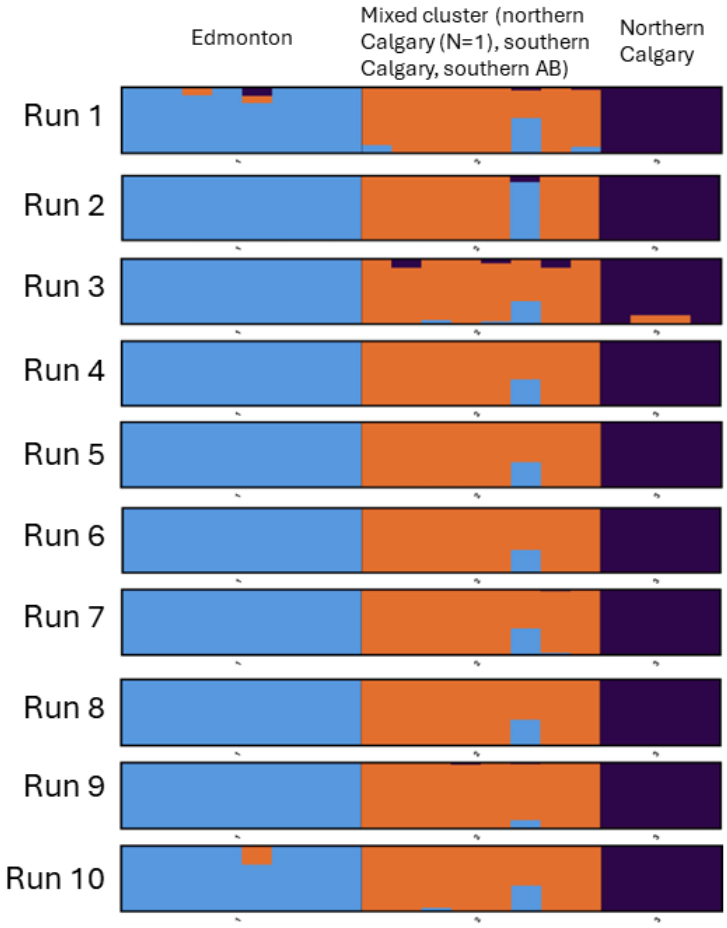
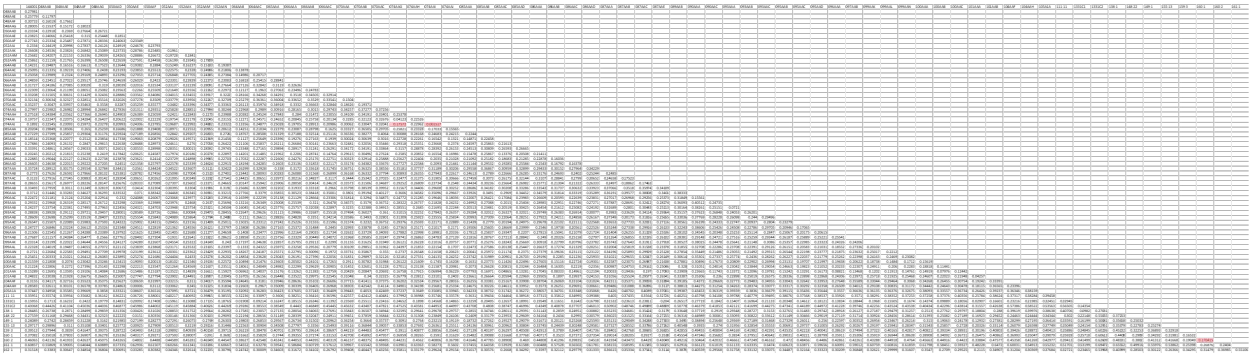


Figure D10: K=3 ADMIXTURE plots for ten datasets correcting for unbalanced sampling. Each dataset (runs 1-10) included eight random samples from Edmonton and all samples from non-Edmonton sites (i.e. southern Alberta).

