8-2017

FLEAS OF THE AMERICAN PIKA: DIVERSITY AND BIOGEOGRAPHY IN NORTH AMERICA’S INTERMOUNTAIN WEST

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Recommended Citation
Wijewardena, Niyomi, "FLEAS OF THE AMERICAN PIKA: DIVERSITY AND BIOGEOGRAPHY IN NORTH AMERICA’S INTERMOUNTAIN WEST" (2017). *All NMU Master's Theses*. 156.
https://commons.nmu.edu/theses/156

FLEAS OF THE AMERICAN PIKA: DIVERSITY AND BIOGEOGRAPHY IN NORTH AMERICA'S INTERMOUNTAIN WEST

By

Niyomi Wijewardena

THESIS

Submitted to
Northern Michigan University
In partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Office of Graduate Education and Research

June 2017

SIGNATURE APPROVAL FORM

FLEAS OF THE AMERICAN PIKA: DIVERSITY AND BIOGEOGRAPHY IN NORTH AMERICA'S INTERMOUNTAIN WEST

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ABSTRACT

FLEAS OF THE AMERICAN PIKA: DIVERSITY AND BIOGEOGRAPHY IN NORTH AMERICA'S INTERMOUNTAIN WEST

By

Niyomi Wijewardena

American pikas (*Ochotona princeps*) are small mammals that are widely distributed across North America's Intermountain West. Previous investigations revealed five geographically distinct mitochondrial lineages within *O. princeps* associated with different mountain systems of the Intermountain West. In contrast, diversity of endoparasitic helminths of pikas is not structured geographically in the same way. Instead, there are two primary parasite assemblages, one distributed across southwestern pika populations and one found across the northeastern part of the host range. These contrasting patterns suggest that the shared history of pikas and their parasites had different consequences for the evolutionary trajectories of these organisms. Here I investigate whether or not patterns in diversity of fleas associated with pikas suggest a history that is more similar to that of the host or that of the endoparasites. I characterized the flea diversity and distribution within American pikas based on a sample of 837 flea specimens collected from 34 localities in the Intermountain West. I identified 11 flea species, two of which are common and known to be specific to pikas. I examined the population genetic structure of the most common flea species, *Ctenophyllus armatus,* for phylogeographic concordance between host and parasite diversity. I generated DNA sequences from the mitochondrial COII gene for 71 fleas representing 24 localities and showed general congruence between the phylogeographic structure of the fleas and that of the endoparasites.

DEDICATION

For my family and my fiancé, James House

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to all the people who helped me on this journey. First, my advisor Dr. Kurt Galbreath for being the greatest advisor and mentor that anyone could ever ask for. Thank you for taking me into your lab and believing in me. You always made sure to have time for me when I needed your advice. I am also grateful for your financial support that made my project possible. Without the brilliant insight you provided, this study would not have been possible. You set a good example of a professional scientist that helped me set my future goals. I was fortunate to have you as my advisor; I hope that our journey together will continue with many publications in the future.

My sincere gratitude to Dr. Ralph Eckerlin who agreed to serve as a committee member even from far away. Thank you for passing down your knowledge about fleas. Everything I know about fleas, I learnt from you. This project would not have been possible otherwise. Thank you for believing in me and most of all, thank you for travelling all the way from Virginia to be there for me. I would also like to thank Dr. Neil Cumberlidge for agreeing to serve in my committee. Your expertise in taxonomy will greatly help me in getting my thesis published.

I also want to thank my friends and fellow graduate students at Northern Michigan University, Department of Biology. My lab mates, Heather Toman, Gena Haas, Sarah Gallagher and Katie Nehiba helped me with everything lab related and were always there when I needed help with my project. Especial thanks to Sarah and Katie, who were also my officemates; you two were the best at keeping me on course and not letting me wander off. I am sorry you had to listen to me talk about fleas all the time, but I learned a lot from both of you about life and science. Thank you so much for that. Amanda Vanderplow, Danielle Brogren, Alex Graeff, Luke Van Osdol, Umair Riyas, Katie Bjornen and Marissa Kane – you all helped me with my project and most of all, thank you for keeping me sane and giving me a life outside of grad school. I love you people and will remember you always.

Lastly, my deep gratitude goes out to my father, Kapila Wijewardena, my mother Marina De Mel, and my brother Dileep Wijewardena for believing in me and supporting me in my journey far away from home. James House my fiancé – thank you for being patient and loving. I am truly lucky to have such a kind, loving person who always challenges me intellectually. Thank you for being my designated proofreader. I am happy to have you in my life and I look forward to spending the rest of my life with you.

PREFACE

The cost of this research project was covered by various grants including a Development Grant from the NMU Department of Biology, Excellence in Education Awards, a Charles C. Spooner Award, and a Graduate Research and Scholarly Activities Award. Some aspects of this research were also supported by NSF grants DEB 0506042 and DEB 1258010.

This thesis follows the format prescribed by the Journal of Biogeography and the Department of Biology.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 1

CHAPTER 2

LIST OF FIGURES

CHAPTER 1: SIPHONAPTERA (FLEA) DIVERSITY AND DISTRIBUTION AMONG AMERICAN PIKA POPULATIONS IN NORTH AMERICA'S INTERMOUNTAIN WEST

INTRODUCTION

North America's Intermountain West is a region with high-elevation mountain ranges connected by low, intervening valleys, resulting in varied environmental conditions along steep elevation gradients (Thompson et al., 1993). Tectonic and climatic changes in the past have influenced the topography of this landscape over millions of years (Badgley et al., 2014). This topographical complexity, along with past alternating periods of warming and cooling of climate, influenced the genetic structure of the species that are found in montane habitat islands of western North America (Hewitt, 1996). Species that show range expansion during glacial periods and range retraction during interglacials (e.g., Galbreath et al., 2009) have moved across an elevation gradient from and to sky islands (restricted high-elevation patches of habitat) (Guralnick, 2007). Climatic oscillations between glacial and interglacial periods resulted in expansion and fragmentation of populations in cold-adapted organisms. As a direct response to climate cooling, alpine species expanded their range, thus increasing gene flow between populations (Galbreath et al., 2009). Conversely, during climate warming, populations of these cold adapted species underwent fragmentation and were geographically isolated, restricting gene flow among fragmented populations. However, warm periods did facilitate the dispersal of warm-adapted species that are acclimatized to such conditions. For example, climate warming during the Miocene Climatic Oscillation (17-14 million years ago) promoted diversification in most mammalian groups in the Great Basin region, but it was followed by a period (13-12 million years ago) of extinction with climate cooling (Badgley et al., 2014). This trend toward climate cooling can be observed throughout the glacial history leading up to present day. Periodic climatic oscillations shaped the diversity of many mammalian groups in this Intermountain West, which therefore offers an excellent model for examining biogeographical patterns of species diversification.

The Pleistocene epoch (2.6 million years ago - 11,700 thousand years ago) was a cold period in history during which dispersal of alpine species was generally facilitated. During this period, continental ice sheets shaped the ecology and biogeography of high-altitude ecosystems (Hewitt, 2004). Species that took advantage of open dispersal corridors show mixing of genetic diversity in their population structure (Latch et al., 2009), whereas poor dispersers, such as the American pika (*Ochotona princeps* Richardson 1828), show a population structure that reflects regional isolation over deep time (Galbreath et al., 2010). During the Last Glacial Maximum (LGM), which spanned 18,000-21,000 thousand years ago (Clark et al., 2009), species distributions in temperate areas of western North America were considerably different from what is observed today (Waltari et al., 2007). The ice sheets covered a great part of North America, restricting species to ice-free refugia in Beringia and south of the continental ice sheets (e.g., in the Pacific Northwest; Shafer et al., 2010). Glacial and interglacial periods that consisted of periodic climate cooling and warming, respectively, influenced the current fragmented distribution of alpine species across this topographically complex landscape (Galbreath et al., 2009). Glacial cycles were responsible for intraspecific genetic differences that arose from isolation between populations of alpine species such as thin horn sheep (Worley et al., 2004) and pikas (Galbreath et al., 2010).

Alpine species such as the American pika are generally restricted to sky islands usually above 2300 m in elevation (Rickart, 2001). Ideal habitat for pikas is talus (rocky boulder fields) where they can store food for winter and escape from predators (Smith, 1974). Their restriction to high-elevation habitats arises from their low tolerance for high temperatures. This physiological property of pikas allows suitable habitat to be detected based on regional climatic conditions (Simpson, 2009). As a result, climate change has a great impact on these cold-adapted species. Phylogeographic studies of pikas show deep genetic divergence across their range that can be explained by their isolation among mountain systems associated with past climatic oscillations (Galbreath et al., 2010). According to phylogenetic analysis using mitochondrial DNA data, there are five geographically distinct lineages of *O. princeps* that are associated with different mountain systems of the Intermountain West. These include the Northern Rocky Mountains, Southern Rocky Mountains, Cascade Range, Sierra Nevada, and Central Utah (Fig. 1.1) (Galbreath et al., 2009, 2010). Historical movements of pikas along elevation gradients and latitudes during Pleistocene climatic cooling events allowed regional lineages to expand, bringing into contact pikas from different lineages. Conversely, the warm interglacial periods isolated pika populations on cool high-altitude areas that fragmented them into smaller populations across the Intermountain West. However, periodic fragmentation within mountain systems did not prevent the periodic exchange of alleles between populations, and cohesion of regional genetic lineages was maintained (Galbreath et al., 2009).

Parasites can provide insight into the history of hosts (Brooks & McLennan, 1993; Hoberg, 1997; Galbreath & Hoberg, 2015). Parasite population genetics and demographic history can shed light on the evolution of the host and its demographic history (Whiteman & Parker, 2005). Pikas harbor a variety of both endo- and ecto-parasites. A parasite that can live on or in the epidermis of the host is classified as an ectoparasite (Wall & Shearer, 2008). Conversely, endoparasites live inside the body of a host. Endoparasites of pikas, specifically host-specific pinworms and cestodes, have distributions that appear to have been mediated by climate-driven host range shifts (Galbreath & Hoberg, 2012, 2015). In this study, I provide the first range-wide exploration of patterns of diversity in an ectoparasite of American pikas. Unlike endoparasites, ectoparasites are exposed to the external environment, which suggests the possibility that in addition to host dispersal, environmental factors might have played a greater role in influencing parasite dispersal than do endoparasites. I specifically focus on fleas, which offer a diverse assemblage of morphologically identifiable species whose taxonomy is reasonably well established.

Current distribution of flea species from North America shows fleas from both Nearctic and Palearctic origins parasitizing many different mammalian orders (Krasnov, 2008). Connectivity between North America and Asia across the Bering land bridge promoted dispersal of fleas between the Nearctic and the Palearctic, giving rise to similarities in flea assemblages (Medvedev, 1996). For example, lagomorphs (including pikas and hares) harbor species of fleas that have a Holarctic distribution (Krasnov, 2008). There is a greater diversity of fleas found in the Palearctic than in the Nearctic, which suggest that host-flea associations in the Palearctic have a much deeper history (Krasnov, 2008; Krasnov et al., 2011), yet studies of the fleas of small mammals from western North America have revealed a number of flea species associated with multiple hosts (Vashchenok, 1988) including rodent hosts (Foley et al., 2017).

Two primary objectives of this study are to record the flea species associated with *O. princeps* and to map this diversity across the host's geographic distribution. These results will allow me to test alternative hypotheses regarding the factors that structured large-scale patterns of diversity in the pika-parasite assemblage. Hypothesis 1: Climate-driven pika movement across the landscape led to contact and parasite-sharing among individuals from different lineages facilitated the dispersal of fleas across host lineage boundaries. If so, the distribution of flea species across the Intermountain West should show geographically widespread flea species that span host lineage boundaries, and species distributions should be partitioned into two geographically distinct assemblages, with a biogeographic distinction between the southwestern and northeastern portions of the host's range similar to that of the two major helminth assemblages (Galbreath et al., 2009; Galbreath & Hoberg, 2015). Hypothesis 2: Flea distribution patterns are concordant with the five major genetically distinct pika lineages, suggesting that fleas tracked host lineages with strong fidelity and, if historical episodes of ephemeral contact between host lineages did occur, the fleas did not disperse across those boundaries (Galbreath et al., 2009).

METHODS

Study system

Siphonaptera (fleas) is an order of insects with highly specialized morphology and life history characteristics associated with their parasitic life strategy. Fleas are blood-feeding, obligate parasites of mammals and birds that are distributed worldwide across diverse habitats (Whiting et al., 2008). Given that fleas are exposed to both the environment created by their host's skin and hair and the external environment that lies beyond their host's body, flea evolution is influenced by potentially conflicting pressures associated with both the host and the broader ecosystem (Krasnov et al., 1997). Thus, dispersal of fleas depends on both host dispersal, and on off-host environmental factors such as local climate (Krasnov, 2008).

Existing records of American pika fleas are predominantly derived from the collections of C. A. Hubbard and G. F. Augustson who were early flea researchers. These records show multiple flea species associated with the North American pikas (Hubbard, 1941, 1947; Augustson, 1942) some of which have reported host associations exclusive to pikas. Other flea species found on pikas are categorized as 'accidental' fleas (Hubbard, 1947), because of their preference for other hosts. Pikas living at lower elevations often share their habitat with other species like rodents that result in flea parasites infecting different hosts (Foley et al., 2017). When analyzing the patterns of distribution of fleas from the collection used for this study, I incorporate other reported host associations to explain possible distribution patterns.

Study sites and sampling

I obtained ectoparasites from 219 individual *O. princeps* collected in 2004 and 2005 by Kurt Galbreath (Northern Michigan University). These specimens were collected from 37 different localities spanning the full range of the host (Fig. 1.1). From this ectoparasite collection I first separated the fleas from other ectoparasites, which also included ticks, lice, and mites. A total of 839 fleas were detected from 34 of the 37 sampled localities. No fleas were collected from localities 5, 12 and 25 (Fig. 1.1). The specimens had been stored in 70% EtOH since the day they were collected. To morphologically identify the fleas it was necessary to mount them on slides, but to preserve DNA for future analyses I first extracted genomic DNA from all flea specimens using Epicentre Biotechnologies' MasterPure^{TM} genomic DNA extraction kit (Epicenter Technologies, Inc., Madison, Wisconsin, United States of America).

Morphological identification

I mounted fleas on slides according to protocols provided by Ralph Eckerlin, Northern Virginia Community College. Following DNA extraction, I soaked the flea exoskeleton in 50% EtOH for approximately 10 minutes to ease the hydration process. I then transferred the flea into 10% KOH for 10 hours for partial clearing, followed by dehydration through a series of ethanol solutions (70%, 95%, 100%) for 12 hours in each before finally clearing in xylene for 4 hours. I mounted the cleared specimens on microscope slides using Canada balsam. All mounted specimens are stored in the parasite collection of Northern Michigan University. I identified the specimens to species using keys by Hopkins and Rothschild (1971), Holland (1985) and Lewis (2000). I took digital images of representatives of each species using an Olympus BX53 microscope with Nikon D7200 dSLR.

RESULTS

Species identification and distribution

Morphological identification of the flea specimens revealed 11 flea genera belonging to three families that are associated with *O. princeps* (Table 1.1). The three families were Ceratophyllidae, Ctenophthalmidae, and Leptopsyllidae, which all are commonly found in the Nearctic (Holland, 1985). The two most common and widespread flea species were *Ctenophyllus armatus* (Wagner, 1901) and *Amphalius runatus necopinus* (Jordan, 1925) (Fig. 1.5, 1.6), which both have reported host associations with *Ochotona* spp. in North America (Holland, 1985). These two species have been categorized as host-specific and restricted to only *Ochotona* spp. (Hopkins & Rothschild, 1971; Holland, 1985). However, there have been reports of these species occurring on accidental hosts, including birds. I discuss these host associations in the following sections.

Ctenophyllus armatus made up 45% of the 827 fleas in the collection. The 375 records of *C. armatus* spanned almost the entire range of the host, while most other species revealed more restricted and patchy distributions (Fig. 1.2-1.4). The other most commonly found species, *Amphalius runatus necopinus* was recorded 219 times and spread across all five lineages of the host. However, *A. runatus necopinus* was found in fewer localities than *C. armatus*. The flea species *Geusibia ashcrafti* Augustson, 1941 (Fig. 1.7) is also known to have a preference for pikas (Hubbard, 1947). However, it was only recorded here from two counties in the USA: Alpine Co., California and Mesa Co., Colorado (locality 24 and 34; Fig. 1.4), one of which (Mesa) is a new locality record that adds to current knowledge of the geographical range of the species. Previous reports indicate the presence of *G. ashcrafti* in two other counties in California and Colorado. The absence of *G. ashcrafti* from other localities across the pika range raise questions regarding the factors that limit their distribution. For example, *Aetheca wagneri* Baker, 1904 (Fig. 1.8) was the only flea species that was found widely distributed across the Sierra Nevada host lineage. Its distribution was not restricted to one host lineage, but was found in all other host lineages except for the Cascade Range. Other identified flea species such as *Orchopeas* spp. Jordan, 1933 (Fig. 1.9); *Rhadinopsylla* sp. Jordan and Rothschild, 1912 (Fig. 1.10); *Eumolpianus eumolpi* Rothschild 1905 (Fig. 1.12); *Conorhinopsylla* sp. Stewart, 1930; *Peromycopsylla* sp. I. Fox, 1939 (Fig. 1.11); *Megarthroglossus* sp. Wagner, 1936 (Fig. 1.14); and *Catallagia* sp. Rothschild, 1915 (Fig. 1.13) were a small proportion of the total flea collection. Moreover, these species are mostly reported from hosts other than pikas; therefore, their patterns of distribution in relation to the hosts they are found on may not reflect the population history of pikas. Lastly, I was not able to identify 38 flea specimens from the collection, which if identified would provide additional insight into the flea fauna associated with pikas and probably represent additional species-level diversity. In some flea species, only males can be identified with confidence.

Distinguishing morphological characteristics

Ctenophyllus armatus –This flea species has an armor of pigmented spiniforms in its preantennal region. One or two rows of spiniforms are clearly visible in both males and females. A pronotal ctenidium and arc of tentorium are present and visible, however a genal ctenidium is absent. The female's spermatheca head has a sub-globular shape (Holland, 1985). Compared to other flea species, *C. armatus* has a darkly pigmented exoskeleton (Fig. 1.5).

Amphalius runatus necopinus – Males and females have different identifiable characteristics. Males possess a movable process with one long pigmented spiniform at the apex and two thick spiniforms at the distal margin. Their fixed process is very slender and about the same length as the movable process. Females are easily identifiable by their bisinuated sternum VII and undifferentiated spermatheca (Holland, 1985) (Fig. 1.6).

Orchopeas spp. – Both males and females have one lateral seta on the fore femur. Males are easier to identify than females. Their sternum VIII is narrow and has no setae. The movable process of the clasper has 4-6 short pointy spiniforms with one long seta near the top margin. The bulga of the female spermatheca is barrel-shaped with the hilla including an apical process. The ventral margin of the anal sternum is curved to the inside in the middle (Holland, 1985) (Fig. 1.9).

***Aetheca wagneri* -** This species is listed under the synonym *Monopsyllus wagneri* (Baker) in Holland (1985). Males can be identified by their triangular movable process with three dark spiniforms at the posterior apex. The uppermost spiniforms are short and lie close together. The lower spiniform is about 5 times longer than the others. Females are characterized by their worm-like spermatheca where the hilla appears to be broader than the bulga (Holland, 1985) (Fig. 1.8).

