Revision and phylogenetic analysis of the verrula and alberta species of Rhyacophila pictet 1834 with description of a new species (Trichoptera: Rhyacophilidae)

by Jonathan Joseph Giersch

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Entomology

Montana State University

Abstract:

Adult, larval, and pupal characters, and data from newly associated life stages supported the monophyly of the Rhyacophila verrula- and alberta-species groups. The verrula-group is comprised of R. haddocki Denning, R. leechi Denning, R. potteri Denning in Denning and Schmid, R. rickeri Ross, R. singularis Botosaneanu, and R. verrula Milne, with a new inclusion of R. chandleri Denning. Rhyacophila autumnalis Nimmo was found to be a junior synonym of R. potteri. The monophyly of the verrula-group is based on synapomorphies that include the expanded dorsal appendage of the phallic apparatus, closed m-cell in the forewing and morphology of the larvae. The morphology of the known larvae of this group supports the hypothesis of phytophagous feeding habits, which served as an opportunity for the evolution and speciation within the group.

Rhyacophila chandleri was found to be a basal member of the verrula-group, although autapomorphies suggest an early isolation from the rest of the verrula-group. Rhyacophila rickeri is basal to the rickeri-subgroup, with R. singularis and R. potteri as sister species. Rhyacophila verrula, R. leechi, and R. haddocki form the verrula-subgroup. The wide distribution of R. verrula suggests a wider ecological tolerance than other species of the group.

The alberta-group is comprised of two subgroups, R. alberta, R. tucula, and R. n. sp. comprise the alberta subgroup, and R. kincaidi and R. glaciera comprise the glaciera-subgroup.

Phylogenetic reconstructions of the alberta- and verrula-groups suggest the evolution of these species groups was driven by post-Pleistocene isolation of populations in headwater streams.

REVISION AND PHYLOGENETIC ANALYSIS OF THE VERRULA AND ALBERTA SPECIES GROUPS OF *RHYACOPHILA* PICTET 1834 WITH DESCRIPTION OF A NEW SPECIES (TRICHOPTERA: RHYACOPHILIDAE)

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APPROVAL

Of a thesis submitted by

Jonathan Joseph Giersch

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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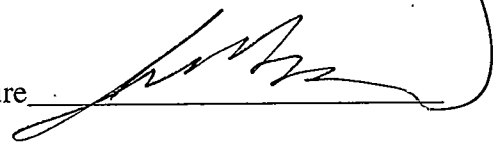
Signature 

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DEDICATION

This work is dedicated to Dr. Andrew Peebles Nimmo, who brought to my attention the vast diversity of *Rhyacophila* in northwestern Montana through his pioneering the work on the *Rhyacophila* of Alberta, thereby awakening my love for alpine Trichoptera and alpine stream habitats in general. While I have attempted to provide thorough graphical representations of the species described in the following document, the illustrations Dr. Nimmo's work set the standard to which remain unsurpassed in Trichoptera literature. I also owe much to Dr. Nimmo for the use of his extensive library on Trichoptera and his generosity with bibliographic references, as well as being a gracious host during my short visit to Edmonton during the winter of 2001.

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ABSTRACT

Adult, larval, and pupal characters, and data from newly associated life stages supported the monophyly of the *Rhyacophila* verrula- and alberta-species groups. The verrula-group is comprised of *R. haddocki* Denning, *R. leechi* Denning, *R. potteri* Denning in Denning and Schmid, *R. rickeri* Ross, *R. singularis* Botoşăneanu, and *R. verrula* Milne, with a new inclusion of *R. chandleri* Denning. *Rhyacophila autumnalis* Nimmo was found to be a junior synonym of *R. potteri*. The monophyly of the verrula-group is based on synapomorphies that include the expanded dorsal appendage of the phallic apparatus, closed m-cell in the forewing and morphology of the larvae. The morphology of the known larvae of this group supports the hypothesis of phytophagous feeding habits, which served as an opportunity for the evolution and speciation within the group.

Rhyacophila chandleri was found to be a basal member of the verrula-group, although autapomorphies suggest an early isolation from the rest of the verrula-group. *Rhyacophila rickeri* is basal to the rickeri-subgroup, with *R. singularis* and *R. potteri* as sister species. *Rhyacophila verrula*, *R. leechi*, and *R. haddocki* form the verrula-subgroup. The wide distribution of *R. verrula* suggests a wider ecological tolerance than other species of the group.

The alberta-group is comprised of two subgroups, *R. alberta, R. tucula,* and *R.* n. sp. comprise the alberta subgroup, and *R. kincaidi* and *R. glaciera* comprise the glaciera-subgroup.

Phylogenetic reconstructions of the alberta- and verrula-groups suggest the evolution of these species groups was driven by post-Pleistocene isolation of populations in headwater streams.

Disclaimer: This thesis is not intended to meet the provision of the ICZN (1999) regarding publication of new nomenclatural acts [Art. 8.2]. No name or nomenclatural act proposed herein should be considered available as defined by the ICZN.

CHAPTER 1

INTRODUCTION

Statement of the problem

The inception of this thesis began with studies in alpine streams of Glacier National Park for F. Richard Hauer at the Flathead Lake Biological Station. This work awakened my appreciation for these unique habitats in which the genus *Rhyacophila* Pictet is particularly well represented, many species of which very little had been previously published.

The purpose of this thesis was to learn the methods of modern cladistics by investigating two species groups of *Rhyacophila*, each of which include both wide and narrowly distributed species. Species groups in *Rhyacophila* are informal groupings, used to bring order to a genus of more than six hundred species. Much of the previous work on *Rhyacophila* phylogeny has been based largely on the male morphology. In the analyses of the verrula- and alberta-groups, I used expanded character sets incorporating data from newly associated females, larvae, and pupae.

Of the two species groups studied, the alberta-group is fairly straightforward. Group synapomorphies are clear, and the membership of the group have been undisputed. In contrast, the synapomorphies for the verrula-group had not been clearly defined, and the inclusion of two species (*Rhyacophila haddocki* Denning and *R. rickeri* Ross) has been disputed. Once the synapomorphies of the verrula-group had been defined, I looked for other species that may have previously been unplaced, but fit within the group. The

result was the inclusion of the previously unplaced *R. chandleri* Denning into the verrula-group.

The resulting phylogenetic hypotheses were then used to examine the impact of biology and biogeography on the evolution of the two species groups.