A



B

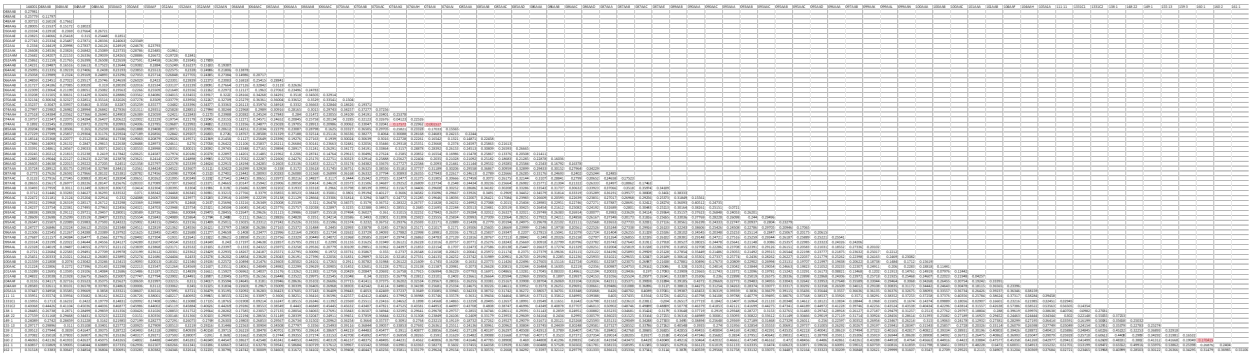


Figure D11: Kinship coefficients for 71 *Porcellio spinicornis* individuals from Alberta, calculated from (A) 39,978 SNPs, multiple SNPs allowed per locus (dataset 1) and (B) 11,800 SNPs, one per locus (dataset 2). Kinship coefficients greater than zero are highlighted in red; values greater than 0.177 indicate second-degree relatives (see Manichaikul *et al*. (2010) for interpretation of kinship coefficients).