***Geusibia ashcrafti* -** Females are easy to identify by the unique shape of the spermatheca, which looks like a sickle. A small handle-like extension of the spermatheca can be observed at the posterior end (Hopkins & Rothschild, 1971) (Fig. 1.7).

Peromyscopsylla sp. – The head is shaped like a helmet with a series of thick, pigmented setae at the anterior margin. Pronotal and genal ctenidium are present. Only 2 spines are present in the genal ctenidium (Holland, 1985). The single female specimen from Nevada could not be identified to species level (Fig. 1.11).

***Eumolpianus eumolpi* -** Listed as *Monopsyllus eumolpi* in Holland (1985), this species is darker in color than other species with darkly pigmented eyes. The posterior margin of the movable process in males has three dark, blunt spiniforms. The ventral spiniform appears to be longer than the upper two (Holland, 1985) (Fig. 1.12).

***Catallagia* sp. –** This genus has vestigial eyes, no genal ctenidium, and a pronotal ctenidium consisting of roughly 14 spines. Pre- and post-antennal areas have two and three rows of setae respectively. The single female specimen from Nevada could not be identified to species level (Holland, 1985) (Fig. 1.13).

***Rhadinopsylla (Actenophthalmus) fraterna* –** A genal ctenidium is present with five spines. Uppermost spines are broader and about two-thirds of the length of the second spine. Sternum VIII has a fairly large sinus (Holland, 1985). Only three females and no males were present in the collection (Fig. 1.10).

***Megarthroglossus* sp. –** Eyes are vestigial. Five segments are present in the labial palpus with last segment being long. No genal ctenidium, but pronotal ctenidium is present. Female spermatheca has a ‘collar’ on the bulga (Holland, 1985) (Fig. 1.14).

***Conorhinopsylla* sp. –** No trabecular centralis, but tentorial arms are visible near vestigial eyes. Labial palpus is long with 5-8 segments. Female sternum VII does not have a lobe on the sinus. Bulga of the spermatheca is twice as long and wide as the hilla (Holland, 1985).

DISCUSSION

The distribution of the flea species across the geographic range of *O. princeps* suggests that the fleas did not track their host’s population history with strong fidelity. They may have obtained their distributions before host lineages differentiated, or later via dispersal between regional mountain systems. The latter scenario suggests episodes of historical contact between populations representing different host lineages that allowed fleas to disperse across lineage boundaries. Pika-specific endoparasite distribution patterns also provide evidence for this scenario, showing distributions that span host-lineage boundaries (Galbreath & Hoberg, 2015). As presented by my first hypothesis, the distribution of pika-specific flea species across the Intermountain West shows species distributed across all host lineages, without a clear biogeographic distinction between the southwestern and northeastern portions of the host's range. The two major endoparasite assemblages – one spanning the northeastern portion of the host's range and the other spanning the southwest – suggest climate-driven pika movement and contact between some of the northeast and southwest host populations, but not all (Galbreath & Hoberg, 2015). Looking at the distribution of the fleas, which span several host-lineage boundaries, there is evidence supporting the hypothesis that historical contact between pika individuals from multiple host lineages occurred. However, the apparent lack of pika specialist fleas such as *Ctenophyllus armatus* and *Amphalius runatus necopinus* in the Sierra Nevada host lineage suggests the possibility of past barriers to dispersal between this area and other regional mountain systems. A similar pattern of distribution was detected in two strongylid nematodes of American pikas: *Graphidiella ochotonae* and *Murielus harpespiculus*. These two host-specific species were absent in many of the populations in the southwest indicating barriers for dispersal into southwestern populations (Galbreath & Hoberg, 2015). The most widely distributed flea species in the Sierra Nevada pika lineage, *Aetheca wagneri*, has been reported as a species that prefers rodent hosts (Foley et al., 2017); therefore, its dispersal throughout the southwest may have been facilitated by hosts other than pikas. However, limited sampling efforts and a relative lack of flea specimens from those localities representing the Sierra Nevada host lineage suggest that conclusions regarding the availability of suitable habitats for specific flea species in that region should be viewed with caution

Other factors besides the distribution of pika populations probably are playing important roles in shaping this flea assemblage. For example, a possible explanation for the presence of *A. wagneri* in the Sierra Nevada where pika-specific flea species are absent may derive from its primary association with *Peromyscus maniculatus*. Distribution of *P. maniculatus* across multiple habitats probably facilitated the dispersal of *A. wagneri* by its rodent host (Egoscue, 1976) rather than by other accidental hosts like pikas. *Peromyscus maniculatus* is abundant in western North America and is commonly found in the nests and burrows of other mammals, facilitating easy transfer of fleas to other small mammals that they come into contact with (Egoscue, 1976). Conversely, my finding that *Geusibia sp*. only parasitized pikas from a restricted geographic area could be explained by their characteristic host-habitat dependence as opposed to dependence on any particular host species (Krasnov et al., 1997; Liang & Houyong, 2005). In the Palearctic these fleas have known associations with several species of pikas, but their distribution is not strictly dependent upon a specific host (Liang & Houyong, 2005).

Observed flea diversity and distribution patterns from this study, which represent the Nearctic flea fauna, can be compared to the recorded distribution of the Palearctic flea fauna to infer historical centers of origin of the observed flea species. Given the strong evidence of Asian ancestry for *O. princeps* (Hafner & Sullivan, 1995), it is worthwhile to first explore the suggested origins of higher level flea taxonomy. I describe the three flea families and associated genera in each family in the following section.

Flea families and genera

The family Ceratophyllidae is composed of 2 sub-families, 47 genera and 414 species. I identified four genera (*Aetheca, Amphalius, Eumolpianus* and *Orchopeas*) that belong to this family, including *Amphalius*, the second most common flea genus among the pikas of the Intermountain West. This genus was only reported on *Ochotona* in the Nearctic; however in the Palearctic, *Amphalius* has host associations with other alpine small mammals of genera *Cricetulus* and *Lagomyidae* (Medvedev, 1996). It was also reported on an avian host of genus *Oenanthe* (Kiefer et al., 2010). Nevertheless, Ceratophyllidae in general associate primarily with rodents rather than lagomorphs (Medvedev, 1996). In the Intermountain West region, *Aetheca*, *Eumolpianus* and *Orchopeas* were mainly reported on *Peromyscus, Tamias* and *Neotoma* (Foley et al., 2017). Based on the first molecular phylogeny of fleas mapped with host associations, ancestral hosts of this family were found to be sciurids and cricetids, showing deep historical associations (Whiting et al., 2008).

Family Leptopsyllidae consists of two sub-families comprising 29 genera and 121 species. Three genera that belong to this family are *Ctenophyllus, Geusibia* and *Peromyscopsylla*. Genus *Ctenophyllus* was the most common and widespread flea genus among all sampling localities, comprising more than 50% of the sampled flea specimens. In the Nearctic this genus is usually reported on *Ochotona,* and it was therefore not surprising to detect numerous *Ctenophyllus* on the pikas. In the Palearctic fleas of this genus are also more common among pikas than on other mammals, but they are also reported on other hosts such as *Alticola sp*. and the avian host *Oenanthe sp.* (Kiefer et al., 2010). Although leptopsyllids are more common and have many host associations in the

Palearctic, they are also very abundant in the Nearctic. The origin of this family is probably in the Palearctic based on the greater diversity of species reported in the Palearctic (Medvedev, 1996). Medvedev (1996) suggested that this family may have originated in Asia and then migrated into North America with rodents of the family Aplodontidae during the Eocene. Later, species representing genera including *Ctenophyllus, Geusibia* and *Peromyscopsylla* may have migrated to North America on Cricetidae and Muridae via the Bering land bridge. To date there is only one record of *Ctenophyllus* on a host other than *Ochotona* spp. in North America. It was reported on a ground squirrel (*Urocitellus undulatus)* in Alaska by (Hopla, 1965). However, in the Palearctic, it was reported on a bird (*Oenanthe* sp.) and a rodent (*Alticola* sp.) (Kiefer et al., 2010). Results of my study showing high abundance of *C. armatus* throughout the sampled pika populations indicate a preference for pika hosts by this flea species as suggested previously (Hubbard, 1941).

CONCLUSION

Upon investigating the diversity and distribution of fleas from *O. princeps*, I detected a pattern in the distribution of fleas which is partially congruent with that of host-specific helminths of the pikas (Galbreath & Hoberg, 2015). I found no clear correlation between the distribution of flea species and pika lineages, thus indicating that fleas have historically dispersed between pikas from different lineages. For host-specific fleas of pikas such dispersal may have been mediated by historical range expansions and contractions during glacial-interglacial cycles, but distributions of accidental parasites of pikas presumably were more strongly influenced by factors determining the distributions of their primary hosts.

Table 1.1: Flea families and genera documented from *O. princeps* in this study.

Flea family	Leptopsyllidae	Ceratophyllidae	Ctenophthalmidae
Flea genera	*Ctenophyllus* *Geusibia* *Peromyscopsylla*	*Aetheca* *Amphalius* *Eumolpianus* *Orchopeas*	*Catallagia* *Rhadinopsylla* *Megarthroglossus* *Conorhinopsylla*

Table 1.2: Collection localities for pika flea samples. Locality numbers identify localities shown in Figures 1.1-1.4.

Locality number	**State or Province**	**County**	**Locality**	**Field latitude/longitude (ddd mm ss.ss)**	
1	British Columbia		Coast Land District Range 3, 20 km S, 12 km E Hagensborg	52 13 10.99	-126 22 5.16
2	British Columbia		Railroad Mountain; 17 km W, 30 km N Pemberton	50 34 57.66	-123 1 40.03
3	British Columbia		2km E, 5km N McBride	53 21 52.74	-120 7 33.7
4	British Columbia		Raft Provincial Forest, Raft Mt., 11 km E, 8 km N Clearwater	51 43 27.38	-119 51 10.48
6	Alberta		Bighorn Wildland Provincial Recreation Area: 4 km S 2 km E Landslide Lake	52 3 39.74	-116 31 4.31
7	Washington	Okanogan	Okanogan National Forest, 2 km SE of Washington Pass	48 30 37.72	-120 38 23.24
8	Washington	Skamania	Gifford-Pinchot National Forest, 0.5 km E Sunrise Peak	46 19 45.2	-121 44 54.47
9	Washington	Skamania	Gifford-Pinchot National Forest, 19 km W Trout Lake	46 3 7.92	-121 45 33.27
10	Oregon	Linn	Willamette National Forest, 1 km W McKenzie Pass	44 14 40.16	-121 49 18.83
11	Oregon	Baker	Whitman National Forest, 1 km S, 2 km E Anthony Lakes	44 56 41.78	-118 12 43.95
13	Idaho	Boundary	Panhandle National Forest, Roman Nose Lakes	48 37 53.48	-116 34 29.53
14	Idaho	Adams	Payette National Forest, 1 km W of Black Lake	45 11 12.11	-116 34 53.63
15	Idaho	Boise	Boise National Forest, 14 km W of Featherville	43 36 52.93	-115 26 10.01
16	Idaho	Custer	Challis National Forest, 10.5 km N, 4 km W of Doublespring Pass	44 18 41.57	-113 53 45.87

17	Montana	Ravalli	Bitterroot National Forest, 9 km W of Darby	46 1 47.45	-114 17 32.2
18	Montana	Judith Basin	Lewis & Clark National Forest, 9 km E of Neihart	46 56 11.04	-110 37 25.85
19	Montana	Carbon	Custer National Forest, 1 km E of Emerald Lake	44 59 50.69	-109 30 38.36
20	Wyoming	Teton	Shoshone National Forest, 2 km E Togwotee Pass	43 45 10.05	-110 2 34.82
21	Wyoming	Big Horn	Bighorn National Forest, 4 km N Duncum Mountain	44 51 25.64	-107 50 37.03
22	Wyoming	Carbon	Medicine Bow National Forest, 2 km SE Bridger Peak	41 10 40.3	-107 0 50.47
23	California	Modoc	Modoc National Forest, East slope Warren Peak	41 22 43.06	-120 12 44.7
24	California	Alpine	Stanislaus National Forest, 0.5 km NW Ebbetts Pass	38 32 44.95	-119 48 58.33
26	Nevada	Nye	Humboldt-Toiyabe National Forest, 5 km N of Arc Dome	38 52 37.09	-117 20 58.79
27	Nevada	Nye	Humboldt-Toiyabe National Forest, 2 km S of South Summit of Mount Jefferson	38 43 31.43	-116 55 32.49
28	Nevada	Elko	Humboldt National Forest, 16 km S, 8 km E Lamoille	40 34 51.62	-115 23 34.09
29	Utah	Summit	Wasatch National Forest, 22 km E, 5 km N Oakley	40 45 24.55	-111 2 19.46
30	Utah	Sanpete	Manti-LaSal National Forest, W slope Heliotrope Mountain	39 6 35.1	-111 28 10.41
31	Utah	Wayne	Fish Lake National Forest, NW slope Flat Top Mountain	38 26 26.19	-111 28 54.04
32	Utah	Millard	Fish Lake National Forest, 3 km E, 2 km S, Mt. Baldy	38 22 55.64	-112 24 2
33	Colorado	Garfield	White River National Forest, 1 km W of N end Trapper's Lake	39 58 17.61	-107 15 28.26
34	Colorado	Mesa	Grand Mesa National Forest, 5 km S, 33 km E Grand Junction	39 2 43.99	-108 4 12.12
35	Colorado	Clear Creek	Arapaho National Forest, W side Berthoud Pass	39 48 8.59	-105 46 54.62
36	New Mexico	Taos	Carson National Forest, 2.5 km NW Twining (Taos Ski Area)	36 36 50.24	-105 30 5.89
37	New Mexico	Santa Fe	Santa Fe National Forest, W slope of Lake Peak	35 47 48.84	-105 46 31.96

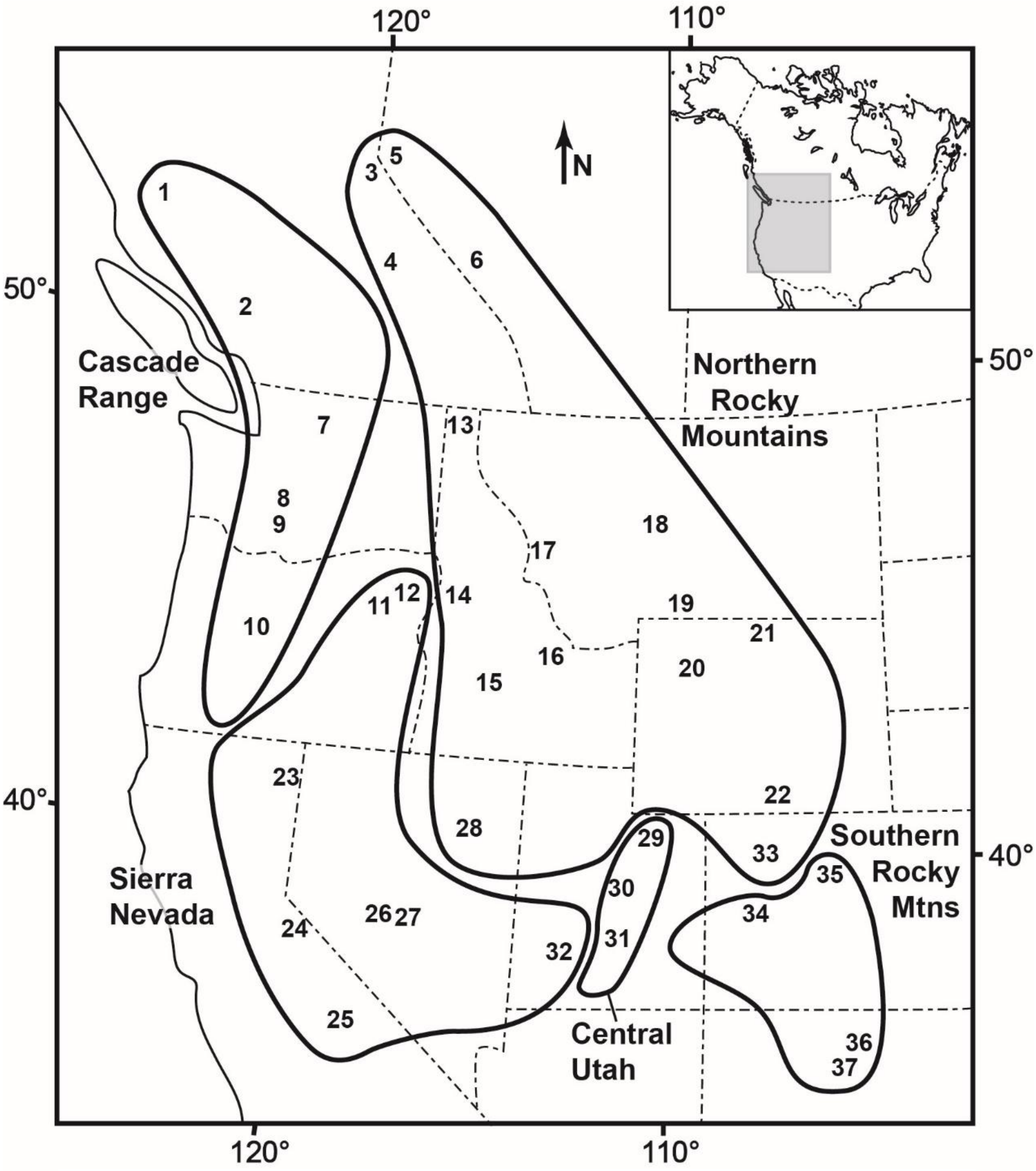

Figure 1.1: Specimen sampling localities and regional host lineages. Collection locality numbers cross-reference with Table 1.1. The thick black lines show five geographically distinct mitochondrial lineages of *O. princeps* (Galbreath et al. 2009, 2010).