Introduction to the order Trichoptera

The order Trichoptera is considered to be the sister group of the Lepidoptera, together comprising the Amphiesmenoptera (Kristensen 1991). The order includes over 10,000 extant species that inhabit a diverse array of freshwater habitats worldwide (excluding Antarctica) (Morse 1997). The success and diversity of the Trichoptera in freshwaters is attributed to their use of silk to assist in mobility, food acquisition, and retreat construction (Mackay and Wiggins 1979). The Trichoptera are hypothesized to have evolved in cold, headwater streams (Ross 1956 and 1967), with the oldest undisputed Trichoptera fossils dating to the Triassic (Wiggins 1984). The diverse selective pressures of freshwater habitats, with their diverse thermal, morphological and hydrologic characteristics contributed to the adaptive radiation and diversification of the Trichoptera (Huryn and Wallace 1988).

Synapomorphies of the Trichoptera include a modified hypopharynx in the adult, the absent proximal articulations and musculature of the adult labrum, elongate prealar arms, apneustic, aquatic larvae, and reduced larval antennae and tentorium (Morse 1997).

The higher-level phylogeny of the Trichoptera has been investigated by several authors (Milne and Milne 1939, Ross 1967, Weaver 1984, Weaver and Morse 1986,

Wiggins and Wichard 1989, Ivanov 1997a, Frania and Wiggins 1997, and Kjer, et al. 2001). The Trichoptera are generally considered to be comprised of three suborders: Annulipalpia, Integripalpia, and the Spicipalpia. Whereas the monophyly of the Annulipalpia and Integripalpia are well supported (Kjer, et al. 2001), problems in the classification of the order have centered on the potential polyphyly of the Spicipalpia (Morse 1997).

The Annulipalpia are considered to be the sister clade of the Integripalpia plus Spicipalpia (Kjer et al. 2001). The Annulipalpia are confined to lotic (running water) habitats, and the larvae construct fixed retreats from which they spin nets to capture small prey or particulate matter. Families included in the Annulipalpia are the Hydropsychidae, Philopotamidae, Polycentropodidae, and their relatives (Wiggins 1996).

The Integripalpia are a large and diverse suborder, containing many families such as the Limnephilidae, Phryganeidae and Brachycentridae. Larvae of this suborder construct portable cases of various types of materials, and occur in diverse aquatic habitats, from lentic to lotic, cold and warm waters (Wiggins 1996).

The Spicipalpia include the families Rhyacophilidae, Hydrobiosidae, Glossosomatidae, and Hydroptilidae. The Hydrobiosidae is a warm adapted lineage that occurs in Australian, Oriental, and Neotropical regions (Wold 1974), whereas the Rhyacophilidae, Glossosomatidae, and Hydroptilidae occur nearly worldwide (with the exception of Antarctica) (Wiggins 1996). Ivanov (1997a), Frania (1997), and most recently, Kjer et al. (2001) have disputed the monophyly of the Spicipalpia. In contrast to

the Annulipalpia and Integripalpia, which build a permeable pupal cocoon, the Spicipalpia are largely defined by the construction of closed, semipermeable cocoons. These problems with the competing hypotheses of the phylogeny for the Trichoptera result from the use of different datasets (adult and larval morphological vs. molecular) or differences of opinion on character polarity. Further studies will no doubt continue to clarify the higher-level phylogeny of the order.

Family Rhyacophilidae

Ross (1956) recognized two subfamilies in the Rhyacophilidae, the Rhyacophilinae and Hydrobiosinae. Schmid (1970) elevated these subfamilies to family status. The resulting family Rhyacophilidae *sensu* Schmid consists of four extant genera: *Fansipangana* Mey 1996, *Himalopsyche* Banks 1940, *Philocrena* Lepneva 1956, and *Rhyacophila* Pictet 1834. *Fansipangana* is monospecific, based on *F. vernalis* Mey from North Vietnam. The phylogenetic placement of this species is of interest, as the phallic apparatus of the male has an elongate dorsal appendage and closed m-cell in the forewing, as in the *Rhyacophila* verrula-group (Mey 1996). *Himalopsyche* is almost entirely oriental in distribution, with a single species, *H. phryganea*, occurring in the Pacific Northwest of North America (Wold 1974). *Philocrena* is represented by a single species, *P. trialetica*, from the Caucasus of Georgia. A single fossil genus, *Rhyacophilites* Piton 1935 has also been placed in the family. This genus is monospecific, based *R. hydropsychiformis*, described from two fragments of a forewing from mid-Pliocene

sediments in France. The phylogeny of the Rhyacophilidae has not been addressed by workers, and therefore no hypothesis of relationships of these genera is available.

Genus *Rhyacophila*

The bulk of the family is placed in *Rhyacophila*, with over 600 recognized species, about 120 of which occur in the Nearctic region (Morse 1999). *Rhyacophila* is most diverse in the Holarctic with nearly 350 species. The synapomorphies of the Rhyacophilidae include the presence of ocelli, the maxillary palps with the first two segments being short, the second of which is subglobular, with an acute point apically. Mesothoracic legs of the female are rounded in cross section, as opposed to being flattened as in the Hydropsychidae and Glossosomatidae.

Studies of the evolutionary relationships of *Rhyacophila*

Schmid (1970) hypothesized that *Rhyacophila* dates from the Cretaceous, originating in Asia. *Rhyacophila* is considered plesiomorphic, resembling the postulated ancestral trichopteran. Plesiomorphic characters exhibited by this genus include ocelli, complete wing venation, with a curved CU_2 vein and short anal veins, the unspecialized pupa, free-living larva, and the membranous meso- and metanota of the larva (Ross 1956). The two-segmented inferior appendages of the male genitalia, with the basal coxopodite and distal harpago are also considered to be plesiomorphic characters (Ross 1956).

Due to the diversity of the genus *Rhyacophila*, several workers have attempted to construct a classification of species groups or subgenera. Banks (1939), Döhler (1950), Fischer (1971), and Kimmins (1952) named seven subgenera of *Rhyacophila*. However, many were limited to a small number of isolated, derived species, and were not based on large-scale revisions. Most revisions have therefore not recognized subgenera.

Ross (1956) published the first major work on the phylogeny of *Rhyacophila*, recognizing nine main branches of the genus, and 44 species groups. Species occurring in North America were represented in eighteen of these groups.

Schmid's (1970) pre-cladistic revision of *Rhyacophila* considered the phylogeny of the genus on a nearly global scale and added over one hundred new species. His work mainly used the morphology of the male genitalia, but also included details of a limited number of female genitalia, as well as the mechanics of copulation. In Schmid's phylogeny, the genus was divided into four main branches, which were separated into seven twigs, further delineated into 72 species groups. Seventeen of these species groups are represented by species occurring in North America. Schmid mainly accepted the species groups named by Ross, but disagreed in the relationships among the groups.