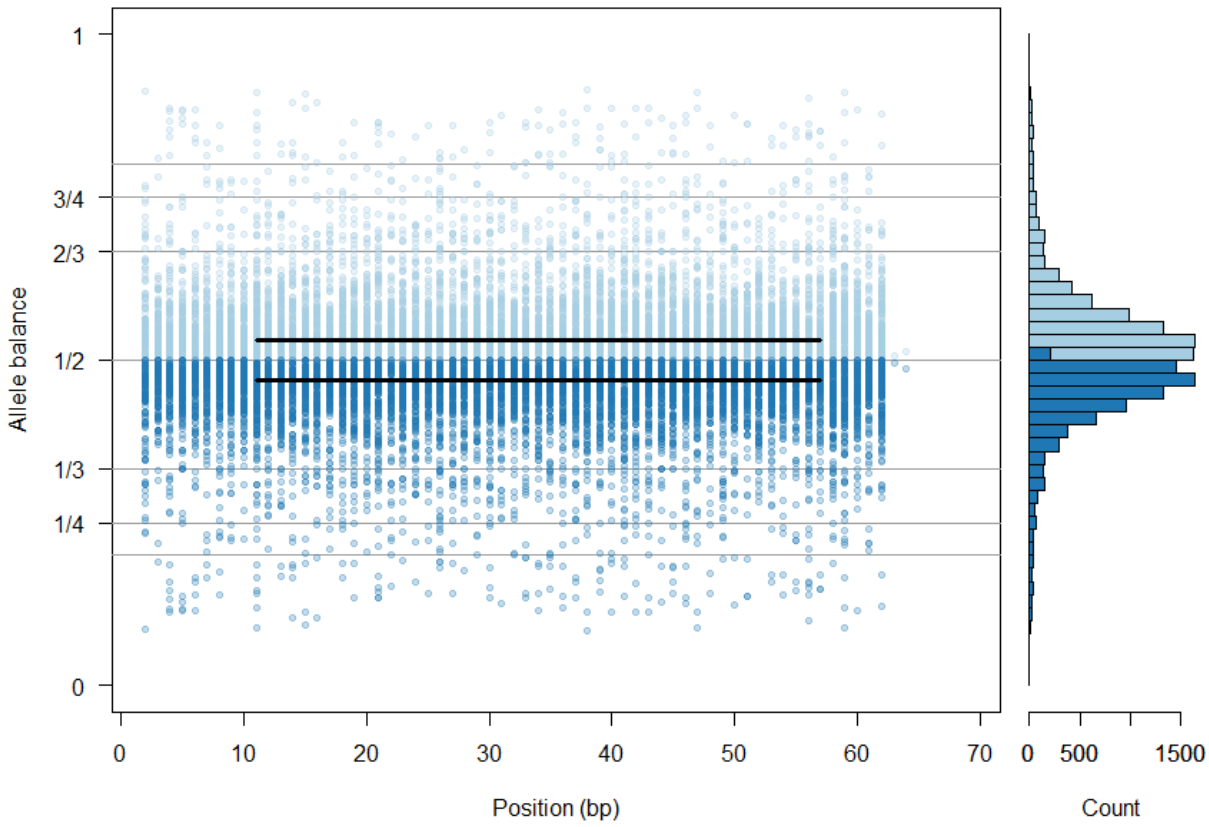


Figure D12: Allele balance for 39,978 SNPS from 13,262 loci (63 bp long) from 71 *Porcellio spinicornis* individuals from Alberta. The average allele balance is centered around 1/2, indicating that this species is diploid (see main text).

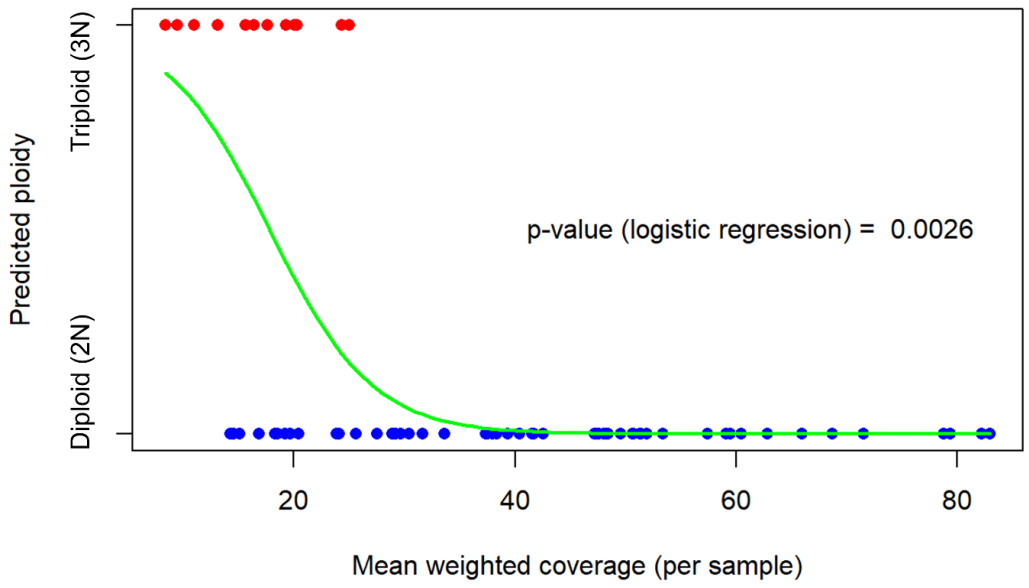


Figure D13: Predicted ploidy (based on allele balance) of 71 *Porcellio spinicornis* individuals from Alberta as predicted by the mean weighted coverage (average weighted read depth). Ploidy is significantly predicted by mean weighted coverage, where individuals with low coverage tend to have also been predicted to be triploid based on their average allele balance (see main text).