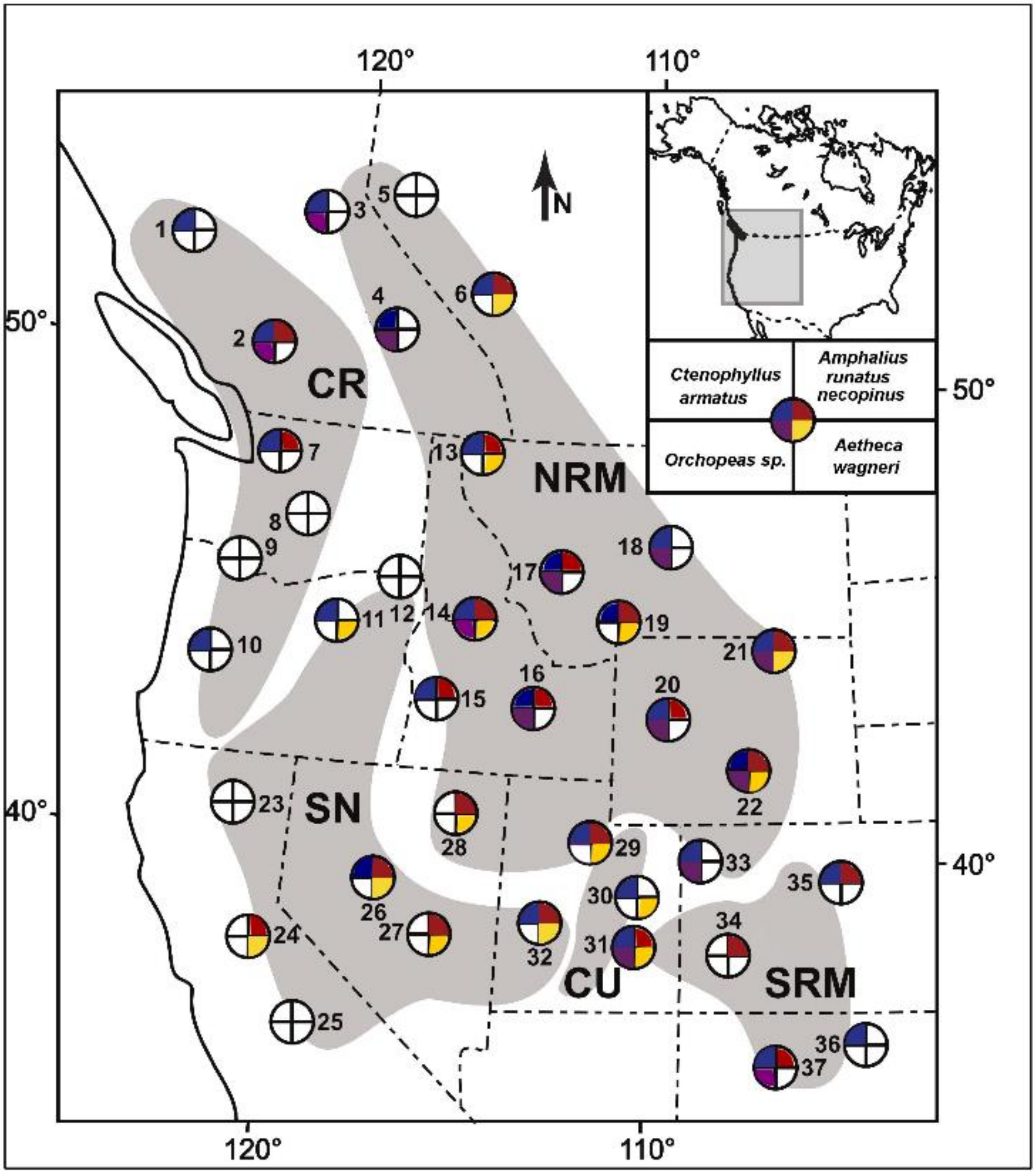

Figure 1.2: Distribution map for *Ctenophyllus armatus* (blue), *Amphalius runatus necopinus* (red), *Orchopeas spp.* (purple) and *Aetheca wagneri* (yellow). Wedges that are empty indicate that the species was not found at that locality. Collection locality numbers cross-reference with Table 1.1.

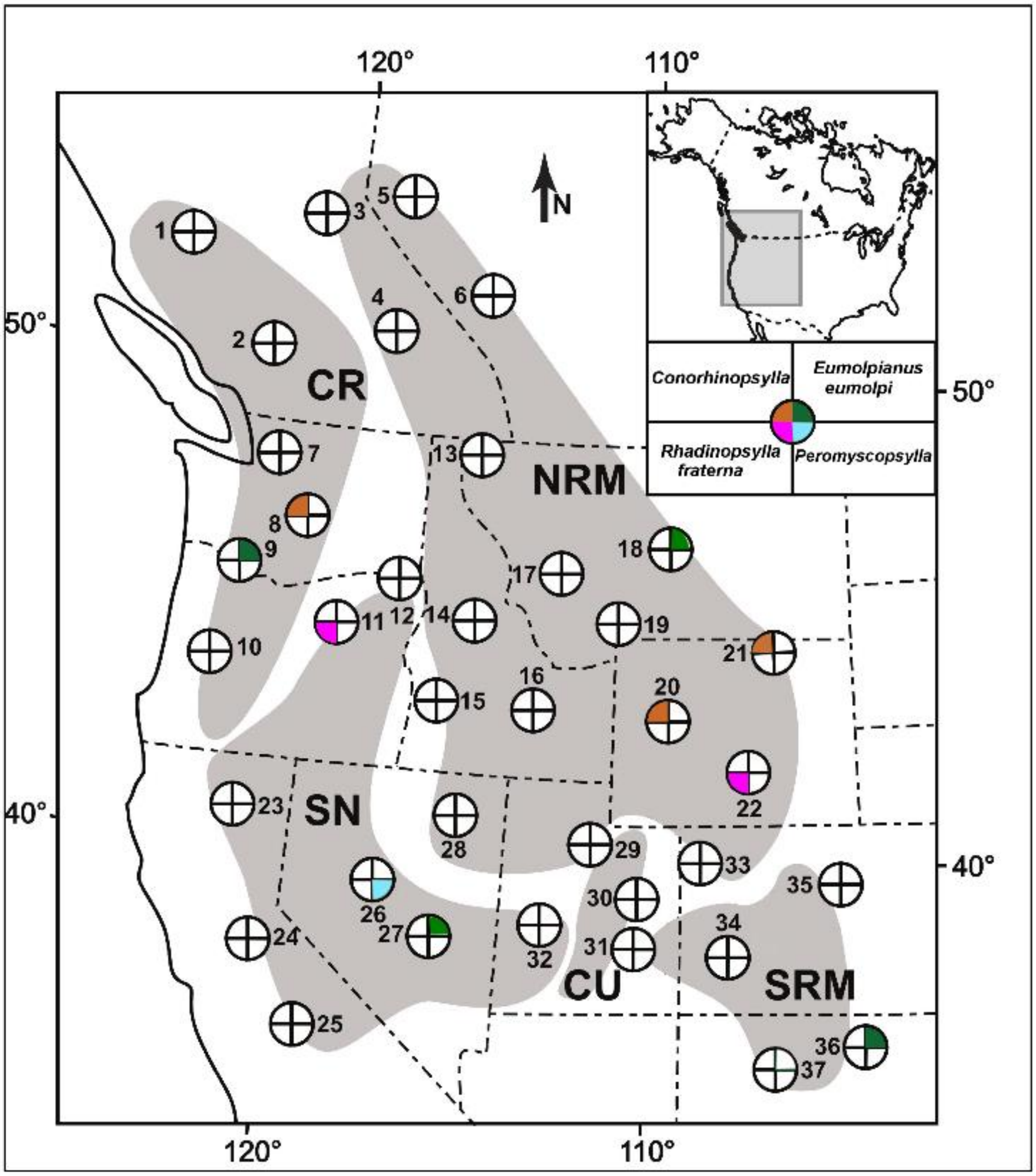

Figure 1.3: Distribution map for *Conorhinopsylla sp*. (brown), *Eumolpianus eumolpi* (green), *Rhadinopsylla fraterna* (purple) and *Peromyscopsylla* (blue). Wedges that are empty indicate that the species was not found at that locality. Collection locality numbers cross-reference with Table 1.1.

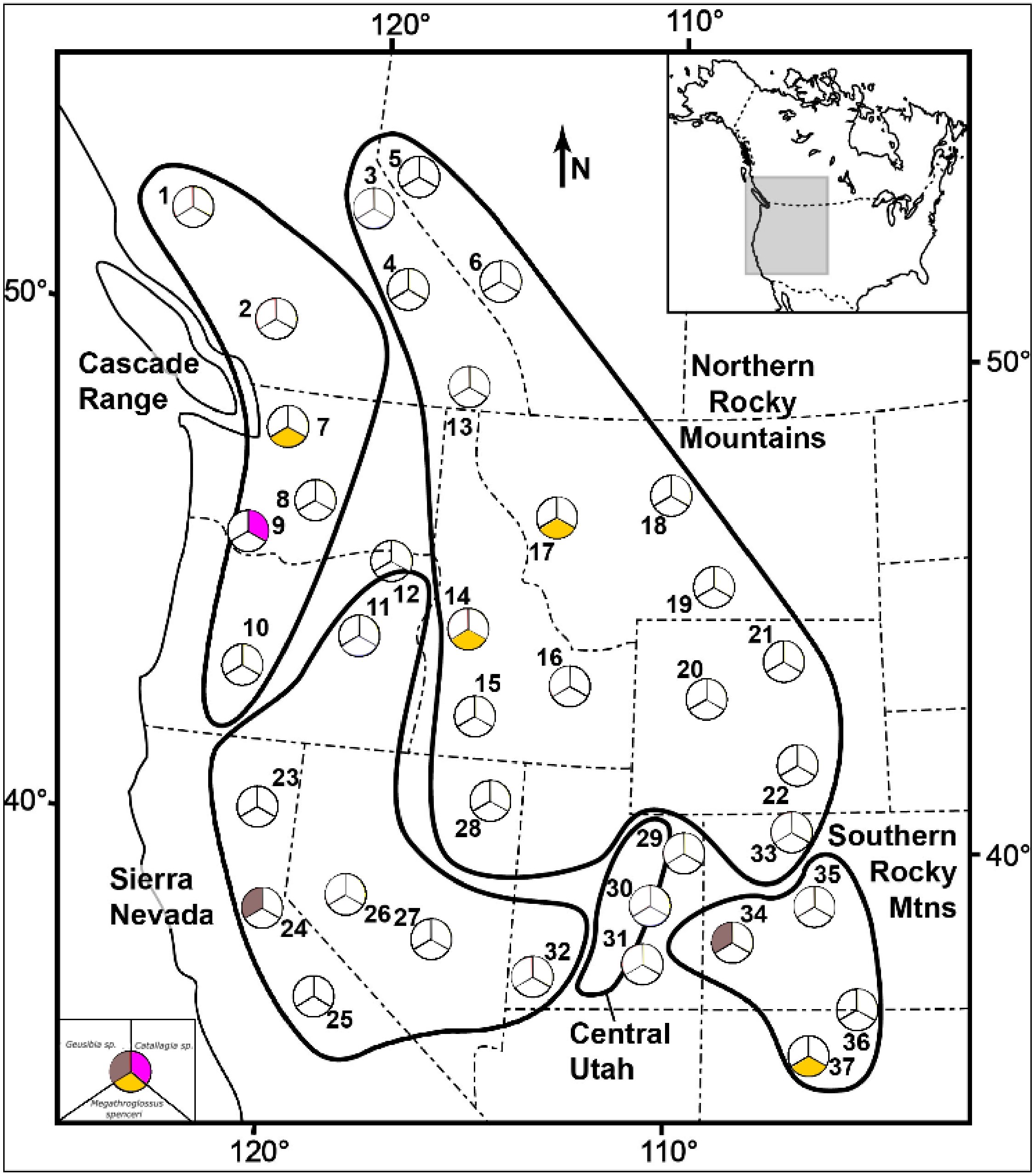

Figure 1.4: Distribution map for *Geusibia sp*. (brown), *Catallagia sp.* (purple) and *Megarthroglossus spenceri* (yellow). Wedges that are empty indicate that the species was not found at that locality. Collection locality numbers cross-reference with Table 1.1.

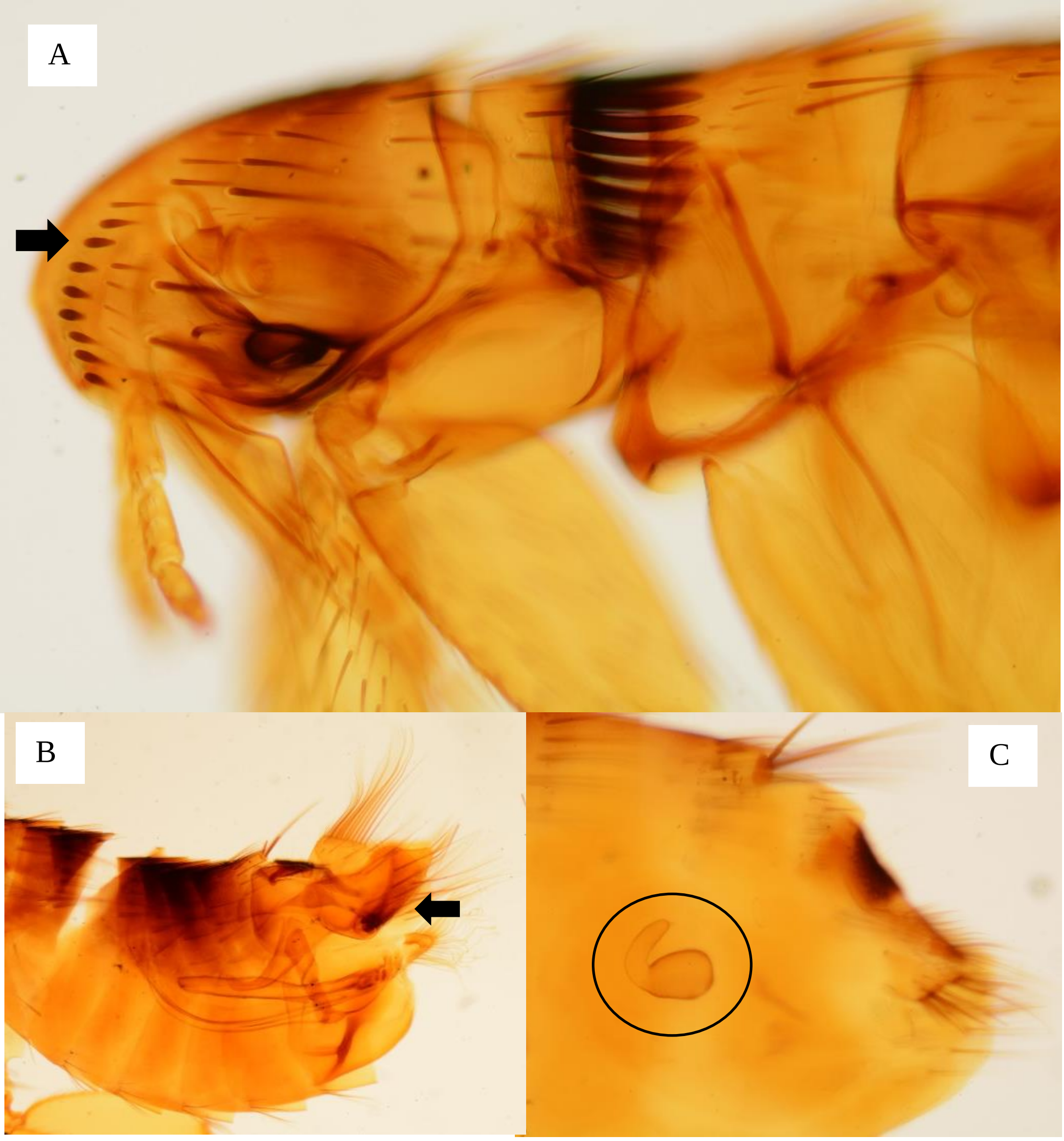

Figure 1.5: *Ctenophyllus armatus.* A) Head with spine-like setae on the frontal margin, B) Clasper process of male, C) Female spermatheca.

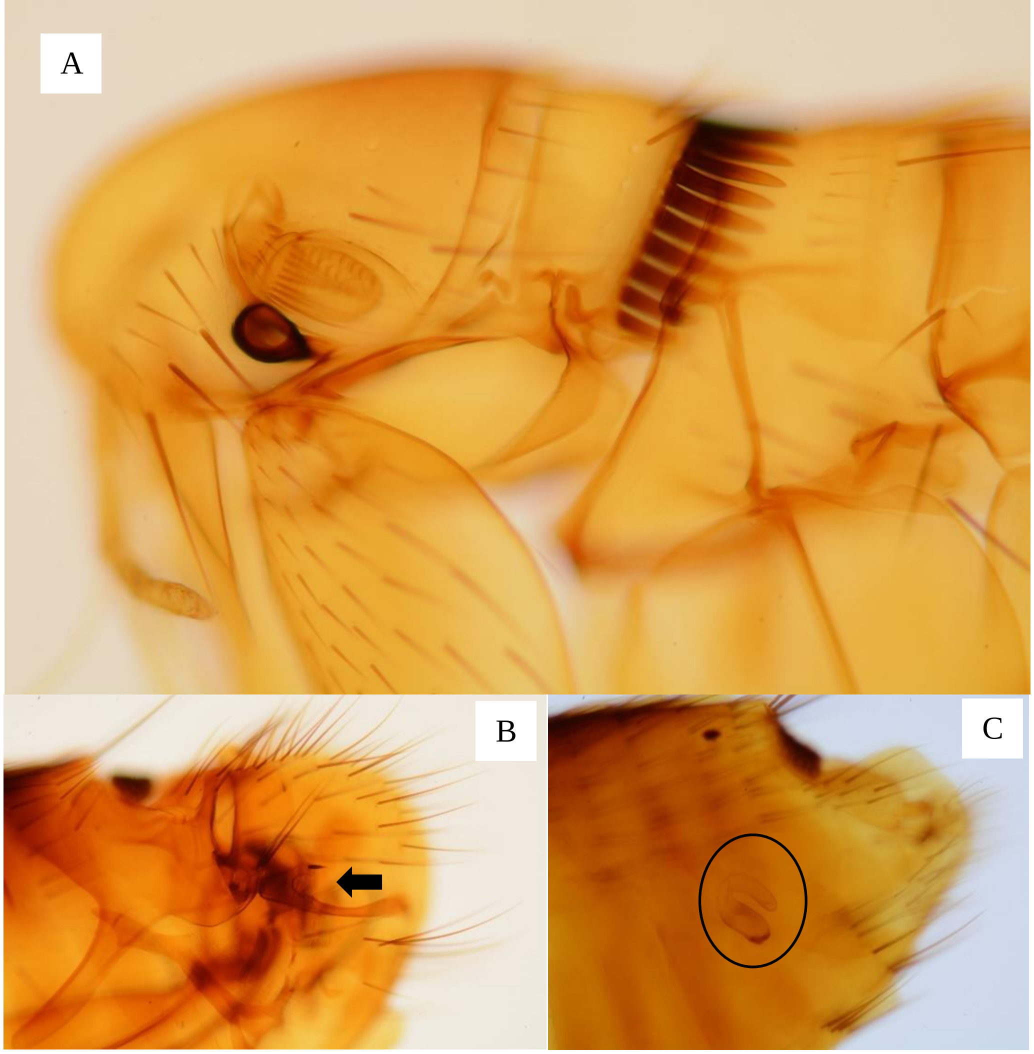

Figure 1.6: *Amphalius runatus necopinus*. A) Head, B) Male genitalia with arrow pointing at the clasper process, C) Female spermatheca.