The phylogenies of Ross (1956) and Schmid (1970) were based mainly on characters of the male genitalia, and tests of those hypotheses that incorporate larval characters have not supported their conclusions. Flint (1962) associated several larvae from the eastern United States, but did not find larval characters from these species to be congruent with Ross' species groups. Lepneva (1970) used Döhler's (1950) classification of the subgenera of *Rhyacophila* as the basis for her study of the Russian *Rhyacophila*

larvae, recognizing his subgenera as species groups. Wold (1974) incorporated characters from recently associated larvae to test Schmid's (1970) phylogeny for the *Rhyacophila* species of the western United States.

The works of Ross (1956), Schmid (1970), Lepneva (1970) and Wold (1974) were all conducted prior to the widespread use of cladistic methods, and therefore hypothetical relationships may not be based on shared derived characters. The first to use cladistics to address this genus in North America were Prather (1998) and Prather and Morse (2001), in a revision of the eastern Nearctic *Rhyacophila*, including a revision of the large *R. invaria* species group. These analyses used morphological data and modern phylogenetic methods to produce a hypothesis of phylogeny, therefore avoiding the inclusion of paraphyletic taxa.

Life history of *Rhyacophila*

Species of *Rhyacophila* exhibit a wide range of life histories, including univoltinism, bivoltinism, and multivoltinism with spring to fall emergence (Ross 1956). *Rhyacophila* in North America are largely univoltine (Anderson and Wold 1972, Singh et al. 1984), however, some species that are univoltine in lower elevation temperate streams may be semivoltine in higher latitudes or altitudes where the growth season is too short for larvae to complete development in a single year (Irons 1988).

Rhyacophila species are often sympatric, with several occurring together at one site. Short and Ward (1980) reported collecting six species from a single riffle in Colorado, and Gustafson (1990) collected eight species at one site in Montana.

Asynchronous life cycles not only reduce competition for resources between several species at a single location, but assure that not all species will emerge simultaneously, discouraging the chance for nonproductive mating between different species (Martin 1985). However, competition between congeneric species may increase during periods of decreased resource availability, such as spates during spring runoff or after heavy rains (Martin and Mackay 1983).

In some species, adult emergence, mating, and oviposition may occur throughout the year, while others are more specific, usually limited to either spring or fall emergence depending on the region and species. Other species emerge early in the spring. In some normally fall emerging species, individuals that do not make the fall emergence overwinter as larvae or pupae and emerge in the early spring (Manuel and Folsom 1982, Huryn and Wallace 1988, Edington and Hildrew 1995). Larvae of *Rhyacophila* can be found in streams throughout the year, and any given instar of several species of *Rhyacophila* occur throughout the year (Thut 1969, Gustafson 1990).

The eggs of *Rhyacophila* can be very resilient. Thut (1969) reported that eggs of *Rhyacophila vagrita* Milne remained viable up to seven months after oviposition.

Rhyacophila feeding ecology

With the exception of the verrula-group, *Rhyacophila* have been shown to be almost entirely predaceous, feeding on aquatic insects such as Simuliidae, Chironomidae, Ephemeroptera, Plecoptera, other Trichoptera, and other invertebrates such as Copepoda, Acari, and Oligochaeta (Thut 1969, Mecom 1972, Shapas and Hilsenhoff 1976, Manuel

and Folsom 1982, Martin and Mackay 1983, Singh et al. 1984, Irons 1988, Otto 1993, Wotton et al. 1993, and Oberndorfer et al. 1984). Predation on fish eggs has also been reported (Brown and Diamond 1984, and Fox 1978).

Gut content analyses have been used to investigate the feeding ecology of *Rhyacophila*, though this method may not provide accurate, quantitative results. Rather than engulfing their prey whole, they only consume soft parts of their prey, hollowing out the thorax and discarding chitinous structures such as legs and head capsules (Martin and Mackay 1982). The morphology of the gut of predaceous *Rhyacophila fuscula* Walker and *R. dorsalis* (Curtis) have been reported to lack a proventriculus, which may limit their ability to digest large, well sclerotized prey fragments (Martin and Mackay 1982).

Rhyacophila that are generally considered to be obligate predators but may ingest non-animal material to a small degree, including filamentous algae, diatoms, detritus, and bryophytes (Mecom 1972, Irons 1988, Thut 1969 and Singh et al. 1984). While the presence of this plant material may be accidental when feeding on insects within plant material, it has been suggested that some predatory *Rhyacophila* occasionally intentionally feed on mosses and algae (Edington and Hildrew 1995). Detritus of leaf origin may also be from the gut contents of the prey items themselves (Irons 1988).

Feeding patterns may also change throughout the life of some *Rhyacophila* species. Species may exhibit phytophagy in the early instars, with a diet dominated by bryophyes, diatoms, and detritus. However, after the third instar, the diet may change to include more animal material (Singh et al. 1984 and Cereghino 2002).

A few species of *Rhyacophila* have been shown to have associations with bryophytes. *Rhyacophila tova* Hagen has been found to be associated with mosses on the vertical faces of waterfalls in the eastern United States (Roback 1975). It is not known whether this species uses the moss as a food source, but larval morphology of this species suggests that it is predaceous and exploits the prey species within the moss mats rather than feeding on the mosses themselves (Roback 1975).

In North America, *R. verrula* Milne is the only *Rhyacophila* species recorded to be entirely phytophagous (Smith 1968, Thut 1969, Gustafson 1990). *Rhyacophila laevis* Pictet, a member of the sibirica-group, is the only other known species in the genus that has been reported to be phytophagous (Botoşăneanu 1953).

The concept of functional feeding groups is important to benthic macroinvertebrate studies (Merritt and Cummings 1984, Resh and Rosenberg 1984). In many studies using rapid bioassesment protocols, *Rhyacophila* larvae are often identified to only family or genus level, which can cause errors in interpretation because of more widespread phytophagy reported (Cereghino 2002).

Physical factors that determine the distribution of *Rhyacophila*

Most *Rhyacophila* species occur on mineral substrates in clean riffles (Gustafson 1990), although some species, such as *Rhyacophila rotunda* Banks, are found in silt-laden streams (Smith 1968). The genus as a group is considered to be intolerant to pollution, and has therefore been useful in biomonitoring studies (Lenat 1993).