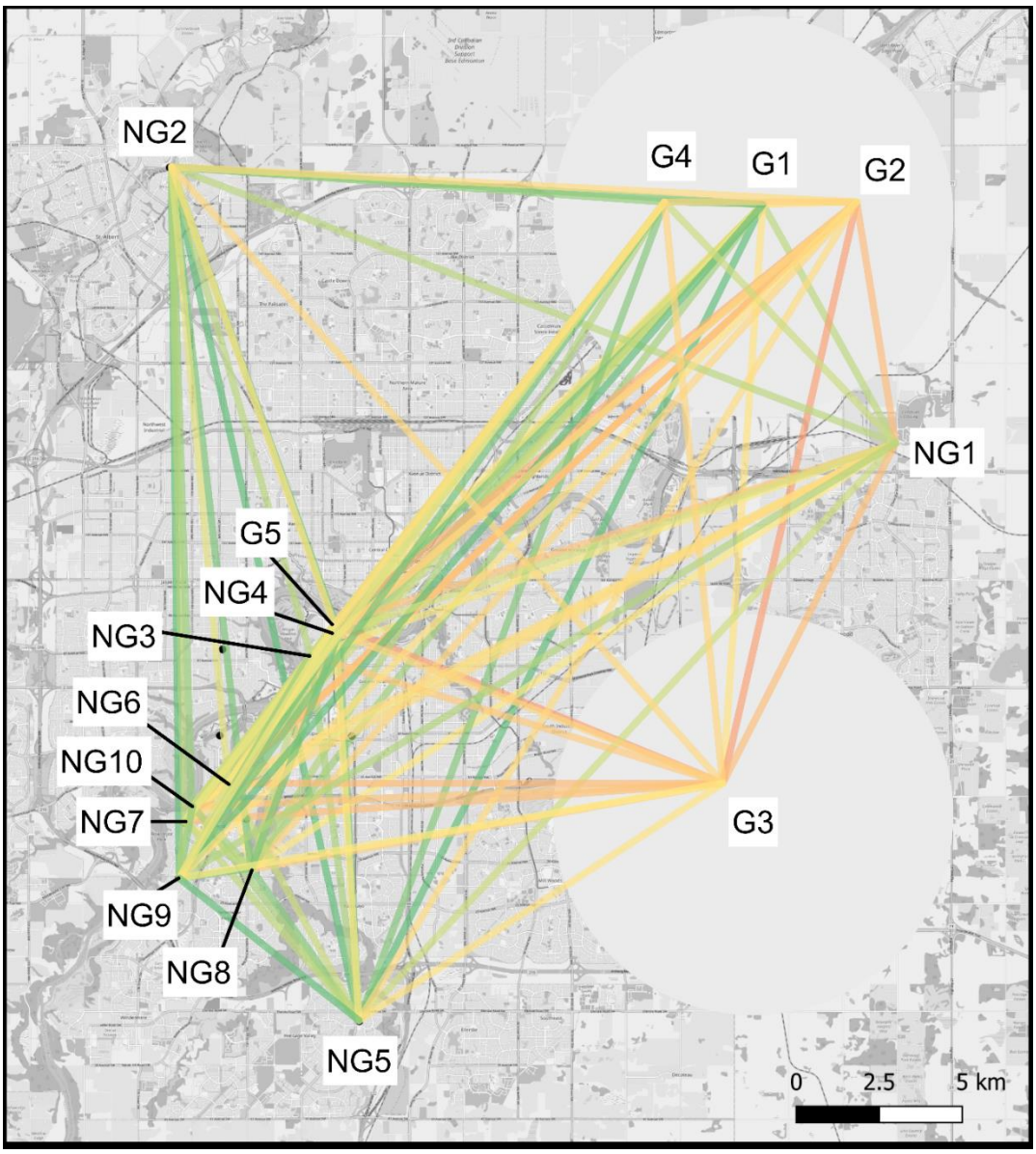


Figure D14: Collection localities and pairwise F_{ST} for populations of *Porcellio spinicornis* from five greenhouses (G) and 10 non-greenhouse sites (NG) in Edmonton. Greener lines connect sites with lower pairwise F_{ST} values, and oranger lines connect sites with higher F_{ST} values. See Table 4.2 for F_{ST} values and associated p-values. Greenhouse locations are obscured for greenhouses 1-4.