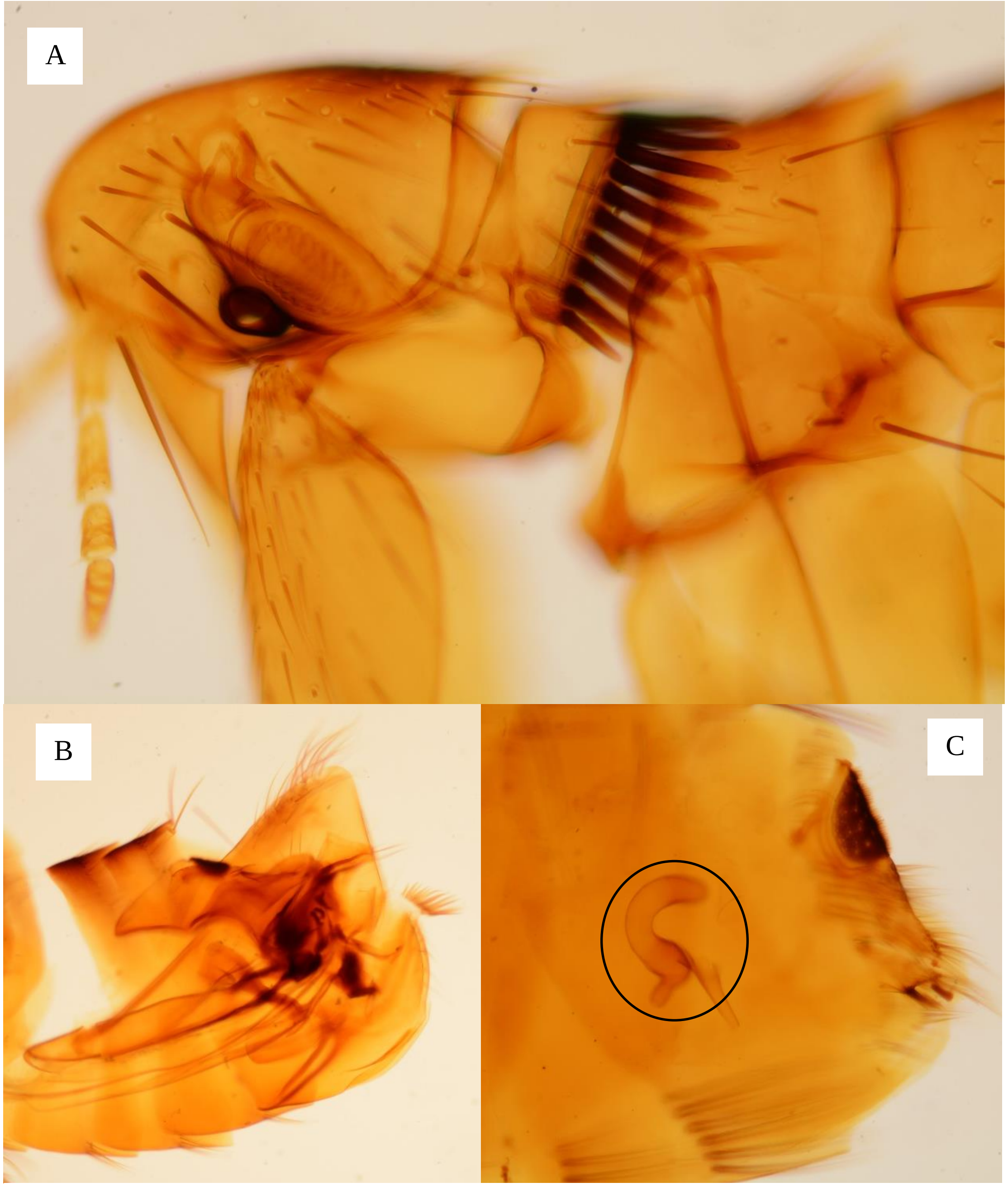

Figure 1.7: *Geusibia ashcrafti*. A) Head, B) Male genitalia, C) Female spermatheca.

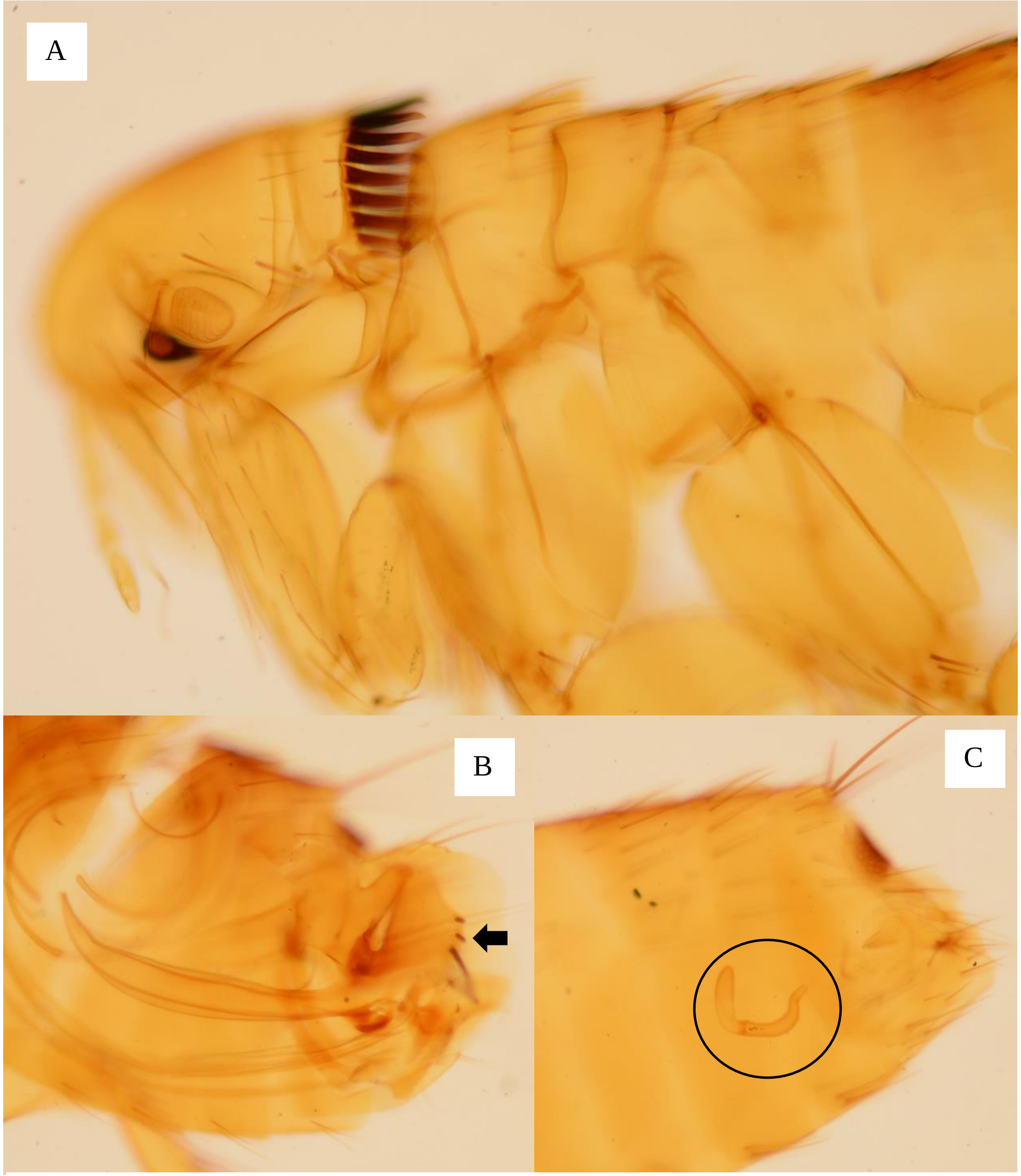

Figure 1.8: *Aetheca wagneri.* A) Head, B) Male genitalia with arrow pointing at the movable process with thick, blunt, spiniforms, C) Female spermatheca.

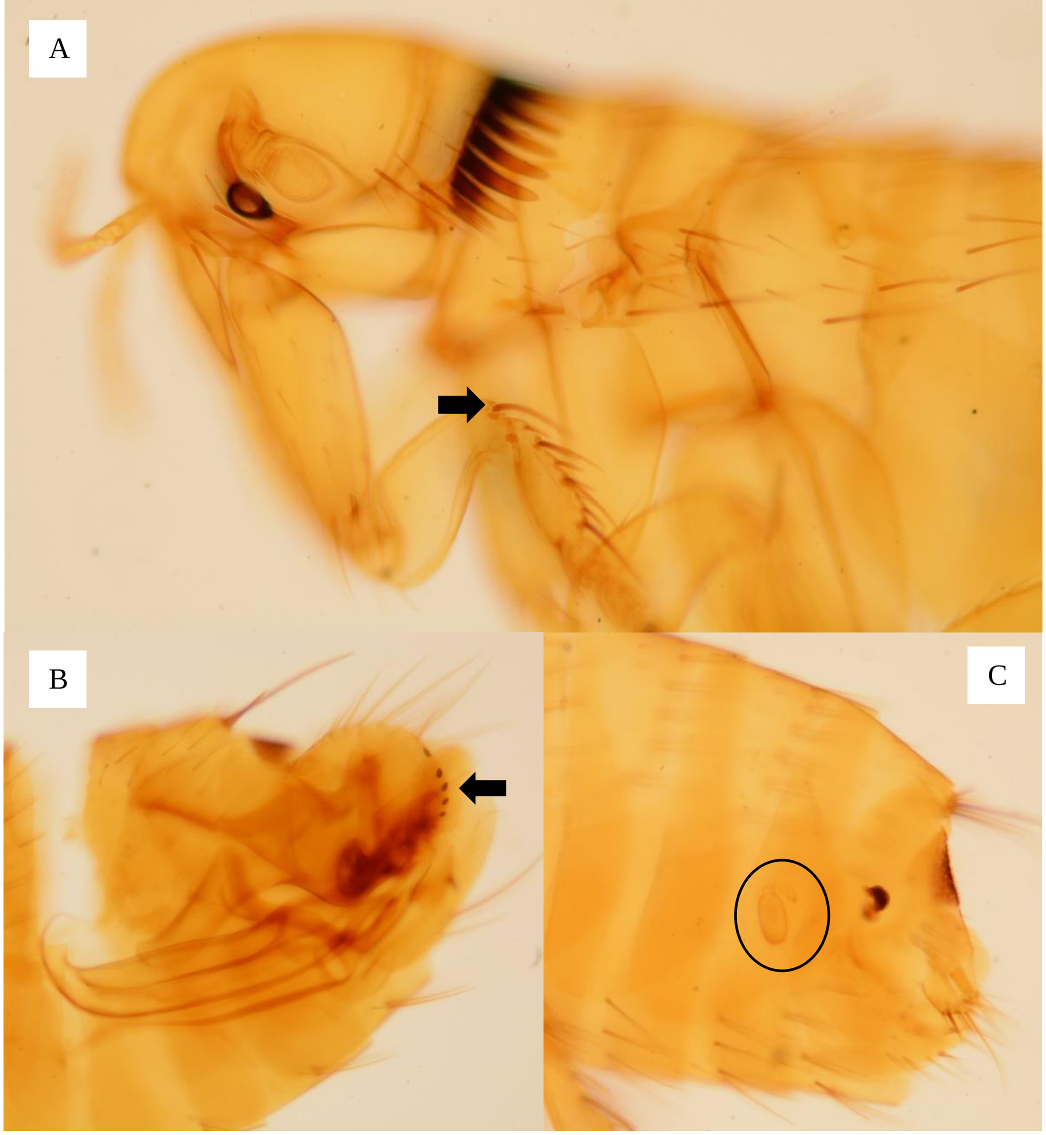

Figure 1.9: *Orchopeas spp.* A) Head with arrow pointing at the lateral setae on the fore femur. B) Male genitalia with arrow pointing at the movable process with short pointy spiniforms. C) Female spermatheca.

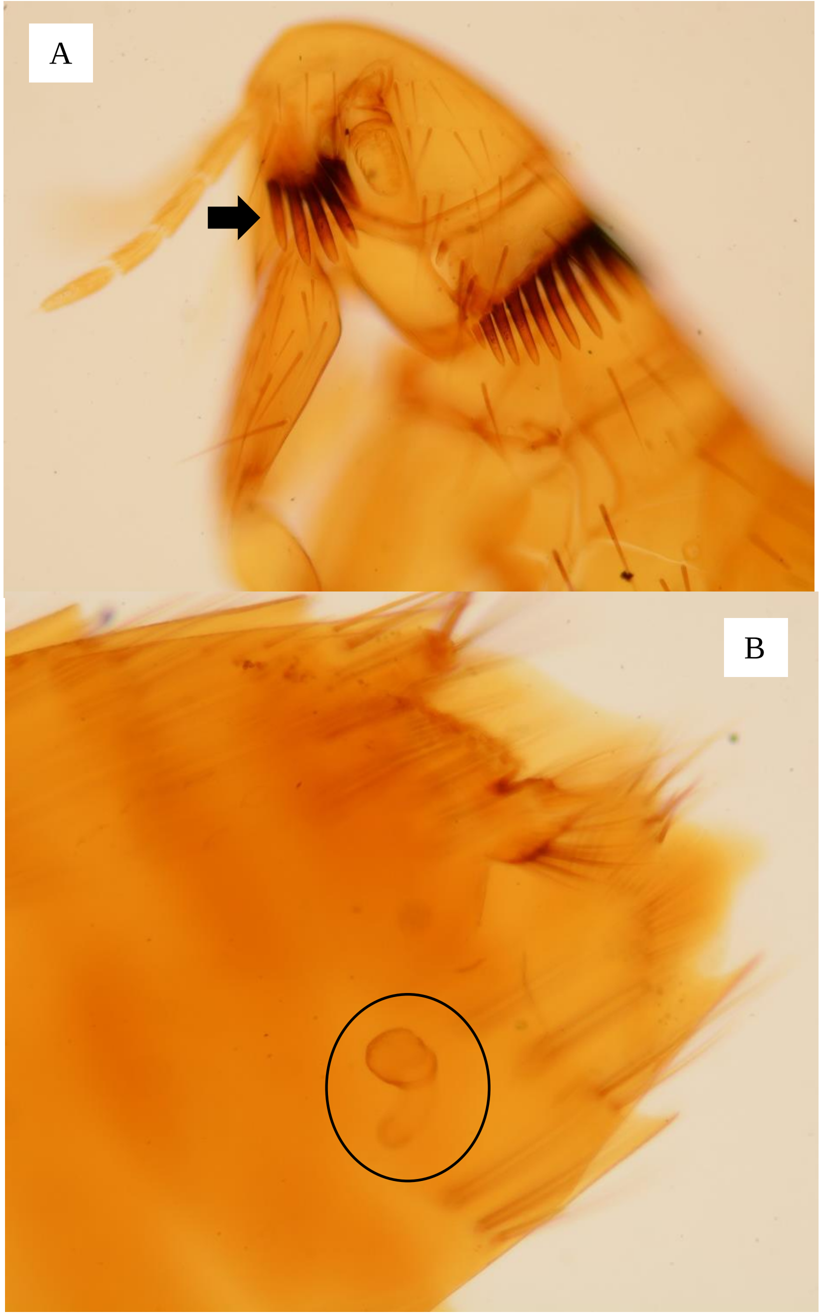

Figure 1.10: *Rhadinopsylla fraterna*. A) Head with arrow pointing at the genal ctenidium. B) Female spermatheca.

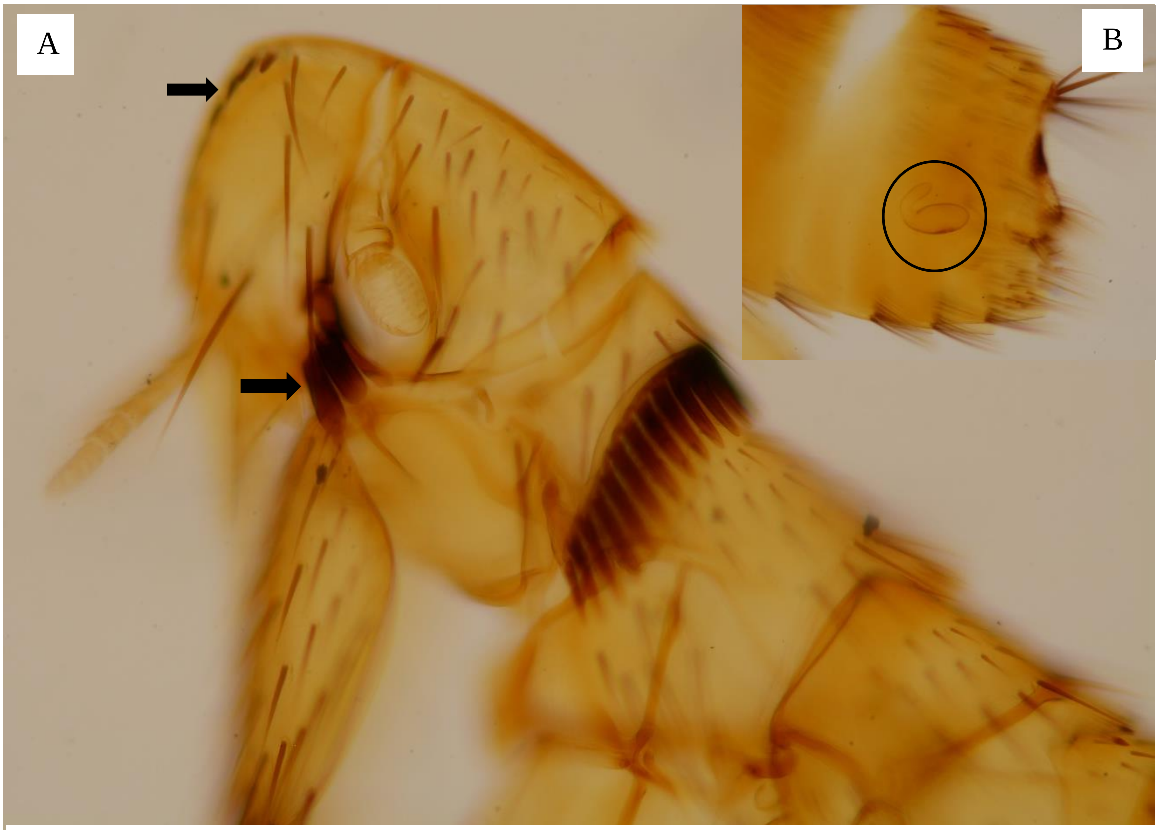

Figure 1.11: *Peromyscopsylla* sp. A) Head with top arrow pointing at the pigmented setae on the anterior margin. Bottom arrow is showing the two spines in the genal ctenidium. B) Female spermatheca.