The thermal ecology of *Rhyacophila* species, coupled with the special characteristics of alpine stream habitats, is important to understanding the distribution of the genus. *Rhyacophila* are confined to cool, swift, mountain streams, with many species geographically restricted to single mountain ranges (Ross 1956, Schmid 1970). Temperature is a major factor affecting the physiology and life history of insects, and can determine the distribution of these animals (Ward and Stanford 1982). The distribution of closely related Trichoptera species along stream gradients has been correlated with the effects of temperature on metabolism (Lowe and Hauer 1999). For species occurring over a wide range of elevation, life cycles and emergence times may correspond to a thermal gradient along the stream continuum (Donald and Anderson 1977, Nebeker 1971). The extreme thermal and morphological conditions of alpine streams result in a unique fauna. Several species of *Rhyacophila*, such as *R. kincaidi* Schmid, *R. glaciera* Denning, and *R. rickeri* Ross are confined to alpine streams. Snow and ice-melt fed streams are characterized as having cold temperatures, high gradients, cobble boulder substrate, and high shear stress, limiting the fauna to those species adapted to such environments (McGregor et al. 1995). Because alpine streams accumulate a small number of annual degree-days, the growth of insect larvae is slow. Alpine areas offer a diverse range of stream habitats, including icefield and glacier melt streams, spring brooks, and seasonal snow-melt driven streams (Ward 1994). Small water volumes, such as those in alpine streams, respond rapidly to changes in temperature (McGregor et al. 1995). The lower reaches of alpine streams exhibit wide daily temperature fluctuations during the hottest days of the summer due to the lack of canopy cover and shallow laminar flow over

bedrock (Ward 1994). Therefore, temperatures change rapidly with distance from the source, isolating species adapted to those habitats. Ice and snowmelt as well as spring-fed stream habitats types may exist in close proximity along the longitudinal gradient of an alpine stream, therefore resulting in a high degree of thermal heterogeneity in a limited spatial area (fig. 1).

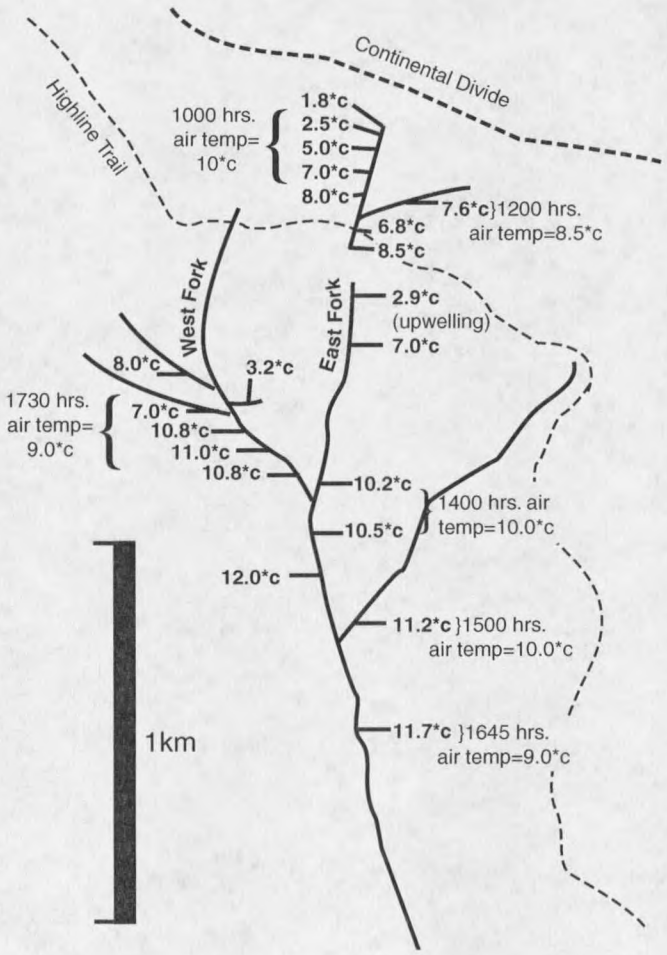

Figure 1: Example of the thermal complexity of alpine stream systems. Temperature data recorded from the Upper Mineral Creek drainage, Glacier National Park, MT. on 28 August 1997 (Hauer and Giersch, unpublished data).

In contrast to forested stream catchments in which the heavy input of leaf litter drives stream metabolism (Fisher and Likens 1973, and Vannote et al. 1980), hardwood canopy cover is absent from alpine streams (fig. 2). Leaf inputs are limited to those from low lying woody shrubs and tundra plants (Ward 1994).

Figure 2: Typical alpine stream habitats at Logan Pass, Glacier National Park, Montana.

The alpine stream faunal community largely lacks the shredder functional feeding group that is a main component of headwater communities. Often, phytophagous species in alpine streams feed on bryophytes, which can be plentiful in those habitats. Since any increase in allochthonous inputs allows an increase in diversity in an otherwise depauperate community, an increase in plant cover along alpine stream gradients is reflected in an increase in macroinvertebrate species (Lillehammer and Brittain 1978). As temperatures, channel stability, and allochthonous inputs increase downstream, the

distinctive community of high alpine stream habitats is replaced with species occurring over a wider range of thermal regimes and habitats.

In contrast to the harsh environment of glacial and snowmelt streams, the stable chemical, hydrological, and thermal conditions in springs result in a different species composition, often with a lower species diversity than other stream types (Ward and Stanford 1982). The constant groundwater input to these streams results in colder temperatures in the summer than adjacent, lower-order streams. As a result, springs are often refugia for glacial relict species, which can lead to speciation through isolation (Erman and Erman 1990). During the winter, the insulating layer of snow and ice further allow streams with groundwater influence to retain relatively warmer temperatures throughout the winter (McGregor et al. 1995).

Rhyacophila Studies in the Rocky Mountain Region

This study on the alberta- and verrula-species groups of *Rhyacophila* relied heavily on previous work published on *Rhyacophila* in the Rocky Mountain region, particularly Montana. Roemhild (1982) published a species list of the Trichoptera of Montana, providing limited habitat information. Nimmo (1971, 1977) contributed to the taxonomy and biology of the Alberta Rhyacophila, providing hypotheses about the Post Pleistocene recolonization of Alberta by *Rhyacophila*. This study provided much of the information on the ecology of alpine *Rhyacophila* that occur in Montana, but did not include many of the species that may be encountered in southern Montana. The work of Smith (1968) in Idaho contributed greatly to the knowledge of the distribution, biology,

as well as providing larval descriptions of western *Rhyacophila*. Wold's (1974) work on Oregon *Rhyacophila* added more distributional data, as well as more larval associations. In the Gallatin River drainage of Montana, Gustafson (1990) contributed greatly to the knowledge of the biology of *Rhyacophila* in our area.