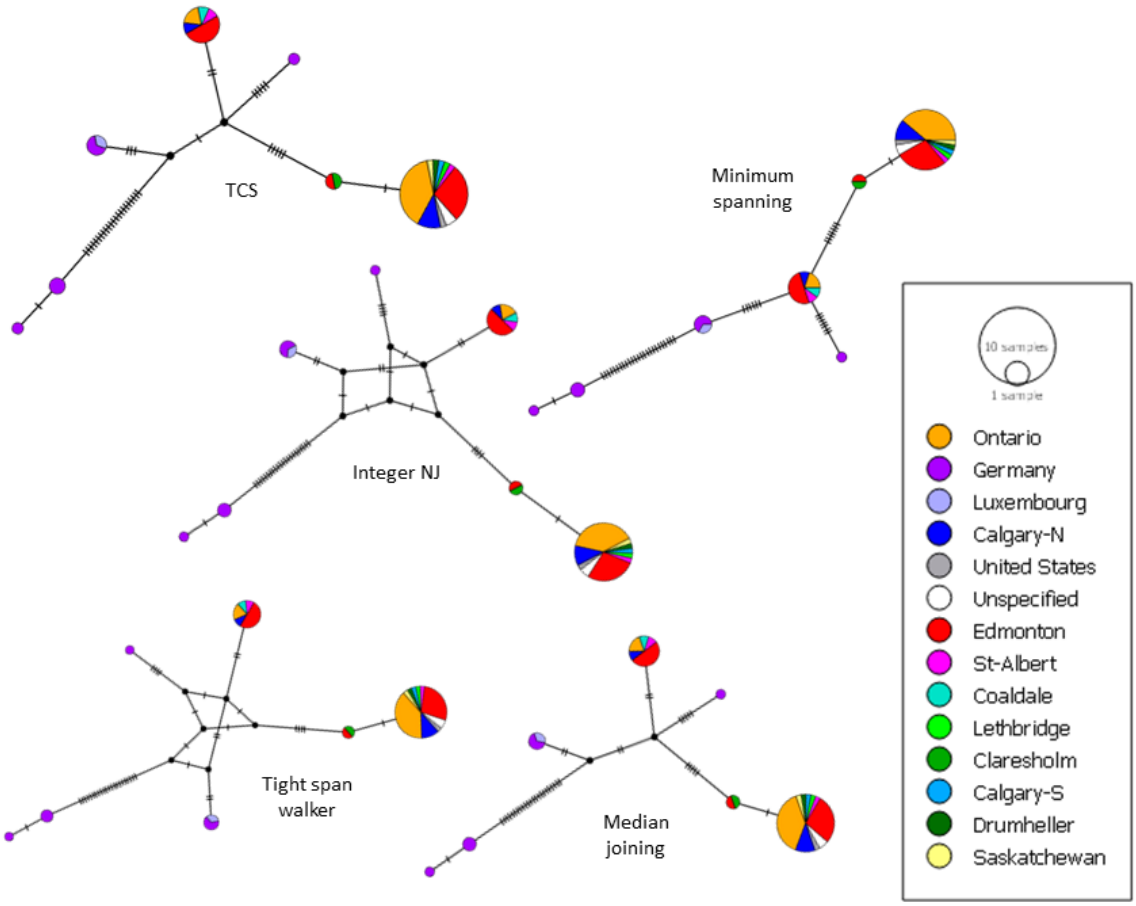


Figure D15: Haplotype networks of 55 *Porcellio spinicornis* COI sequences from North America (Canada and Minnesota) and Europe (Germany and Luxembourg). Labels for each network indicate the algorithm used to create it. Marks on the lines connecting haplotypes indicate the number of nucleotide differences. Samples are colored by collection locality. European haplotypes are in shades of purple, and inferred unsampled haplotypes are colored black. Calgary-N = northern Calgary, Calgary-S = southern Calgary.