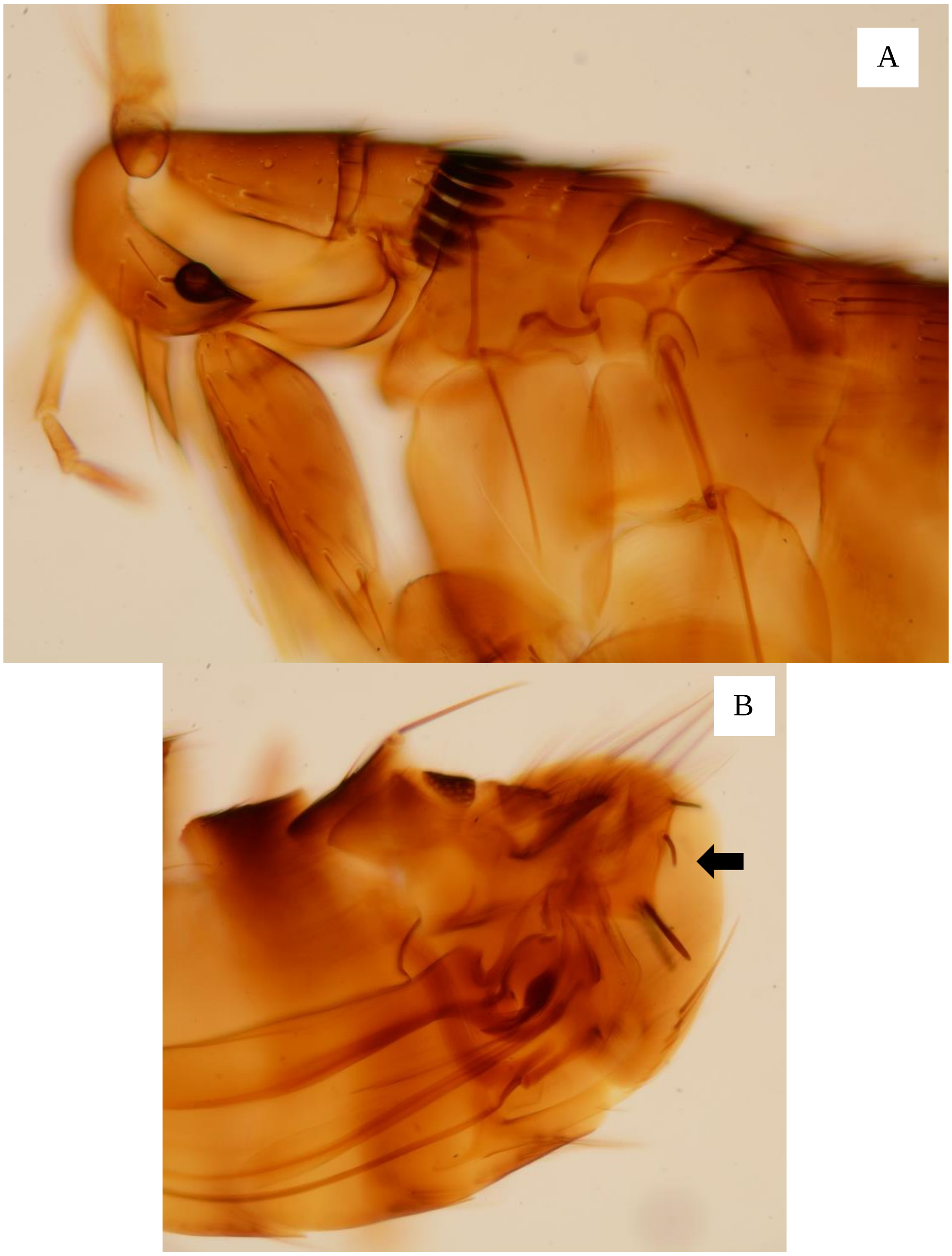

Figure 1.12: *Eumolpianus eumolpi.* A) Head showing darkly pigmented eyes. B) Male genitalia with arrow pointing at the movable process with three dark, blunt spiniforms.

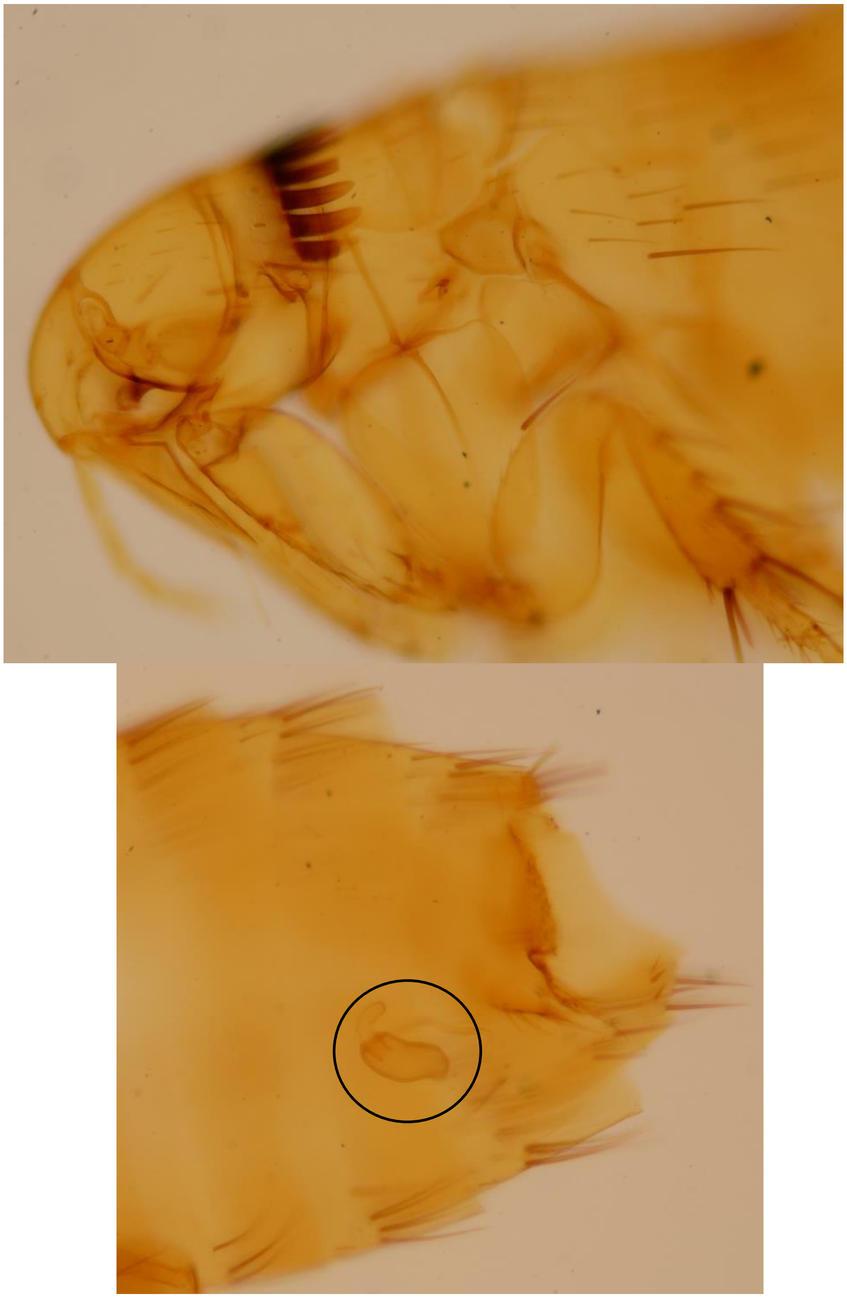

Figure 1.13: *Catallagia* sp. A) Head showing vestigial eyes. B) Female spermatheca.

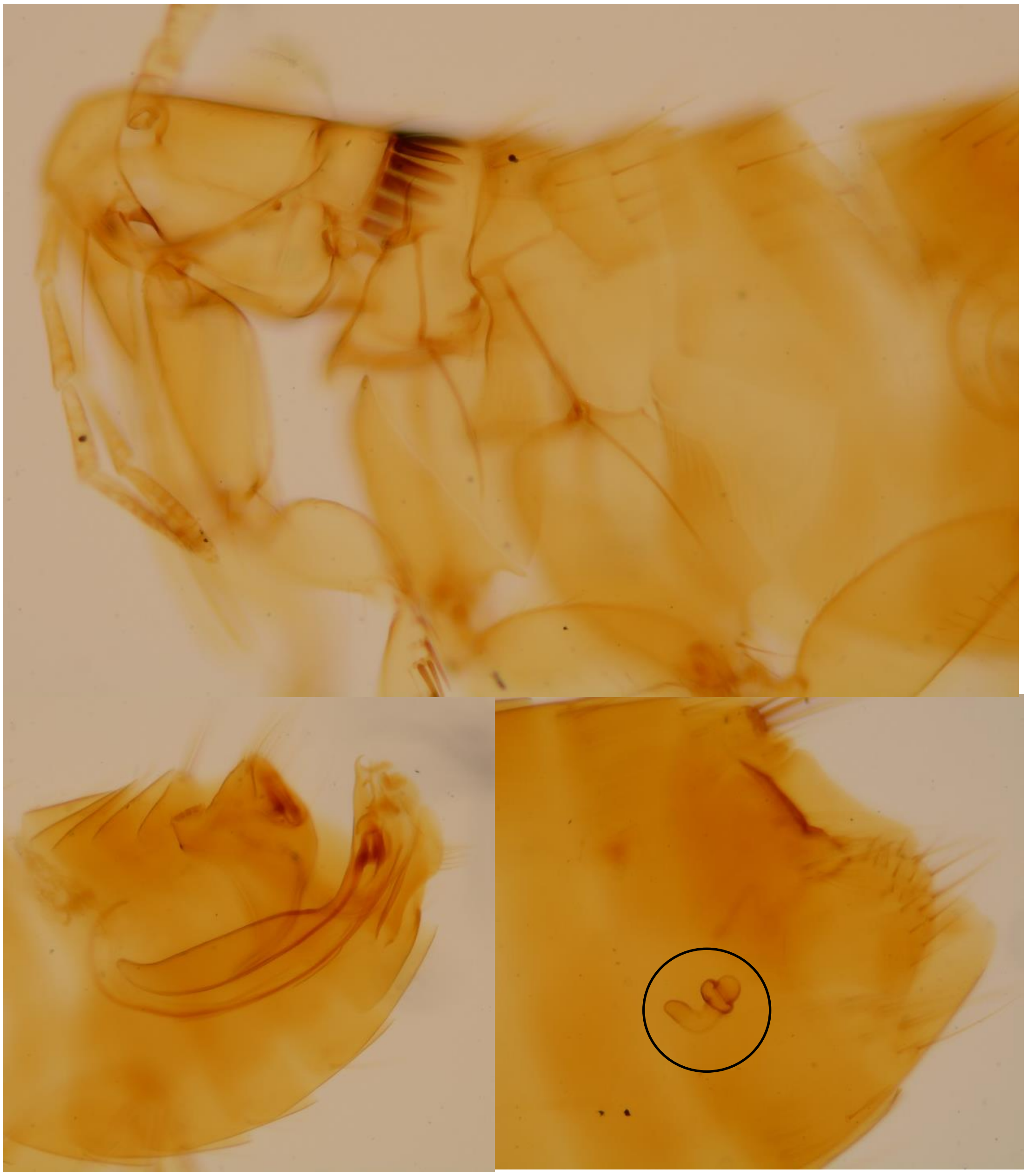

Figure 1.14: *Megarthroglossus* sp. A) Head showing vestigial eyes. B) Male genitalia. C) Female spermatheca.

REFERENCES

Augustson, G.F. (1942) Ectoparasite-host records from the Sierran region of east-central California. *Bull. South. Calif. Acad. Sci*, **40**, 146–157.

Badgley, C., Smiley, T.M., & Finarelli, J.A. (2014) Great Basin mammal diversity in relation to landscape history. *Journal of Mammalogy*, **95**, 1090–1106.

Brooks, D.R. & McLennan, D.A. (1993) Parascript: Parasites and the language of evolution. *Smithsonian series in comparative evolutionary biology (USA).*

Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., & McCabe, A.M. (2009) The Last Glacial Maximum. *Science*, **325**, 710–714.

Egoscue, H.J. (1976) Flea exchange between deer mice and some associated small mammals in western Utah. *The Great Basin Naturalist*, 475–480.

Foley, P., Roth, T., Foley, J., & Ray, C. (2017) Rodent–Pika Parasite Spillover in Western North America. *Journal of Medical Entomology*, tjxo85.

Galbreath, K.E., Hafner, D.J., & Zamudio, K.R. (2009) When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, *Ochotona princeps*). *Evolution*, **63**, 2848–2863.

Galbreath, K.E., Hafner, D.J., Zamudio, K.R., & Agnew, K. (2010) Isolation and introgression in the Intermountain West: contrasting gene genealogies reveal the complex biogeographic history of the American pika (*Ochotona princeps*). *Journal of Biogeography*, **37**, 344–362.

Galbreath, K.E. & Hoberg, E.P. (2012) Return to Beringia: parasites reveal cryptic biogeographic history of North American pikas. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 371–378.

Galbreath, K.E. & Hoberg, E.P. (2015) Host responses to cycles of climate change shape parasite diversity across North America's Intermountain West. *Folia Zoologica*, **64**, 218–232.

Guralnick, R. (2007) Differential effects of past climate warming on mountain and flatland species distributions: a multispecies North American mammal assessment. *Global Ecology and Biogeography*, **16**, 14–23.

Hafner, D.J. & Sullivan, R.M. (1995) Historical and ecological biogeography of Nearctic pikas (Lagomorpha: Ochotonidae). *Journal of Mammalogy*, **76**, 302–321.

Hewitt, G.M. (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, **58**, 247–276.

Hewitt, G.M. (2004) Genetic Consequences of Climatic Oscillations in the Quaternary. *Philosophical Transactions: Biological Sciences*, **359**, 183–195.

Hoberg, E.P. (1997) Phylogeny and historical reconstruction: host-parasite systems as keystones in biogeography and ecology. *Biodiversity II: understanding and protecting our biological resources*, 243–261.

Holland, G.P. (1985) The fleas of Canada, Alaska and Greenland (Siphonaptera). *Memoirs of the Entomological Society of Canada*, **130**, 3–631.

Hopkins, G.H.E. & Rothschild, M. (1971) *An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History) with Keys and Short Descriptions for the Identification of Families, Genera, Species and Subspecies. Vol. V. Leptopsyllidae and Ancistropsyllidae.*

Hopla, C.E. (1965) Alaskan hematophagous insects, their feeding habits and potential as vectors of pathogenic organisms. 1. The Siphonaptera of Alaska. .

Hubbard, C.A. (1941) Ectoparasites of western Lagomorpha. Part I. The ectoparasites of 100 western conies (*Ochotona*). Part II. The ectoparasites of western rabbits (*Lepus-Sylvilagus-Brachylagus*). *Pac. Univ. Bull*, **37**, 1–8.

Hubbard, C.A. (1947) Fleas of Western North America. Their relation to the Public Health. 533pp.

Kiefer, D., Pfister, K., Tserennorov, D., Otgonbaatar, D., Samjaa, R., Sumjaa, D., Burmeister, E.G., & Kiefer, M.S. (2010) Distribution of fleas (Siphonaptera) in bird-nests, bird Siphonaptera on mammalia and the medical importance of interspecific flea transmission in Mongolia. *Digitalcommons.unl.edu*.

Krasnov, B.R. (2008) *Functional and Evolutionary Ecology of Fleas: A Model for Ecological Parasitology.* Cambridge University Press.

Krasnov, B.R., Poulin, R., & Mouillot, D. (2011) Scale-dependence of phylogenetic signal in ecological traits of ectoparasites. *Ecography*, **34**, 114–122.

Krasnov, B.R., Shenbrot, G.I., Medvedev, S.G., Vatschenok, V.S., & Khokhlova, I.S. (1997) Host–habitat relations as an important determinant of spatial distribution of flea assemblages (Siphonaptera) on rodents in the Negev Desert. *Parasitology*, **114**, 159–173.

Latch, E.K., Heffelfinger, J.R., Fike, J.A., & RHODES Jr, O.E. (2009) Species-wide phylogeography of North American mule deer (*Odocoileus hemionus*): cryptic glacial refugia and postglacial recolonization. *Molecular Ecology*, **18**, 1730–1745.

Lewis, R.E. (2000) A taxonomic review of the North American genus Orchopeas Jordan, 1933 (Siphonaptera: Ceratophyllidae: Ceratophyllinae). *Journal of Vector Ecology*, **25**, 164–189.

Liang, L. & Houyong, W. (2005) Morphological phylogeny of Geusibia Jordan, 1932 (Siphonaptera: Leptopsyllidae) and the host–parasite relationship with pikas. *Systematic Parasitology*, **61**, 65–78.

Medvedev, S.G. (1996) Geographical distribution of families of fleas (Siphonaptera). *Entomological Review*, **76**, 978–992.

Rickart, E.A. (2001) Elevational diversity gradients, biogeography and the structure of montane mammal communities in the intermountain region of North America. *Global Ecology and Biogeography*, **10**, 77–100.

Shafer, A.B.A., Cullingham, C.I., CôTé, S.D., & Coltman, D.W. (2010) Of glaciers and refugia: a decade of study sheds new light on the phylogeography of northwestern North America: PHYLOGEOGRAPHY OF NORTHWESTERN NORTH AMERICA. *Molecular Ecology*, **19**, 4589–4621.

Simpson, W.G. (2009) American Pikas Inhabit Low-Elevation Sites Outside the Species' Previously Described Bioclimatic Envelope. *Western North American Naturalist*, **69**, 243–250.

Smith, A.T. (1974) The distribution and dispersal of pikas: influences of behavior and climate. *Ecology*, **55**, 1368–1376.

Thompson, R.S., Whitlock, C., Bartlein, P.J., Harrison, S.P., & Spaulding, W.G. (1993) Climatic changes in the western United States since 18,000 yr BP. *Global climates since the last glacial maximum*, 468–513.

Vashchenok, V. (1988) *Fleas (Siphonaptera)-vectors of disease agents of man and animals.*

Wall, R.L. & Shearer, D. (2008) *Veterinary Ectoparasites: Biology, Pathology and Control.* John Wiley & Sons,

Waltari, E., Hijmans, R.J., Peterson, A.T., Nyári, Á.S., Perkins, S.L., & Guralnick, R.P. (2007) Locating Pleistocene Refugia: Comparing Phylogeographic and Ecological Niche Model Predictions. *PLoS ONE*, **2**, e563.

Whiteman, N.K. & Parker, P.G. (2005) Using parasites to infer host population history: a new rationale for parasite conservation. *Animal Conservation*, **8**, 175–181.

Whiting, M.F., Whiting, A.S., Hastriter, M.W., & Dittmar, K. (2008) A molecular phylogeny of fleas (Insecta: Siphonaptera): origins and host associations. *Cladistics*, **24**, 677–707.

Worley, K., Strobeck, C., Arthur, S., Carey, J., Schwantje, H., Veitch, A., & Coltman, D.W. (2004) Population genetic structure of North American thinhorn sheep (*Ovis dalli*). *Molecular Ecology*, **13**, 2545–2556.

CHAPTER 2: COMPARATIVE PHYLOGEOGRAPHY OF THE FLEAS OF AMERICAN PIKAS (*OCHOTONA PRINCEPS*) IN NORTH AMERICA’S INTERMOUNTAIN WEST

INTRODUCTION

Many parasites have complex evolutionary histories that were shaped by both their hosts’ population histories and broader environmental influences. Understanding the underlying processes involved in shaping host-parasite distribution helps to understand the drivers of parasite evolution (Barrett et al., 2008). Typically, hosts with a large geographic range or a large body size have the capacity to carry a high parasite load (Krasnov et al., 2004). This may be a disadvantage to the host itself but it can offer the opportunity for researchers to use the parasites as study species to infer biogeographical history (Whiteman & Parker, 2005). Parasites have been used in molecular studies as indicators of host evolutionary history. Assessing species population genetic structure and phylogenetic relationships are useful ways to investigate species ancestry across a variety of temporal and geographical scales (Avise, 2009). Parasites can be good targets for comparative phylogeographic studies because of their tendency to track host population dynamics. Changes in genetic structure of a parasite could provide insight into the history of the host that is otherwise hard to detect through only looking at the host genetic structure (Paterson & Gray, 1997). Comparative phylogeographic studies can assess the degree of congruence between host and parasite phylogenies and to look for shared patterns of structure across a geographical range (Avise, 2009). Perfect congruence between host and parasite phylogenies is possible in theory but is rarely observed. Incongruence could arise due to multiple reasons such as different rates of lineage sorting, lineage extinctions, host-lineage switching, or failure to track the host

(Paterson & Gray, 1997). All of these events could be informative to illuminate historical events that shaped the host-parasite history.