CHAPTER 2

MORPHOLOGY OF *RHYACOPHILA*

Overview of studies of *Rhyacophila* larvae

Much of the published work on the morphology of *Rhyacophila* has been in the form of species descriptions based on the male genitalia. However, several detailed studies on the morphology of this genus have been published. Nielsen (1942) described and gave a very detailed morphological study of one species of *Rhyacophila*, with homologization of larval and pupal morphology. Pryor (1951) homologized the structure and musculature of the anal proleg of *Rhyacophila*. Flint (1962) published a major work on *Rhyacophila* larvae from eastern North America, describing the larvae of sixteen species (Flint 1962). Smith (1968) published the first descriptions of larvae the Western United States, describing the larvae of 14 species of *Rhyacophila* from the Salmon River drainage of Idaho. The larval *Rhyacophila* of the western United States was also the focus of Wold's (1974) unpublished thesis, and included 24 additional larval descriptions. Smith (1995) has compiled an unpublished key to the larvae of species groups of *Rhyacophila* for North America. Most recently, in a major synthesis of the *Rhyacophila* of the eastern United States, Prather (1998) and Prather and Morse (2001) included descriptions of 24 species and two new larval and adult associations.

The chaeotaxy, or arrangement of setae, of *Rhyacophila* larvae can reveal useful characters (Giersch, this work). Several authors have addressed the chaeotaxy of *Rhyacophila*. To homologize and standardize the chaeotaxy of Trichoptera larvae,

Williams and Wiggins (1981), described the setal patterns and names of setae for the head, thorax and abdomen (Williams and Wiggins 1981). Mathis (1977) provided a further homology of Trichoptera setae, with the addition of setae on the anal prolegs.

Larval morphology

Ross (1956) addressed the evolutionary relationships of *Rhyacophila* larvae, considering the general morphology of the larvae to be plesiomorphic for the order. Ross' assertion was based on characters of the anal proleg and the free-living habits of the larvae. In the dataset used by Frania and Wiggins (1997), several of the larval characters of *Rhyacophila* were coded as basal.

The overall body shape of *Rhyacophila* is campodeiform. The head is generally parallel-sided to wedge shaped, and in a typically prognathous aspect. However, in the phytophagous verrula-group, the head of the larva approaches a hypognathous condition, and is rounded and nearly spherical.

The head capsule is composed of five main sclerites. Expanding laterally around the head capsule are the parietal sclerites. The sclerites meet ventrally along the ventral ecdysial line, and dorsally along the dorsal ecdysial lines. The paired frontal arms of the dorsal ecdysial lines of the head capsule enclose the frontoclypeus, the fusion of the frons and clypeus (Nielsen 1942). The frontoclypeus is a large sclerite that covers most of the dorsum of the head, and articulates anteriorly with the labrum. The frontoclypeus of species of the verrula-group is much shorter than that of other *Rhyacophila* species, extending less than half the length of the head capsule. The dorsal ecdysial line is Y-

shaped, with the base extending forward from the occipital foramen, and forking partway along the dorsal surface of the head. Each of the anterior forks of the dorsal ecdysial line is roughly sigmoid, and extends to the anterior margin of the head. The line is inflected at a point roughly halfway along its length. The tentorium of *Rhyacophila* is reduced, appearing as a pair of fibers rising from the most ventral section of the occipital foramen and dorsally inserting at the point of inflection of the anterior forks of the dorsal ecdysial line (Babcock 1961).

Mathis (1997) homologized the major setae of the parietal sclerites of the head capsule. The anterior tactile setae, A_1 and A_2, are inserted below the antenna and anterior the stemmata, respectively. Each eye is surrounded by three tactile setae, the S_1 on the ventral margin of the stemmata, the S_2 dorso-lateral to the stemmata, and the S_3, on the posterior margin of the stemmata. The posterior tactile seta, P_1, is located in a position dorso-posterior to the stemmata.

The major setae of the frontoclypeus occur in two groups. The frontoclypeal tactile setae, FC_1, FC_2, and FC_3, are inserted from the anterolateral margin of the frontoclypeus, mesally along the frontoclypeal margin. Of these, the FC_1 seta is the shortest, on the anterolateral corner of the frontoclypeus, curved mesad, and is colorless. The FC_4-FC_6 frontoclypeal tactile setae are inserted along the lateral margins of the frontoclypeus, inserted anterad to posterad.

The antennae of *Rhyacophila* are near the anterior margin of the head, anterior to the eyes, near the dorsal articulation of the mandibles. The structure of the antennae are

considered to be plesiomorphic, as they are composed of two large, basiconic sensilla on either side of a single, trichoid sensillum (Frania and Wiggins 1997).

The labium is composed of the postmentum, prementum, and submentum (fig. 3). The postmentum is a triangular sclerite on the anterior edge of the ventral surface of the head capsule. The prementum is a transverse sclerite fused to the postmentum. The submentum is a short, transverse sclerite with a concave anterior margin that floats in the membrane anterior to the postmentum. This sclerite bears a seta on each side and is reduced in some members of the verrula-group. In *R. verrula*, the submentum is expressed as only a small sclerite at the base of each submental seta.

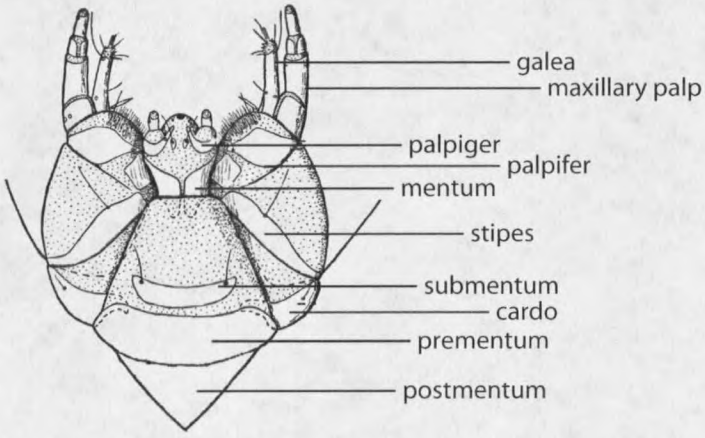

Figure 3: Ventral view of labium, maxilla and mentum of *Rhyacophila* (after Nielsen 1942).