Assessing host-parasite associations can permit inferences of past climate-mediated host movements. Alpine mammals and their parasites are suitable candidates to evaluate species responses to climatic oscillations in the past because of their preference for a well-defined habitat type and narrow climatic range (Trizio et al., 2005; Mráz et al., 2007). Habitat preferences may vary for different alpine species (Reichel, 1986) but their overall preference for alpine climate makes them vulnerable to any extreme change in climate.

This study focuses on a mammal-parasite assemblage in North America's Intermountain West, which spans the western part of the United States and southwestern Canadian provinces (Porter et al., 1983). This area provides an excellent system for studying the processes that structured diversity in alpine organisms because of the topographical complexity of the landscape and the past climatic fluctuations that influenced the distributions of species (Galbreath et al., 2010). The composition of the landscape includes high mountain regions (>3000 m) and low intermountain basins (<2000 m) (Porter et al., 1983; Grayson, 1993). During the Pleistocene glacial periods, climatic conditions across the region were unfavorable to many temperate species which resulted in fragmentation and contraction of populations. However, many cold-adapted species more typically associated with alpine environments took advantage of cooler environmental conditions during glacial periods and underwent range expansions, which resulted in increased gene flow (Galbreath et al., 2009).

Genetic consequences from past climatic fluctuations in western North America are documented for many species (Hewitt, 1996; Galbreath & Cook, 2004) including alpine specialists such as pikas. American pikas are small mammals that are widely distributed across North America's Intermountain West (Smith & Weston, 1990; Wilson & Reeder, 2005), and are known to have descended from an ancestor that crossed the Bering land bridge from the Palearctic (Dawson, 1967; Anderson & Kurten, 1980). They have received much attention recently because of local extirpations of Great Basin populations (Beever et al., 2003), which are believed to be associated with climate change. These lagomorphs have limited capacity for thermoregulation (Smith, 1974), leading them to expand and contract their range throughout the Intermountain West during the climatic oscillations of the Quaternary. When the conditions were favorable during the 1st Wisconsinan glaciation, pikas dispersed south of the ice sheets making use of the corridors that were open at the time (Grayson, 2005). This history of pikas was supported by phylogenetic studies based on both mitochondrial (mtDNA) and nuclear DNA (nDNA) of pikas, which showed that pikas achieved their distribution across the Intermountain West before the late Wisconsinan glaciation (Galbreath et al., 2010). Indeed, they are thought to have persisted in this area since the middle Pleistocene. At present, fragmented pika populations restricted to montane sky islands are a consequence of past inter-glacial warming periods (Hafner & Sullivan, 1995).

Phylogeographic analysis of American pikas from the Intermountain West showed genetic consequences of climate-mediated range shifts. These studies revealed five major non-overlapping mtDNA lineages spanning the range of American pikas in North America (Fig. 2.1) (Galbreath et al., 2009). Four out of the five lineages were also distinguished by allozymic variation (Hafner & Sullivan, 1995) suggesting deep histories of isolation which drove differentiation of both mitochondrial and nuclear DNA. The fifth mitochondrial lineage (previously unassigned in the allozymic study) was centered on populations found in central Utah. The five major lineages are associated with the Northern Rocky Mountains (NRM), Southern Rocky Mountains (SRM), Cascade Range (CR), Sierra Nevada (SN), and Central Utah (CU) (Fig. 2) (Galbreath et al., 2009, 2010).

Patterns of phylogeographic structure in American pikas raise the hypothesis that patterns of genetic diversity in associated parasites would be similarly structured. This was tested for host-specific endoparasitic helminths of pikas (Galbreath & Hoberg, 2015). The helminths showed distribution patterns that indicated past dispersal across host lineage boundaries, leading to two assemblages of helminths that were not fully concordant with host phylogeographic structure. These included a southwestern group of helminths associated with the Great Basin and Sierra Nevada Range, and a northeastern group that spans the Cascade Range and Northern and Southern Rocky Mountains (Galbreath & Hoberg, 2015). Incongruence between the host lineages and the endoparasite assemblages suggest historical contact between pika individuals from different lineages at lower elevations when favorable habitat was available, permitting parasites to be transported between host populations (Galbreath et al., 2010; Galbreath & Hoberg, 2015).

The history of the two major assemblages of helminth species is linked to historical climate-driven dispersal of pikas out of major mountain systems (Galbreath et al., 2009). Past dispersal appears to have led to contact between host individuals from neighboring lineages. Though such contact has left little evidence of gene flow in the host, it apparently facilitated dispersal of helminths across host lineage boundaries. On the contrary, in some parts of the Intermountain West helminths showed shallow patterns of co-divergence with their host due to shared isolation events which occurred since the last glacial maximum (Galbreath & Hoberg, 2015). Demographic studies on pikas and their endoparasites that explored the change in effective population size through time revealed a relationship between population fluctuations and historical climatic oscillations (Galbreath et al., 2010). Specifically, during the Pleistocene and Holocene periods, pika populations in the Intermountain West underwent population expansions followed by fragmentation and isolation of populations into high-elevation sky islands. The signature of these demographic changes was apparent in the host mtDNA and nDNA that showed isolation between but genetic admixture within populations in different mountain systems. This signal of both isolation and admixture recorded in DNA is concordant with expectations given the periodic cooling and warming of climate (Galbreath et al., 2010). Looking at the population structure of the endoparasites, it is apparent that patterns of dispersal of these host-specific parasites are not strictly shadowing the host. They seem to show historical dispersal across multiple host lineages suggesting possible contact between pikas from multiple lineages. Sharing of haplotypes across host lineages provided evidence for such historical dispersal, thus placing closely related parasite individuals within deeply divergent host lineages (Galbreath & Hoberg, 2015). Conversely, pikas show deep isolation between mountain ranges that is associated with separate evolutionary trajectories as a consequence of climatic oscillations in the past (Galbreath et al., 2010).

Our developing understanding of the coevolutionary history of pikas and their helminths led me to question the degree to which this history is shared by ectoparasites. Because ectoparasites utilize the hosts' outer body, they are exposed to both the host microenvironment and outer environmental factors. Fleas have eggs that fall off the host to the substrate to develop. The larvae, pupae and adult stages all spend time off a host and are subject to environmental conditions (Holland, 1985). I set out to investigate the intraspecific genetic structure of a representative ectoparasite for similarities to either the endoparasites or the host. Specifically, I investigated the phylogeographic structure of *Ctenophyllus armatus* Wagner, 1901 a common and geographically widespread flea species associated with American pikas. I tested two alternative hypotheses: 1) The phylogeographic structure of the most commonly distributed flea species across the Intermountain West shows genetic structure that is geographically concordant with the two major helminth assemblages, which can be explained by climate-driven host-mediated parasite dispersal across the landscape (Galbreath et al., 2009; Galbreath & Hoberg, 2015). 2) The phylogeographic structure of the fleas are geographically concordant with the five mitochondrial lineages of the host, indicating that factors controlling flea population structure are similar to those that structured pika distribution across the Intermountain West (Galbreath et al., 2009). In addition to testing these hypotheses, I also assessed the history of demographic change for the fleas to test for similarities to histories inferred for the host and the endoparasites.

METHODS

Study sites and sampling

Kurt Galbreath (Northern Michigan University) collected American pika specimens during the summers of 2004 and 2005 to acquire parasites from 37 localities across North America's Intermountain West. These parasites were stored in 70% EtOH, at various times either refrigerated or at room temperature, and I separated all specimens of *C. armatus* from the rest of the collection. *Ctenophyllus armatus* is a well-known pika flea, largely restricted to *Ochotona spp.* except for one instance in which it was reported from a ground squirrel in Alaska (Hopla, 1965). This species was the most abundant and widespread of the fleas recovered from the collection, occurring in 27 of the 37 sampled localities and with a distribution spanning the five lineages of *O. princeps* (Figure 2.1). A total of 375 *C. armatus* individuals were identified from these localities.

Molecular data collection

For this phylogeographic analysis, I selected the flea species *C. armatus* because it was the most common and widely spread species across the sampling localities. This provided me with an opportunity to test for phylogeographic concordance to its host and the endoparasites. To acquire genomic DNA from the collected fleas, I extracted DNA using the MasterPure^{TM} genomic DNA extraction kit (Epicenter Technologies, Inc., Madison, Wisconsin, United States of America). I first made a small incision on the abdomen of the flea exoskeleton to open up the bodily tissues and incubated the exoskeleton for 2 days in a solution of 1µl proteinase K (50µg/µl) mixed with tissue and cell lysis solution at 50^{o}C. Occasional vortexing of the samples during the incubation period encouraged successful tissue digestion. After the incubation period, I removed the exoskeleton from the solution and preserved it permanently by mounting it on a slide in Canada balsam (detailed mounting protocol in Chapter 1).

I amplified a portion (544 bp) of the cytochrome c oxidase subunit II (COII) mitochondrial gene using two published primer sets COII-2a/COII-9b and COII-F-leu/COII-R-lys (Whiting 2002) and one nested primer set (COII_NW_1a CAATAGGTATAAATCTGTG, NW_COII_1b TAGAAAATGACTACTTGG) that I designed. The amplification process involved running polymerase chain reaction (PCR) on a PTC 200 thermal cycler (GMI, Ramsey, Minnesota, United States of America) with the following touch-down protocol: 10 cycles of 1 min. denaturation, 1 min. annealing and 1 min. extension at 95°C, 58°C and 72°C respectively, followed by another 25 cycles of 1 min. denaturation (95°C), 1 min. annealing (48°C) and 1 min. extension (72°C). The final extension period was for 5 minutes at 72°C. I visualized the amplified DNA using gel electrophoresis and submitted the amplified DNA for sequencing by Elim Biopharmaceuticals, Hayward, California, United States of America. I assessed the quality of the DNA sequences by eye using GENEious 10.0.2 (Biomatters, Auckland, New Zealand), and aligned the sequences using MUSCLE as implemented in MEGA7.0 (Kumar et al., 2016).

Phylogeographic analysis

To characterize the phylogeographic structure within *C. armatus,* I used a Bayesian phylogenetic approach implemented in MRBAYES 3.2 (Ronquist et al., 2012). I chose *Ochotonobius hirticus* (GenBank # KM890841) as the outgroup for the analysis because of its close relationship to *C. armatus* (Krasnov et al., 2011). An appropriate nucleotide substitution model of TPM2uf+G was selected using jModelTest (Darriba et al., 2012). I ran a MRBAYES analysis for two runs of five chains each for 10 million generations and sampled every 1000 steps. I used Tracer v1.6 (Rambaut et al., 2013) to assess the quality and congruence between the two runs to ultimately determine the proportion of samples to assign as burn-in. The first 100,000 sampled trees were assigned as burn-in and the results of both runs were combined to generate a consensus Bayesian tree. I visualized the consensus tree using Figtree v 1.4.3 (Rambaut, 2016).

Diversity and Demographic analysis

Given the history of host population fluctuations due to climatic oscillations in the past, the effective population size (N_e) of the fleas was expected to experience similar changes over time. I tested for changes in effective population size using several methods. First, the genetic diversity among flea individuals in each population was analyzed in DnaSP 5.1 by generating a list of unique haplotypes with sample frequencies. Second, I created a minimum spanning network that shows mutational steps and relationships among each unique haplotype. Unlike a phylogeny, these networks allow sampled haplotypes to occupy ancestral nodes in the network and have more than two descendants. They show alternative evolutionary relationships in the form of a network that minimizes genetic distance between haplotypes (Bandelt et al., 1999). I constructed the minimum spanning network using the mathematical algorithm implemented in PopArt (http://popart.otago.ac.nz.).

To detect past demographic events such as sudden population expansions or contractions, I used several methods. Test statistics such as Fu's F_s and Tajima's D provide a test to detect sudden population expansions (Chaves et al., 2011; Schultheis et al., 2012). Significantly negative values for these test statistics imply either population expansion or strong positive selection. For Tajima's D, a positive value would imply a recent population contraction, balancing selection or admixture between divergent ancestral populations whereas positive Fu's F_s value would suggest a population bottleneck (Tajima, 1989; Fu, 1997). I used DnaSP 5.1 (Librado & Rozas, 2009) to calculate Fu's F_s and Tajima's D statistic, and test their significance. As an alternative test of population expansion, I generated a pairwise mismatch distribution in DnaSP 5.10 (Librado & Rozas, 2009) and compared this to expectations based on a sudden population expansion model. Mismatch distributions show the pairwise nucleotide differences between all individuals at the sequenced locus. If the resulting distribution is unimodal with a small raggedness index, a recent population expansion is implied. A multimodal distribution suggests either a contracting or a stable population.

Finally, I used a Bayesian skyline plot (BSP) to estimate fluctuation in the effective population size (N_e) over time. Unlike the tests described above, BSPs show the trajectory of N_e over time. This analysis was implemented in BEAST v2.4.4 (Bouckaert et al., 2014). I used the HKY+I nucleotide substitution model, which was selected by jModelTest. An assumption of a strict molecular clock that assumes the mutations occur at a constant rate was made based on the results of a chi-square log-likelihood test (Felsenstein, 1988). To test for this, likelihood trees and scores were computed in PAUP* (Swofford, 2003) with and without a molecular clock constraint. The score difference between the simpler model (with the clock constraint) and the more complex model (without a clock constraint) was calculated. I could not reject the clock-constrained model because the best ML tree was not significantly better than the unconstrained tree.

RESULTS

Phylogeographic structure

The 71 individuals sequenced for COII yielded 17 unique haplotypes, some of which were shared across different mountain systems (Fig. 2.3). The phylogenetic tree generated from COII mitochondrial gene sequences from *C. armatus* showed that individuals from the same locality or adjacent localities tend to cluster together (Fig. 2.3). The majority of diversity is associated with the southern extent of the NRM, the SRM, SN, and CU. Populations from the Cascade Range exhibit relatively shallow diversity.

Diversity and Demographic Analysis

Based on the minimum spanning network, some haplotypes are associated with multiple host lineages. Five haplotypes (Hap_1, 2, 4, 5, 6) are shared among the NRM, SRM, and CR host lineages. However, the only host lineage that does not seem to share flea haplotypes with other host lineages is the SN (Fig. 2.2). The minimum spanning network suggests that haplotype 6 may be the ancestral haplotype based on its central position in the network, but this conclusion is weak and needs further testing. Test results for Fu's F_s and Taijima's D revealed low but non-significant values (Fu's $F_s = 0.37$, Taijima's $D = -0.07$). These non-significant values indicate that I cannot reject the possibility of long-term population stability. Likewise, the pairwise mismatch distribution rejects the possibility of a sudden population expansion, thus suggesting population contraction or stability. The calculated raggedness index was low ($r = 0.0921$). However, the observed disdribution is clearly multimodal (Fig. 2.5). The BSP is also in agreement with the results of other demographic analyses, indicating a relatively stable population size through time.

DISCUSSION

Ochotona princeps first appeared in North America during the mid-Pleistocene at a time when the Bering Land Bridge was open (Galbreath et al., 2009). Since then, American pikas have differentiated in association with separate mountain systems of the Intermountain West (Galbreath et al., 2010). If the flea species underwent the same differentiation as their host, we would expect to see congruence in the phylogeographic structure of the host and the fleas. Instead, there is more similarity in the phylogeographic structure between the endoparasites and the fleas. Both endo- and ectoparasites seem to have dispersed across host lineage boundaries as indicated by sharing of haplotypes among localities associated with multiple host lineages.

Fleas found on different host lineages near the boundaries of the mountain systems often are closely related, probably because the pikas had a chance to exchange parasites when they came into contact at some point in time when the conditions were favorable for dispersal. Pika fossils dating to the LGM provide evidence for their dispersal at lower elevation and latitude during cooling periods (Hafner & Sullivan, 1995), and subsequent warm periods led them to the fragmented distribution we see today (Galbreath et al., 2009). Results from this study are concordant with my first hypothesis, which states that similar responses to climate-driven host population fluctuations resulted in dispersal of parasites across the Intermountain West. Parasites showing similar patterns of dispersal and not the same as the host could be due to host-lineage switching, in which parasites disperse beyond their ancestral host-lineage boundaries and persist among other host lineages (Paterson & Gray, 1997). The driver for this behavior could be climate-driven range shifts of the host.

Fleas sharing haplotypes among host lineages in high frequency can be explained in two ways: either they were present with the ancestral host population before the host underwent lineage seperation or their widespread distribution was acquired more recently. I found no evidence to support deep historical associations between *C. armatus* and *O. princeps* that could explain wide-spread distribution of closely related individuals. However, absence of *C. armatus* in SN populations does imply apparent physical barriers between this region and elsewhere, as seen in the endoparasites. Failure to track its host or extinction of parasite populations (Paterson & Gray, 1997) also could have resulted in the absence of *C. armatus* in the SN host lineage. In general, the evidence of historical contact between host individuals from separate regional lineages appears to be retained in the genetic structure of the parasites and not the hosts themselves.

The history of *C. armatus* in North America places them with pikas and thus having a preference for high-latitude or high-elevation cold habitats (Holland, 1985). When the host is deceased, *C. armatus* is thought to leave the host body immediately to seek another pika (Holland, 1985). Specificity for pikas is typical except in one instance, in which *C. armatus* was reported on a ground squirrel in Alaska. However, in the time since this early record (Hopla, 1965), there have not been any records of this flea on species other than pikas. If they were common among any other hosts, conclusions drawn from this study regarding host distribution would not strictly apply to pikas.

Persistance of a stable flea population over time may be explained by high effective population size of *C. armatus* among generally stable pika populations. These fleas have been maintaining a high effective population size by associating with a host that also maintains a stable population regardless of local extirpations (Erb et al., 2011). Absence of *C. armatus* from some populations suggests a possible role for competition between flea species to colonize a host body. Alternatively, *C. armatus* may have missed the chance to disperse into those populations historically, or our sampling may have simply been incomplete for those populations. However, lack of *C. armatus* in some populations of the southwestern part of the Intermountain West can be explained by geographical barriers for pika dispersal, which would inhibit contact between individuals to share parasites. Isolation of the pikas in the Sierra Nevada from the rest of the pikas in the Rocky mountains and Central Utah was suggested by ecological niche modelling (ENM) of pika distributions under past and present climatic conditions (Galbreath & Hoberg, 2015). The ENM showed that physical barriers for dispersal into Sierra Nevada may have existed during the LGM, even when the climatic conditions were maximally favorable for dispersal. Further sampling is needed to understand the distribution of *C. armatus* and its genetic diversity across the southwestern portion of the Intermountain West.

CONCLUSION

Results of this study illustrate the potential for parasites to aid in inferring host history. I provide further support for the conclusion that regional pika lineages were in contact historically. Associations between *C. armatus* and *O. princeps* show how micro- and macro- habitat can influence the dispersal and diversification of ectoparasites. Although increased sampling in the SN populations could strengthen conclusions, there is strong evidence of historical contact between pikas from multiple lineages, post-glacial northward range expansion from southern mountain systems, and a distinct separation of populations representing the SN lineage from other lineages.

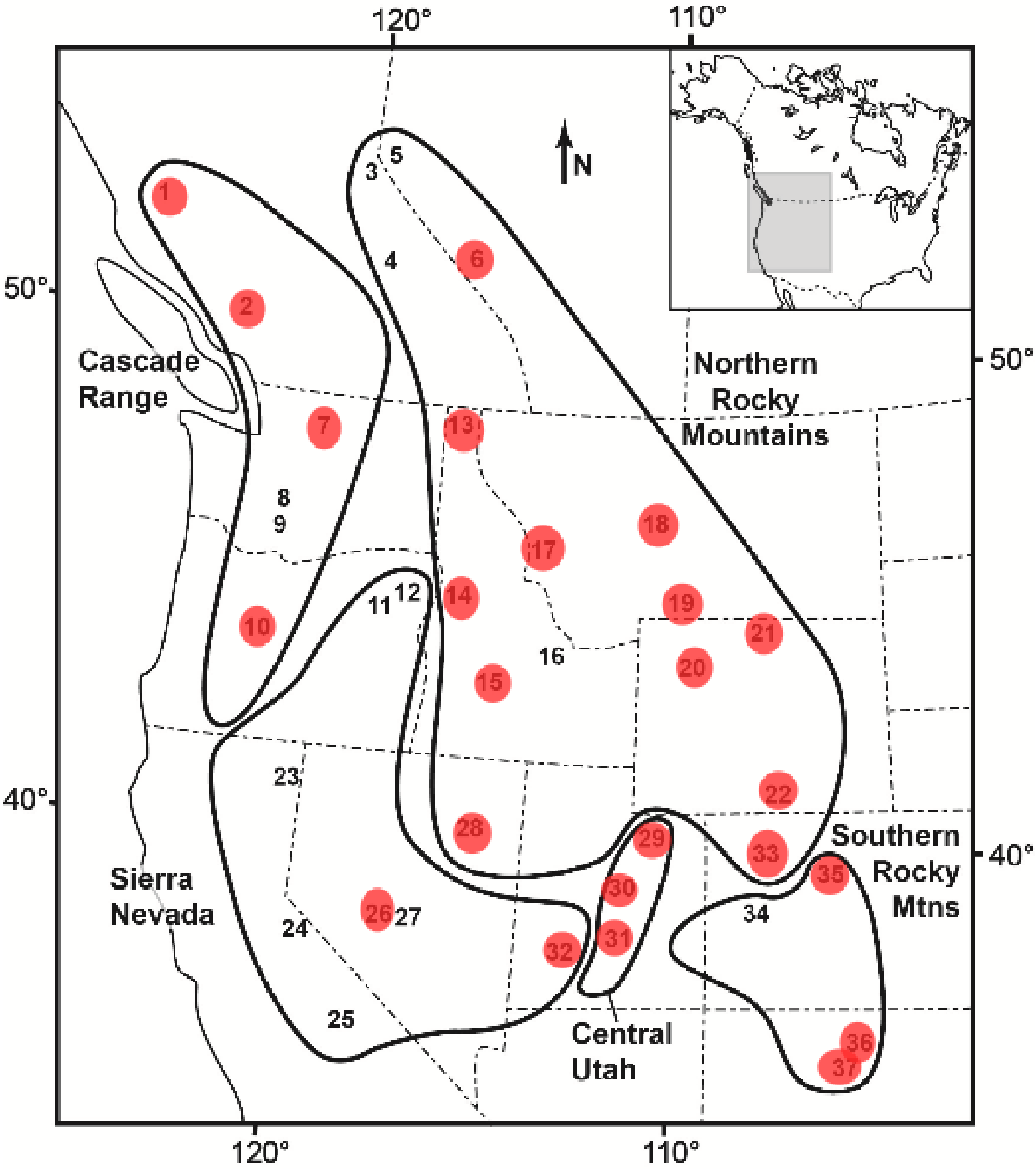

Figure 2.1: Sample localities of *Ctenophyllus armatus* used in the molecular analysis (colored in red). Collection locality numbers cross-reference with Table 1.1.

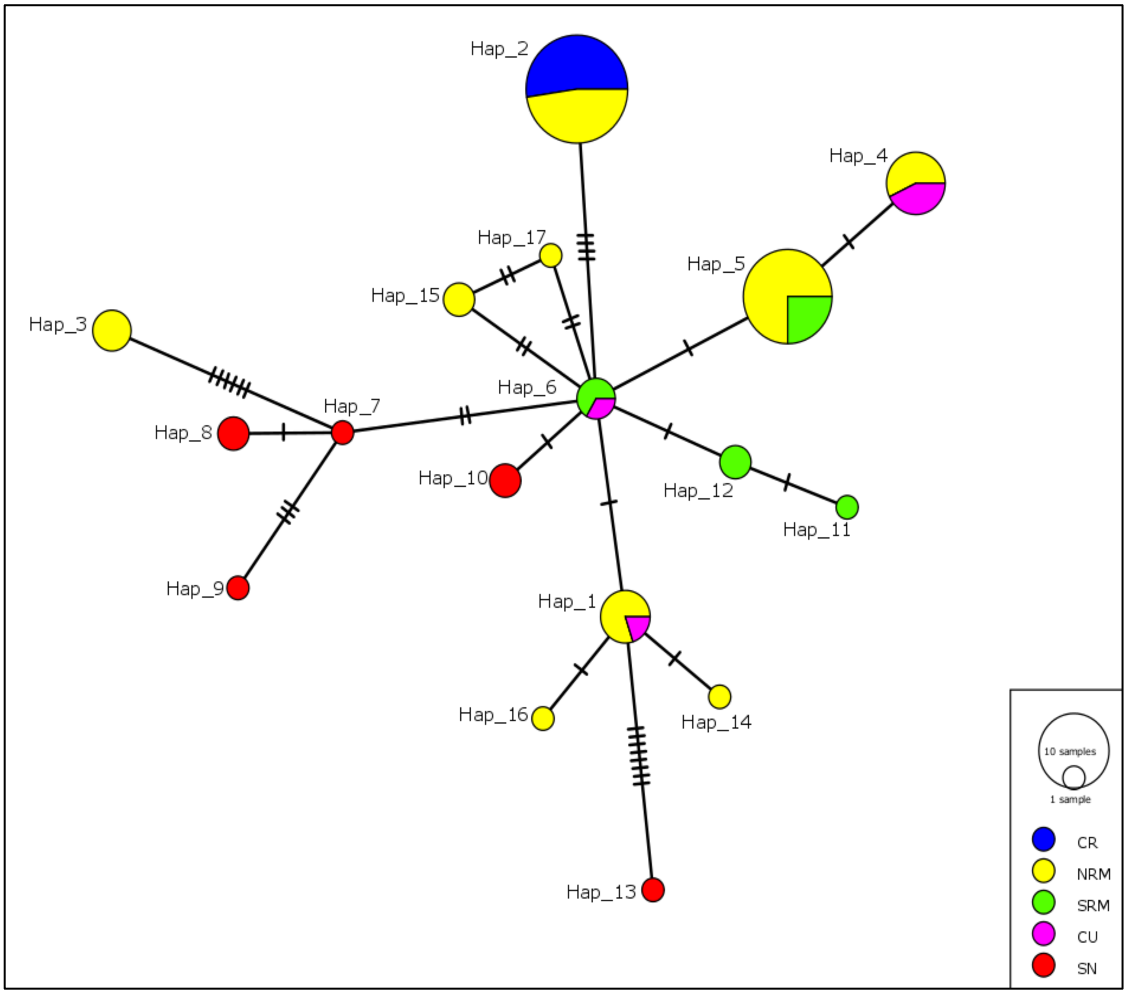

Figure 2.2: Minimum spanning network showing unique haplotypes. Circle size correspond to sample size (see legend). Color coding represent host lineages (CR = Cascade Range, NRM = Northern Rocky Mountains, SRM = Southern Rocky Mountains, CU = Central Utah, SN = Sierra Nevada). Un-sampled haplotypes are denoted by black dash marks.

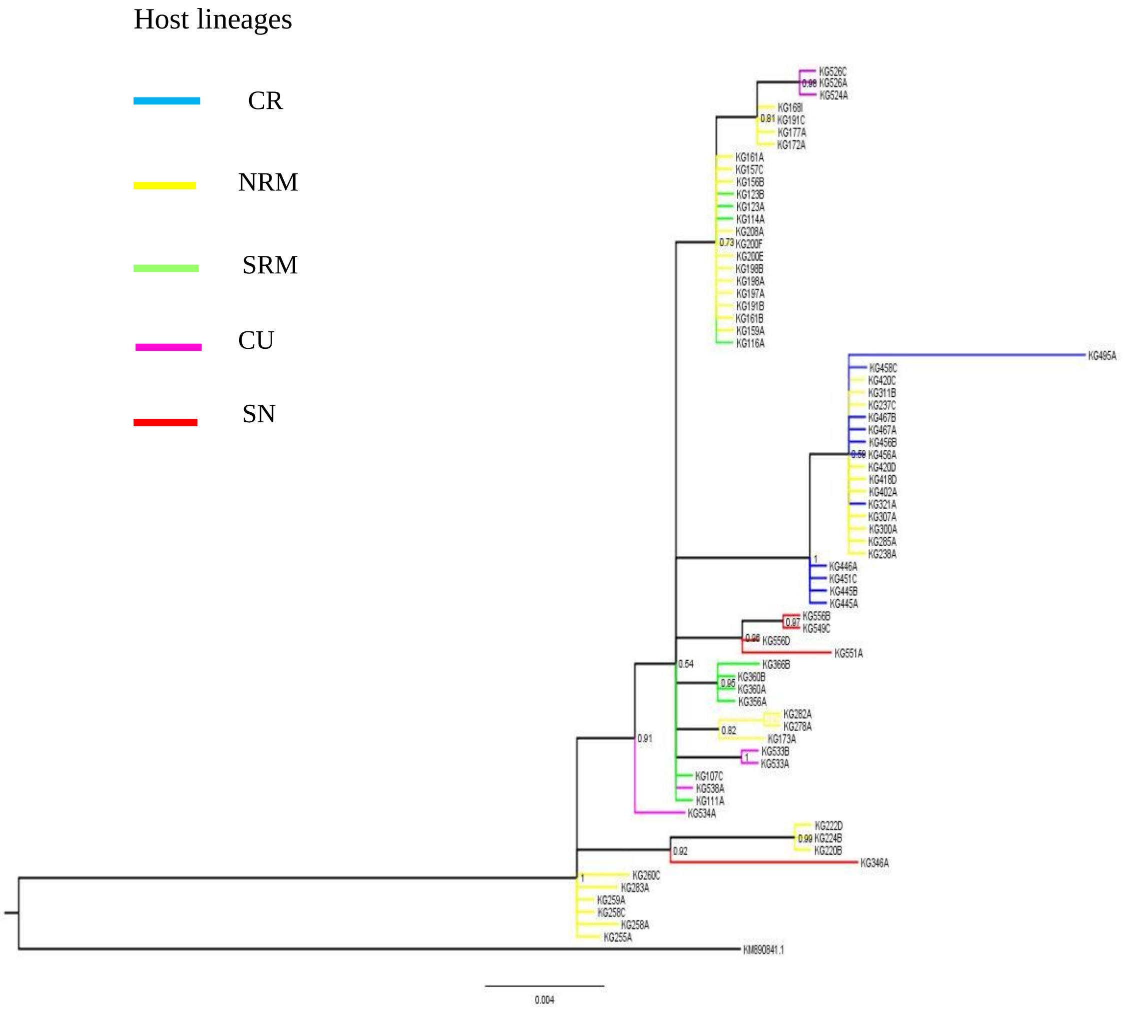

Figure 2.3: Phylogenetic tree for *C. armatus*. Tips are color-coded based on the collection localities associated with host lineages (CR= Cascade Range, NRM= Northern Rocky Mountain, SRM= Southern Rocky Mountain, CU= Central Utah, SN= Sierra Nevada). Posterior probabilities are shown by the node labels.

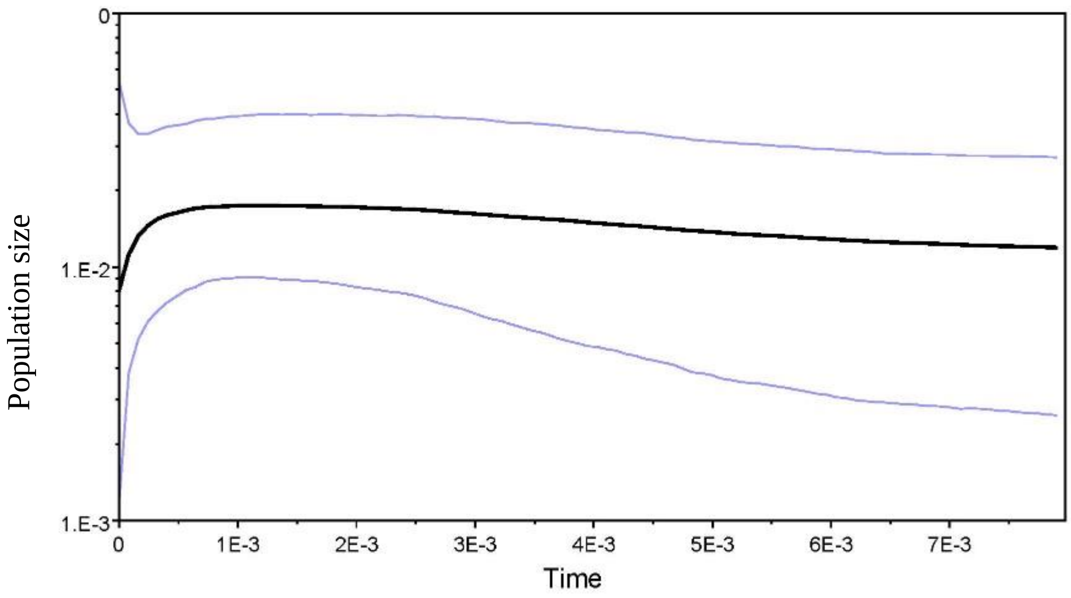

Figure 2.4: Bayesian skyline plot for *Ctenophyllus armatus* showing effective population size. The black line in the middle indicates the median population size. The two blue lines denote the 95% highest posterior density. The X axis shows time in terms of substitutions/site.

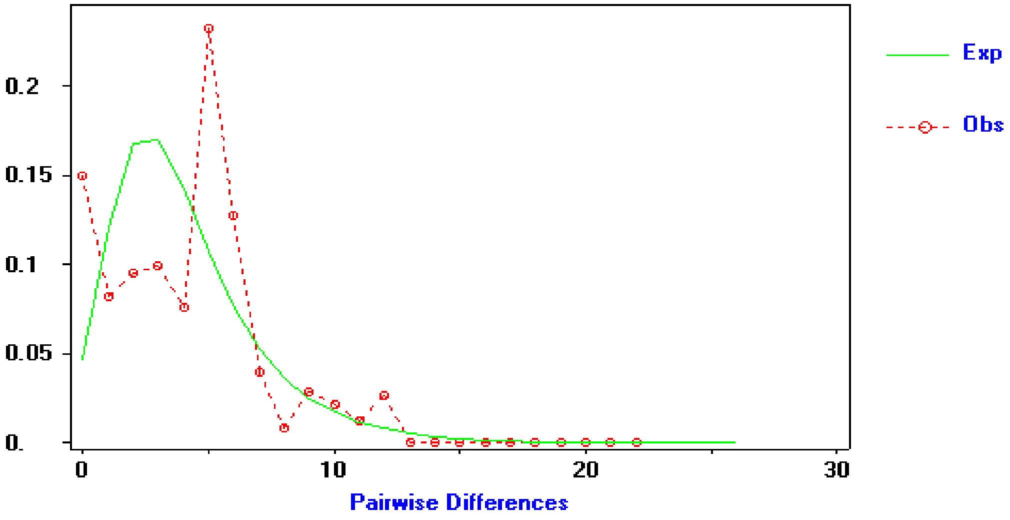

Figure 2.5: Pairwise mismatch distribution under sudden population expansion model. Green line = Expected distribution, Red dashed line = Observed distribution.

Table 2.1: Haplotype number, frequency and flea identification numbers

Haplotype Number	**Number of individuals in each haplotype**	**Flea identification numbers**
1	5	KG260C; KG534A; KG259A; KG258C; KG255A
2	21	KG495A; KG458C; KG446A; KG420C; KG311B; KG237C; KG467B; KG467A; KG456B; KG456A; KG451C; KG445B; KG445A; KG420D; KG418D; KG402A; KG321A; KG307A; KG300A; KG285A; KG238A
3	3	KG222D; KG224B; KG220B
4	7	KG168I; KG526C; KG526A; KG524A; KG191C KG177A; KG172A
5	16	KG161A; KG157C; KG156B; KG123B; KG123A KG114A; KG208A; KG200F; KG200E; KG198B KG198A; KG197A; KG191B; KG161B; KG159A; KG116A
6	3	KG107C; KG538A; KG111A
7	1	KG556D
8	2	KG556B; KG549C
9	1	KG551A
10	2	KG533B; KG533A
11	1	KG366B
12	3	KG360B; KG360A; KG356A
13	1	KG346A
14	1	KG283A
15	2	KG282A; KG278A
16	1	KG258A
17	1	KG173A

REFERENCES

Anderson, E. & Kurten, B. (1980) *Pleistocene mammals of North America.* Columbia University Press, New York.

Avise, J.C. (2009) Phylogeography: retrospect and prospect. *Journal of biogeography*, **36**, 3–15.

Bandelt, H.-J., Forster, P., & Röhl, A. (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular biology and evolution*, **16**, 37–48.

Barrett, L.G., Thrall, P.H., Burdon, J.J., & Linde, C.C. (2008) Life history determines genetic structure and evolutionary potential of host–parasite interactions. *Trends in Ecology & Evolution*, **23**, 678–685.

Beever, E.A., Brussard, P.F., & Berger, J. (2003) Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *Journal of mammalogy*, **84**, 37–54.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M.A., Rambaut, A., & Drummond, A.J. (2014) BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. *PLOS Computational Biology*, **10**, e1003537.

Chaves, P.B., Alvarenga, C.S., Possamai, C. de B., Dias, L.G., Boubli, J.P., Strier, K.B., Mendes, S.L., & Fagundes, V. (2011) Genetic Diversity and Population History of a Critically Endangered Primate, the Northern Muriqui (*Brachyteles hypoxanthus*). *PLOS ONE*, **6**, e20722.

Darriba, D., Taboada, G.L., Doallo, R., & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, **9**, 772–772.

Dawson, M.R. (1967) Lagomorph history and the stratigraphic record. *Essays in paleontology and stratigraphy*, **2**, 287–316.

Erb, L.P., Ray, C., & Guralnick, R. (2011) On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology*, **92**, 1730–1735.

Felsenstein, J. (1988) Phylogenies from Molecular Sequences: Inference and Reliability. *Annual Review of Genetics*, **22**, 521–565.

Fu, Y.-X. (1997) Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*, **147**, 915–925.

Galbreath, K.E. & Cook, J.A. (2004) Genetic consequences of Pleistocene glaciations for the tundra vole (*Microtus oeconomus*) in Beringia. *Molecular Ecology*, **13**, 135–148.

Galbreath, K.E., Hafner, D.J., & Zamudio, K.R. (2009) When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, *Ochotona princeps*). *Evolution*, **63**, 2848–2863.

Galbreath, K.E., Hafner, D.J., Zamudio, K.R., & Agnew, K. (2010) Isolation and introgression in the Intermountain West: contrasting gene genealogies reveal the complex biogeographic history of the American pika (*Ochotona princeps*). *Journal of Biogeography*, **37**, 344–362.