Silk glands open medially at the apex of the mentum. Silk from these glands is used for building the pupal case and cocoon prior to pupation. Silk is also used for mobility in *Rhyacophila*, as the larvae trail a strand behind them, rappelling along the

substrate. In Sweden, *R. nubila* Zetterstedt returned to a particular stone in the stream after hunting, using silk attached to the substrate (Otto 1993).

Each mandible bears a pair of basal setae on the lateral surface. The left mandible in predaceous species has a ventral cutting surface and a dorsal ridge that may have teeth along the edge. The right mandible has a mola on the ventral edge, and may have teeth on the edges. The mandibles of the verrula-group reflect the phytophagous feeding habits of the group, in that they are short, stout, and pyramid-shaped with apical rather than marginal teeth.

The pronotum of *Rhyacophila* is uniformly sclerotized. The anterior margin of the pronotum is entire, without an internal flange present in other Trichoptera. The mesonota and metanota are entirely membranous. The major setae on the thorax of *Rhyacophila* are largely confined to three setal areas on each segment. Sa_1 is on the anterior half of the segment, at a submesal location. In the rare case of *R. rickeri*, some Sa_1 setae on the distal abdominal segments may be forked. Sa_2 is on the posterior half of the segment, farther laterad of Sa_1. Sa_3 is lateral, on the medial part of the segment. Sa_1 is not present on the pronotum. The anterior margin of the pronotum often bears a line of setae, that is variable in length depending on species group. These setae are very long in species of the verrula-group (fig. 20I), and shorter or absent in others. A group of three dorsal anterolateral setae, two long and subequal in length, and a third, shorter seta, are located in a depression on the anterior angle of the pronotum.

The muscle scars mark the points of muscle attachment on the interior of the sclerite, and appear as dark areas on the sclerite, or light areas if the background color is dark. These muscle scars may exhibit species-specific patterns.

On the pleura, the protrochantin is digiform and projected forward. The pleural sclerites on the prothorax are separate from one another, and the ventral portions of these sclerites are membranous. The mesepisternum and metepisternum both have an apodeme that projects anteriorly. At the point of articulation with the pleuron, a large prominence is present on the coxae of the mesothorax and the metathorax (Frania and Wiggins 1997). The legs of the prothorax are generally shorter than the meso- or metathoracic legs, though they are not chelate, and trochanter is closed dorsally.

Segments I-VIII of the larval abdomen are membranous. A single large sclerite covers the dorsum of abdominal segment IX. The shape of this sclerite is variable within species, being roughly triangular to quadrate, and the chaeotaxy corresponds to that of the other abdominal segments. Gills are present in some groups, either as short, broad tubercles (coloradensis-group) single fingerlike projections (alberta-group), or branches with numerous filaments (vemna-group) (Smith 1995).

Anal prolegs are present in all instars, projecting freely from the entire margin of segment IX. The prolegs are largely separate, and can be moved in a vertical plane. This form of the prolegs allows for the larva to firmly grasp the substrate, making it well adapted to the free-living lifestyle of the larvae. This allows for limited lateral movement, but is more conducive to life in the larval retreat (Ross 1956).

The anal proleg is covered by several sclerites. The lateral sclerite of Pryor (1951) [sclerite b of Nielsen (1942) and Lepneva (1970)] covers most of the lateral, outward facing surface of the proleg. In most groups, this sclerite has an oblique suture originating near the dorso-anterior angle. This suture is absent in the vagrita-group (Smith 1995). The long, horizontal position of the lateral sclerite was considered by Ross (1956) to be a basal condition of the Trichoptera.

Two primary setae are present on this sclerite, the PRb_1 seta on the dorsal or distal portion of the sclerite, and the PRb_5 seta on the venter or proximal portion. The membrane at the base of the sclerite may obscure this seta. A short seta is also present on a small sclerite on the membrane ventral to the lateral sclerite. In the verrula-group, this sclerite is particularly well developed, taking on the appearance of a secondary hook (fig. 20J).

The lateral sclerite may have an elongate baso-ventral hook (anterior hook of Pryor 1951, proximal hook of Nielsen 1942) which projects free from the membrane (as in some species of the sibirica-group). A lateral spur is also present in some groups of *Rhyacophila*, either arising as an extension of the lateral sclerite (as in *R. angelita* Banks) or being entirely separate from the lateral sclerite (as in *R. hyalinata* Banks and *R. arnaudi* Denning). This spur may be very reduced and present as a very short process, short and slightly downcurved (*R. amicis* Ross) or long with a smooth, even curvature (angelita-group).

The dorsal articular plate (distal plate of sclerite b by Nielsen) is a roughly quadrate sclerite that articulates proximally with the lateral sclerite, and distally with the

anal claw. The large size of this sclerite was considered to be a basal condition by Ross (1956). The dorsal articular plate bears a pair of long dorsal setae, the PRb_2, on the mesal side of the sclerite, and the PRb_3, on the lateral side of the sclerite.

Located laterally at the base of the anal claw is a pair of the ventral sole-plates. These sclerites may appear to be fused, or one may be very reduced. Sole-plate 1 of Pryor (ventral plate of Nielsen) is the larger of the two sole-plates. Mesally, at the base of the anal claw, is ventral sole plate 2. This sclerite bears the PRc_1 tactile seta.

The anal claw is long, smoothly curving, and well sclerotized, and is secondarily divided by a weakened line, increasing its flexibility. Ventral teeth may be present or absent. The anal claw bears eight main setae. The setal names used here follow Nielsen (1942). Setae 1 through 3 are inserted on roughly the dorsal edge of the claw, from the base to the apex. Seta 5 is on the lateral face, basal on the sclerite, and seta 6 is on the lateral face, distad the split in the claw. Basally, on the ventral edge of the claw, is seta 7. Seta 8 is on a tubercle on the ventral edge, proximad the split in the claw. The tubercle may be expanded, as in the verrula-group. Seta 4 is on the mesal face of the anal claw.

Pupae of Rhyacophila

Descriptions of *Rhyacophila* pupae are relatively rare in the literature, although some comprehensive descriptions exist (Nielsen 1942 and Lepneva 1970). Lepneva (1970) gives a thorough description of pupal case construction. Prior to pupation, the pre-pupal larva will build a case over itself, using rocks, sand, or in the case of *Rhyacophila potteri*, moss (J. Giersch personal observation). This case is porous, and

functions as a protective covering, while allowing for the circulation of fresh water. A separate cocoon is then spun within this case. The larva builds the cocoon by spinning silk along the length of the inside of the outer case. The resulting cocoon is attached to the outer case at the ends (Lepneva 1970). The cocoon is therefore built within the outer covering of rocks and entirely separate from it (Hickin 1949). The composition of the silk differs in the outer case and the cocoon. The outer case is held together by thick, loose silk strands, whereas the cocoon is made up of multiple layers of thin, dense silk threads, with the innermost layer being the most compact (Cianficconi et al. 1993).