Galbreath, K.E. & Hoberg, E.P. (2015) Host responses to cycles of climate change shape parasite diversity across North America's Intermountain West. *Folia Zoologica,* **64**, 218–232.

Grayson, D.K. (1993) *The desert's past: a natural prehistory of the Great Basin.* Smithsonian Inst Pr,

Grayson, D.K. (2005) A brief history of Great Basin pikas. *Journal of Biogeography,* **32**, 2103–2111.

Hafner, D.J. & Sullivan, R.M. (1995) Historical and ecological biogeography of Nearctic pikas (Lagomorpha: Ochotonidae). *Journal of Mammalogy*, **76**, 302–321.

Hewitt, G.M. (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society,* **58**, 247–276.

Holland, G.P. (1985) The fleas of Canada, Alaska and Greenland (Siphonaptera). *Memoirs of the Entomological Society of Canada,* **130**, 3–631.

Hopla, C.E. (1965) Alaskan hematophagous insects, their feeding habits and potential as vectors of pathogenic organisms. 1. The Siphonaptera of Alaska. .

Krasnov, B.R., Poulin, R., & Mouillot, D. (2011) Scale-dependence of phylogenetic signal in ecological traits of ectoparasites. *Ecography*, **34**, 114–122.

Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S., & Allan Degen, A. (2004) Relationship between host diversity and parasite diversity: flea assemblages on small mammals. *Journal of Biogeography,* **31**, 1857–1866.

Kumar, S., Stecher, G., & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, msw054.

Librado, P. & Rozas, J. (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, **25**, 1451–1452.

Mráz, P., Gaudeul, M., Rioux, D., Gielly, L., Choler, P., Taberlet, P., & IntraBioDiv Consortium (2007) Genetic structure of *Hypochaeris uniflora* (Asteraceae) suggests vicariance in the Carpathians and rapid post-glacial colonization of the Alps from an eastern Alpine refugium. *Journal of Biogeography*, **34**, 2100–2114.

Paterson, A.M. & Gray, R.D. (1997) Host-parasite co-speciation, host switching, and missing the boat. *Host–parasite evolution: general principles and avian models*, 236–250.

Porter, S.C., Pierce, K.L., & Hamilton, T.D. (1983) Late Wisconsin mountain glaciation in the western United States. *Late Quaternary environments of the United States. Vol 1, the late Pleistocene* pp. 71–111. University of Minnesota Press, Minneapolis.

Rambaut, A. (2016) Available at: http://tree.bio.ed.ac.uk/software/figtree/.

Rambaut, A., Suchard, M., & Drummond, A. (2013) Available at: http://tree.bio.ed.ac.uk/software/tracer/.

Reichel, J.D. (1986) Habitat Use by Alpine Mammals in the Pacific Northwest, U.S.A. *Arctic and Alpine Research*, **18**, 111–119.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic biology*, **61**, 539–542.

Schultheis, A.S., Booth, J.Y., Perlmutter, L.R., Bond, J.E., & Sheldon, A.L. (2012) Phylogeography and species biogeography of montane Great Basin stoneflies. *Molecular Ecology*, **21**, 3325–3340.

Smith, A.T. (1974) The distribution and dispersal of pikas: influences of behavior and climate. *Ecology*, **55**, 1368–1376.

Smith, A. T. & Weston, M. L. (1990) *Ochotona princeps. Mammalian species*, **352**, 1-8.

Swofford, D.L. (2003) PAUP*. Phylogenetic analysis using parsimony (* and other methods). Version 4. .

Tajima, F. (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, **123**, 585–595.

Trizio, I., Crestanello, B., Galbusera, P., Wauters, L.A., Tosi, G., Matthysen, E., & Hauffe, H.C. (2005) Geographical distance and physical barriers shape the genetic structure of Eurasian red squirrels (*Sciurus vulgaris*) in the Italian Alps. *Molecular Ecology*, **14**, 469–481.

Whiteman, N.K. & Parker, P.G. (2005) Using parasites to infer host population history: a new rationale for parasite conservation. *Animal Conservation*, **8**, 175–181.

Wilson, D.E. & Reeder, D.M. (2005) *Mammal species of the world: a taxonomic and geographic reference.* John Hopkins University Press, Baltimore.

APPENDIX

Flea identification numbers (KG = Kurt Galbreath; number = host identification number; letter = individual fleas collected from that host), flea family, genera, species and locality numbers that cross reference with Table 1.1.

Flea ID	**Family**	**Genus**	**Species**	**Loc#**
KG 101 B			*Unknown*	36
KG 101 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 104 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 107 A			*Unknown*	36
KG 107 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 107 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 107 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 107 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 107 F	Ceratophyllidae	*Eumolpianus*	*Eumolpianus eumolpi*	36
KG 108 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 108 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 109 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 H	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36

KG 110 I	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 J	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 K	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 L	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 M	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 N	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 O	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 P	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 Q	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 R	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 110 S	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 111 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	36
KG 114 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 114 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 114 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus*	35
KG 114 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 114 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus*	35
KG 114 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 116 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 116 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus*	35
KG 116 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 116 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 117 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 117 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 117 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 117 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 117 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35

KG 122 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 122 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 123 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 123 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 123 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus*	35
KG 123 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 123 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 124 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 125 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 125 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 125 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 125 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	35
KG 126 A			*Unknown*	35
KG 126 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 126 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 126 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 126 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 126 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 126 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	35
KG 127 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 127 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 127 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 127 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 127 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 127 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 127 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 127 H	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35

KG 128 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 128 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 128 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 129 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	35
KG 134 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 134 B	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 134 C	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 134 D	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 134 E	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 135 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 B	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 C	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus*	34
KG 136 E	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus*	34
KG 136 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus*	34
KG 136 H	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 I	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 J	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 K	Ceratophyllidae	*Amphalius*	*Amphalius runatus*	34
KG 136 L	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 M	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 N	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 O	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 P	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 136 Q	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34

KG 137 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 137 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 137 C	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 137 D	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 137 E	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 137 F	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 137 G	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 137 H	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 137 I	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 137 J	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 137 K	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 138 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 139 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 139 B			*Unknown*	34
KG 140 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 B	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 C	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 D	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 E	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 F	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 G	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 H	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 140 I	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 J	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 K	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 L	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 M	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34

KG 140 N	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 O	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 P	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 Q	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 R	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 S	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 140 T	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 U	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 V	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 W	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 X	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 Y	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 Z	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 A1	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 140 B1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 C1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 D1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 E1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 F1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 G1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 H1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 I1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 J1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 K1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 140 L1	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 141 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 141 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34

KG 141 C	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 141 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 142 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 142 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 142 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 142 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 142 E	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 142 F	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 142 G	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 142 H	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 145 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 145 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 145 C	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 145 D	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 145 E	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 145 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 145 G	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 145 H	Ceratophyllidae	*Amphalius*	*Amphalius runarus necopinus*	34
KG 145 I	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 145 J	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 145 K	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 145 L	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 145 M	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 145 N	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 145 O	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 146 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 146 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34

KG 146 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 146 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 146 E	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 146 F	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 146 G	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 146 H	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 146 I	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 146 J	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 146 K	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 146 L	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 B	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 C	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 D	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 E	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 F	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 G	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 H	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 I	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 J	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 K	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 L	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 147 M	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	34
KG 148 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	34
KG 150 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	33
KG 155 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 156 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33

KG 156 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 156 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 157 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	33
KG 157 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 157 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 158 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 158 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 158 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 158 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 158 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 159 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 159 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 159 C	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	33
KG 159 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 161 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 161 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	33
KG 167 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 167 B	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	22
KG 168 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 168 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 168 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 168 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 168 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 168 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 168 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 168 H	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 168 I	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22

KG 169 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 169 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 169 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 169 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 169 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 170 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	22
KG 172 AA	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 172 BB	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 172 CC			*Unknown*	22
KG 172 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 172 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 173 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 173 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 173 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 173 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 173 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 177 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 177 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 177 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 177 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 177 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 178 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 180 A			*Unknown*	22
KG 180 B	Ctenophthalmidae	*Rhadinopsylla*	*Rhadinopsylla fraterna*	22
KG 182 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 190 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 190 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22

KG 190 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 190 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 190 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 190 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 190 G	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	22
KG 190 H	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	22
KG 191 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 191 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 191 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 191 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 191 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 191 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	22
KG 195 A			*Unknown*	20
KG 195 B			*Unknown*	20
KG 197 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 197 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 198 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 198 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 198 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 H	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20

KG 200 I	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 J	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 K	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 L	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 M	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 200 N	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 201 A	Ctenophthalmidae	*Conorhinopsylla*	*Conorhinopsylla sp.*	20
KG 201 B	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	20
KG 202 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	20
KG 202 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 202 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 202 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 203 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 203 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 206 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	20
KG 208 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 208 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 208 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 208 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 208 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 208 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	20
KG 208 G			*Unknown*	20
KG 210 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 210 B	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	21
KG 210 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 210 D	Leptopsyllidae	*Amphalius*	*Amphalius runatus necopinus*	21
KG 211 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21

KG 213 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 213 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 213 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	21
KG 214 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	21
KG 215 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 215 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 218 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 220 A			*Unknown*	21
KG 220 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 221 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 221 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 221 C	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	21
KG 222 A			*Unknown*	21
KG 222 B	Ceratophyllidae	*Amphalius*	*Amphaluis runatus necopinus*	21
KG 222 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 222 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 222 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 222 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	21
KG 222 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 222 H	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 222 I			*Unknown*	21
KG 224 A			*Unknown*	21
KG 224 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 224 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 224 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21
KG 225 A	Ctenophthalmidae	*Conorhinopsylla*	*Conorhinopsylla sp.*	21
KG 225 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	21

KG 225 C	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	21
KG 226 A			*Unknown*	21
KG 227 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	18
KG 229 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 229 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 229 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 231 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 231 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 235 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 236 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 236 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 236 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 237 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	18
KG 237 B			*Unknown*	18
KG 237 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 238 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 238 B	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	18
KG 238 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 238 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 238 D	Ceratophyllidae	*Eumolpianus*	*Eumolpianos eumolpi*	
KG 239 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 239 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 239 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 239 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 239 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 239 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	18
KG 239 G			*Unknown*	18

KG 248 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	19
KG 250 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	19
KG 250 B	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	19
KG 251 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	19
KG 253 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	19
KG 254 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	19
KG 254 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	19
KG 255 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	19
KG 256 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	19
KG 257 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	19
KG 257 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	19
KG 257 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	19
KG 258 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	19
KG 258 B			*Unknown*	19
KG 258 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	19
KG 258 D			*Unknown*	19
KG 259 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	19
KG 260 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	19
KG 260 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	19
KG 260 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	19
KG 260 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	19
KG 260 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	19
KG 264 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	17
KG 265 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	17
KG 265 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	17
KG 265 C	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	17
KG 266 A	Ctenophthalmidae	*Megarthroglossus*	*Megarthroglossus sp.*	17

KG 268 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	16
KG 273 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	16
KG 278 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	15
KG 280 A			*Unknown*	15
KG 282 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	15
KG 283 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	14
KG 283 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	14
KG 285 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	14
KG 285 B	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	14
KG 286 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	14
KG 286 B	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	14
KG 289 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	14
KG 289 B	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	14
KG 289 C	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	14
KG 290 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	14
KG 293 A	Ctenophthalmidae	*Megarthroglossus*	*Megarthroglossus spenceri*	14
KG 294 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	14
KG 299 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	13
KG 299 B			*Unknown*	13
KG 300 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 300 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus*	13
KG 300 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus*	13
KG 300 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 300 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 300 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	13
KG 300 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 300 H	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13

KG 300 I	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 300 J	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 302 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	13
KG 302 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 302 C			*Unknown*	13
KG 303 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 303 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 303 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	13
KG 303 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 305 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 306 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 306 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 306 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 307 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 307 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 309 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	13
KG 309 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	13
KG 309 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	13
KG 309 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	13
KG 310 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 311 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 311 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	13
KG 312 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	7
KG 312 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	7
KG 314 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	7
KG 314 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	7
KG 321 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	7

KG 322 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	7
KG 322 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	7
KG 324 A			*Unknown*	7
KG 325 A	Ctenophthalmidae	*Megarthroglossus*	*Megarthroglossus spenceri*	7
KG 336 A	Ctenophthalmidae	*Conorhinopsylla*	*Conorhinopsylla sp.*	8
KG 339 A	Ctenophthalmidae	*Catallagia*	*Catallagia sp.*	9
KG 341 A	Ceratophyllidae	*Eumolpianus*	*Eumolpianus eumolpi*	9
KG 344 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 344 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 344 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 344 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 344 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 344 F	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	26
KG 345 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 345 B	Leptopsyllidae	*Peromyscopsylla*	*Peromyscopsylla sp.*	26
KG 345 C	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	26
KG 345 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 345 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 345 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 345 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 346 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	26
KG 346 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 346 C	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	26
KG 346 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	26
KG 347 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	27
KG 347 B	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	27
KG 349 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	27

KG 349 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	27
KG 351 A	Ceratophyllidae	*Eumolpianus*	*Eumolpianus eumolpi*	27
KG 354 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	37
KG 356 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	37
KG 357 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	37
KG 357 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	37
KG 358 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	37
KG 358 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	37
KG 360 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	37
KG 360 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	37
KG 362 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	37
KG 364 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	37
KG 364 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	37
KG 365 A	Ctenophthalmidae	*Megarthroglossus*	*Megarthroglossus spenceri*	37
KG 366 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	37
KG 366 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	37
KG 366 C	Ctenophthalmidae	*Megarthroglossus*	*Megarthroglossus spenceri*	37
KG 367 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	37
KG 380 A			*Unknown*	23
KG 383 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	24
KG 384 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 384 B	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 384 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	24
KG 384 D	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 384 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	24
KG 384 F	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 384 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	24

KG 384 H	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 384 I	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 384 J	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 384 K	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	24
KG 384 L	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	24
KG 384 M	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	24
KG 384 N	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 384 O	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	24
KG 384 P	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 385 A	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 385 B	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 385 C	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	24
KG 385 D	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 385 E	Leptopsyllidae	*Geusibia*	*Geusibia ashcrafti*	24
KG 390 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 H	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 I	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 J	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 K	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 L	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 390 M	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28

KG 390 N	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 391 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 391 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 391 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 391 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 391 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 392 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 392 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 392 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 392 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 392 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 392 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 392 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 393 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 393 B	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	28
KG 393 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 393 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 393 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 394 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 396 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 396 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 396 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 396 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 396 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 396 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 396 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 396 H	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28

KG 396 I	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 396 J	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 399 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 399 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 399 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 399 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 399 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 399 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 399 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 400 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 400 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 400 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 400 D	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	28
KG 400 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 400 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 400 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	28
KG 401 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 401 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 401 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 401 D			*Unknown*	6
KG 401 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 401 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 402 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 402 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 402 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 402 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 405 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6

KG 405 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 405 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 406 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 406 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 406 C			*Unknown*	6
KG 406 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 408 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 408 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 408 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 408 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 408 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 408 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 408 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 408 H	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 408 I	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 409 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 409 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 409 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 409 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 409 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 409 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 410 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 410 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 410 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 410 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 410 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 410 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6

KG 410 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 410 H	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 410 I	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 410 J	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 411 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 411 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 411 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 413 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 417 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 417 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 417 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 418 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 418 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 418 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 418 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 419 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 420 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	6
KG 420 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 420 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 420 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	6
KG 422 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	3
KG 423 A			*Unknown*	3
KG 427 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	3
KG 427 B	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	3
KG 427 C			*Unknown*	3
KG 427 D	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	3
KG 427 E	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	3

KG 427 F			*Unknown*	3
KG 427 G			*Unknown*	3
KG 427 H	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	3
KG 427 I			*Unknown*	3
KG 428 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	3
KG 438 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 439 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 440 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 441 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 442 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 445 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 445 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 446 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 446 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 448 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 449 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 451 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 451 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 451 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 451 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 451 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 451 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 451 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1

KG 452 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 H	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 I	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 J	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 K	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 L	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 M	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 N	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 O	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 452 P	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 453 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 453 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 453 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 453 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 454 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 454 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	1
KG 456 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 456 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 456 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 457 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 457 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 457 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 457 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 457 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 457 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2

KG 457 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 458 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2
KG 458 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 458 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 458 E			*Unknown*	2
KG 458 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 458 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 458 H	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2
KG 459 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 459 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 459 C	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	2
KG 459 D	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	2
KG 459 E			*Unknown*	2
KG 459 F	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	2
KG 459 G	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	2
KG 461 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 461 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 462 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 462 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 467 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 467 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 467 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2
KG 469 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 469 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 469 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 469 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2
KG 469 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2

KG 469 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 469 G	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2
KG 469 H	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 469 I	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 469 J	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2
KG 469 K	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 469 L	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2
KG 469 M	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 G	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 H	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2
KG 470 I	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 J	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 K	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 L	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2
KG 470 M	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 N	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 470 O	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 471 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 472 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 472 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	2
KG 472 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2

KG 472 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 472 E	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 473 A			*Unknown*	2
KG 473 B			*Unknown*	2
KG 475 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 475 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 475 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 476 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	2
KG 476 B	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	2
KG 481 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	4
KG 486 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	4
KG 495 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	10
KG 504 A	Ctenophthalmidae	*Rhadinopsylla*	*Rhadinopsylla fraterna*	11
KG 511 A	Ctenophthalmidae	*Rhadinopsylla*	*Rhadinopsylla fraterna*	11
KG 517 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	11
KG 517 B			*Unknown*	11
KG 519 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	29
KG 524 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	29
KG 525 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	29
KG 525 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	29
KG 525 C			*Unknown*	29
KG 526 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	29
KG 526 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	29
KG 526 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	29
KG 526 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	29
KG 528 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	29
KG 528 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	29

KG 528 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	29
KG 529 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	30
KG 530 A	Ctenophthalmidae	*Megarthroglossus*	*Megarthroglossus spenceri*	30
KG 530 B	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	30
KG 530 C	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	30
KG 530 D			*Unknown*	30
KG 530 E	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	30
KG 531 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	30
KG 532 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	30
KG 532 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	30
KG 533 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	30
KG 533 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	30
KG 533 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	30
KG 533 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	30
KG 533 E			*Unknown*	30
KG 533 F	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	30
KG 534 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	30
KG 537 A	Ceratophyllidae	*Orchopeas*	*Orchopeas spp.*	31
KG 538 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	31
KG 539 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	31
KG 539 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	31
KG 539 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	31
KG 539 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	31
KG 540 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	31
KG 540 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	31
KG 540 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	31
KG 544 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	31

KG 546 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32
KG 546 B	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	32
KG 549 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	32
KG 549 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32
KG 549 C	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	32
KG 549 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32
KG 549 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32
KG 551 A	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	32
KG 553 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	32
KG 553 B			*Unknown*	32
KG 553 C	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	32
KG 553 D	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	32
KG 553 E	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	32
KG 554 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	32
KG 556 A	Ceratophyllidae	*Aetheca*	*Aetheca wagneri*	32
KG 556 B	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	32
KG 556 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32
KG 556 D	Leptopsyllidae	*Ctenophyllus*	*Ctenophyllus armatus*	32
KG 557 A	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32
KG 557 B	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32
KG 557 C	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32
KG 557 D	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32
KG 557 E	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32
KG 557 F	Ceratophyllidae	*Amphalius*	*Amphalius runatus necopinus*	32