At the prepupal to pupal molt, a hypertonic excretion that is derived from the hemolymph of the larva is released into the cocoon. This fluid remains in the cocoon throughout pupation, forming an osmotic gradient between the cocoon and the surrounding water. This osmotic gradient draws in water, inflating the cocoon, and placing a cocoon in higher concentrations of salt will cause the cocoon to collapse. The cocoon is permeable to oxygen and water, but impermeable to larger molecules (Wichard 1991, Rudolph and Wichard 1993, and Wichard et al. 1993). The isolation of the pupa from the surrounding water presents a problem with respiration. Oxygen diffusion must not only take place across the integument of the pupa, but across the cocoon membrane and through the cocoon fluid. Because the membrane of the cocoon has a relatively small surface area, and the length of the diffusion pathway from this surface to the surface of the pupal cuticle is relatively long, pupae of *Rhyacophila* are restricted to cold, flowing, well-oxygenated water (Wichard 1991).

The pupa of Trichoptera is exarate and ambulatory- having free appendages allowing for a degree of mobility within the cocoon. The pupa must be able to reach the surface of the water prior to emergence of the adult. The pupa superficially resembles the adult, with wing buds, antennae, and functional legs (Hickin 1967). Whereas gills are present on the pupae of some Trichoptera families (such as Hydropsychidae), gills on the larvae of *Rhyacophila* are not reflected in the pupa (Hickin 1967). The pupal mandibles of *Rhyacophila* are sclerotized and well developed (fig. 12I). The inside margins are serrate and have large teeth for tearing out of the pupal case (Lepneva 1970). These mandibles, as well as the associated muscles, are lost at the pupal molt (Lepneva 1970). The antennae are ensheathed in the pupal cuticle, resemble those of the adult, and extend to the middle of the abdomen. The dorsum of the pupal abdomen of *Rhyacophila* bears small sclerotized plates that are used to grip sides of the cocoon as the pupa emerges from the cocoon (Hickin 1949 and fig. 12J). Hook plates are absent from the first abdominal segment of *Rhyacophila* pupae as they do not move while in the pupal case as do pupae of the Annulipalpia that pupate in permeable cocoons (Hickin 1949).

The tarsal segments of the mesothoracic legs have rows of setae for swimming from the cocoon to the surface of the water (Lepneva 1970). The pupae of Trichoptera species living among bryophytes lack swimming fringes on the mesothoracic legs, as they can climb directly out of the water rather than swimming (Hickin 1949) [I have verified this in *R. potteri* and *R. rickeri*, two species that pupate directly within bryophyte mats (J. Giersch personal observation)]. The pupa has fully functional claws for climbing out of the water (Lepneva 1970).

Rhyacophila adult morphology

Diagnosis (from Schmid 1981):

Ocelli present. Maxillary palpi 5-segmented in both sexes. First two segments very short, second subglobular. Last segment of maxillary and labial palpi ending in a small point. Spurs: 3,4,4. Middle legs of female not flattened. Wings smooth ovals. Both pairs in both sexes similarly shaped. Venation complete, with all forks present, I, II, III, IV, and V in front wings and I, II, III, and V in hind wings. R_1 in front wings divided into R_{1a} and R_{1b} at tip. In both pairs of wings, discoidal and median cells open. Thyridial cell in front wings very long. Internal gland of abdominal sternite V small. Abdominal hemogill system absent.

In addition, scent glands are located on the anterior corner of sternite V, posterad of the antecostal suture (fig. 8G). Because this gland is present in both males and females, Nielsen (1980) hypothesized that it has a repulsive function rather than holding sex pheromones. However, Fofstedt et al. (1994) reported that extracts from the fourth and fifth abdominal sternites of *Rhyacophila fasciata* Hagen and *R. nubila* females caused an electrophysiological response in the antennae of males. Although the scent glands are located on the fifth abdominal segments, reservoir cells are also located on the fourth segment (Lofstedt et al. 1994, Larsson and Hansson 1998). A spine is present on the venter of abdominal segments VII and VIII which may be used for drumming, scraping, or other forms of auditory communication (Ivanov 1997b).

Studies of *Rhyacophila* male morphology

The most important references on male *Rhyacophila* genitalic structure are Ross (1956) and Schmid (1970). Nielsen (1957) homologized the genital morphology and illustrated the associated musculature of two species of *Rhyacophila*. Schmid (1970) incorporated Nielsen's study of the musculature to interpret the mechanics of copulation

Rhyacophila male morphology

Male genitalic diagnosis (from Schmid 1981):

Segment IX ring-shaped, occasionally forming an apicodorsal lobe overhanging other genital parts. Segment X variously shaped, with occasionally a highly complex structure. Preanal appendages occasionally present. The anal sclerites are virtually always small and may be present or absent, paired or unpaired. Inferior appendages very large, subhorizontal and 2-segmented, with second segment virtually always indented in a manner characteristic of the species. Phallic apparatus situated between inferior appendages and joined to base of latter by means of a sclerotized connection. The phallic apparatus is relatively primitive and complete in structure. It comprises a phallotheca, endotheca, aedeagus, and generally two more or less spiniform parameres. Occasionally there is a ventral lobe below and a dorsal lobe above aedeagus.

The generalized morphology of the male genital segments are illustrated in figure 4. Segment VIII is annular and unmodified in the vast majority of *Rhyacophila*. However, Schmid (1970) reported that a single species, *R. verrula*, had a modified tergum VIII (Schmid 1970). Later, other species of the verrula-group, including *R. haddocki* Denning,

R. singularis Botoșăneanu and *R. leechi* Denning have been found to have at least a posterior lobe projecting from tergum VIII.

Segment IX is annular, and may have a variously modified apicodorsal lobe that extends over segment X, as in the invaria-twig of the philopotamoides-branch. The morphology of segment X is variable in *Rhyacophila*, taking on a wide variety of simple

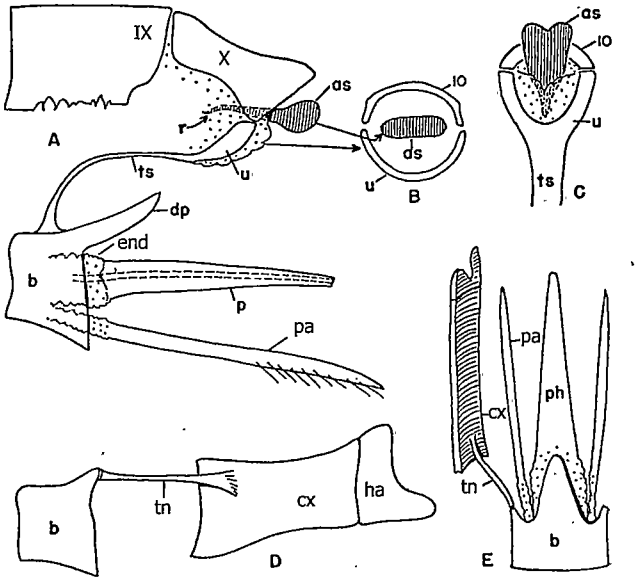

Figure 4: Generalized male genital morphology of *Rhyacophila.* A, lateral aspect of tergites IX, X , and phallic complex; B, posterior aspect of tergite X; C, ventral aspect of tergite X; D, lateral diagram of base of phallic apparatus and inferior appendage; E, dorsal view of phallic apparatus and inferior appendage. *IX*, tergite 9; *X*, tergite 10; *as*, anal sclerite; *b*, phallobase; *end*, endotheca; *cx*, coxopodite; *dp*, dorsal process; *ha*, harpago; *p*, phallicata; *pa*, paramere; *tn*, tendon; *ts*, tergal strap; *u*, apical band (from Ross 1956).

to complex forms. The cerci (preanal appendages of Schmid 1970) are present in some branches of *Rhyacophila*, such as the vulgaris- and divaricata-branches, and entirely

absent in others. Schmid (1970) hypothesized that the ancestral *Rhyacophila* had a pair of prominent preanal appendages, inserted on the median part of segment X.

The anal sclerites are paired or joined into a single, fused process (fig. 4, *as*) that is hinged between the tenth tergite and the membrane attached to the base of the aedeagus, above the opening of the anus (Ross 1956). This structure is homologous to the scaphium of Lepidoptera (Matsuda 1976). It often has a basal projection that extends into the tenth segment, known as the root of the anal sclerite (fig. 4, *r*). Schmid (1970) hypothesized that the anal sclerites were homologous with the epiproct, and that the ancestral *Rhyacophila* had a pair of heavily sclerotized anal sclerites. The anal sclerites undergo a series of specializations throughout the genus, joining together or disappearing completely.

On each side of the end of the abdomen and articulating with segment IX, are the inferior appendages. These have been referred to as claspers by some authors (Ross 1956), as they are used to grasp the female during copulation. The inferior appendages are two-segmented, and consist of the proximal coxopodite (fig. 4, *cx*) and the distal harpago (fig. 4, *ha*). The coxopodite is articulated with the phallotheca by tendons that arise on the basal dorsal edge (fig. 4, *tn*) [the clasper hangers of Ross (1956)]. Matsuda (1976) homologized the tendons with the juxta of the Lepidoptera. The harpago is generally smaller than the coxopodite and is covered with patches of dense spicules on the medial face. The distal margin of this segment tends to be indented to some degree, and the shape of this indentation can be species specific.

The phallic complex lies between the inferior appendages, and consists of the phallotheca, endotheca, parameres and phallicata. The phallotheca (fig. 4, *b*) is the sclerotized base of the phallus. Arising distally from this structure is the endotheca (fig. 4, *end*), which is membranous and erectile. Projecting from each side of the endotheca are the lateral parameres (fig. 4, *pa*), the apices of which may be covered in spines or patches of setae. In some groups, the endotheca may have a prominent ventral lobe that may be expanded into extensile arms that may functionally replace the parameres. This is character is particularly evident in the sibirica and angelita-groups (Schmid 1970). The ejaculatory duct opens at the tip of the sclerotized phallicata (fig. 4, *p*), which extends distally from the endotheca. In some groups, a dorsal appendage (fig. 4, *dp*) arises as an extension of the phallic apparatus from the posterior edge of the phallotheca or the base of the endotheca. This is a chitinous, digiform process, and is especially well formed in the verrula-group (fig. 8C).

The apical band (fig. 4, *u*) is a chitinous, U-shaped structure extending underneath the anus, and dorsally articulating with segment X. Schmid (1970) hypothesized that the apical band was homologous with the paraprocts, and that the arms of the apical band that extend around the anus were prominent and formed appendages in ancestral *Rhyacophila*. In contrast Matsuda (1976) homologized the apical band of *Rhyacophila* with the gnathos of Lepidoptera.

The tergal strap (fig. 4, *ts*) is a longitudinal, dorsal narrow sclerotized ribbon that arises from the phallotheca and connects to the anterior edge of the apical band. The tergal strap may be either sclerotized or membranous. Ross (1956) believed that the

plesiomorphic condition of *Rhyacophila* was an unsclerotized tergal strap, and is therefore a useful phylogenetic character.

Studies of *Rhyacophila* female morphology

In contrast to the large number of males illustrated in his monograph on *Rhyacophila*, Schmid (1970) published illustrations of few females. However, the illustrations of females that he provided were very detailed, including illustrations of the sclerotized vaginal apparatus of the female. Schmid also illustrated the abdomen of the male and female during copulation (Schmid 1970). Included in his revision of the *Rhyacophila* of Canada, Schmid (1981) published descriptions and illustrations of the known females. Smith and Manuel (1984) used female morphology in a study of the acropedes (now brunnea)-group. Prather (1998) and Prather and Morse (2001) provided descriptions and illustrations of females of 32 species from eastern North America Several authors have published studies homologizing structures of the reproductive system *Rhyacophila* females. For example, Matsuda (1976) addressed female *Rhyacophila* in his study of abdominal morphology and Nielsen (1980) provided a very detailed study of the morphology of the female genitalia, including musculature and internal structures.

Rhyacophila female morphology

Female genitalic diagnosis from (Schmid 1981):

Segment VIII in shape of a ring or truncated cone, often with apical notches separating lobes that, in shape, are characteristic of species. Segment IX present or not distinguishable from intersegmental membrane VIII-X. The last segments and their connecting membranes generally stretch considerably into a long, flexible, retractile ovipositor containing 2 pairs of sclerotized apodemal rods serving as sites of insertion for the muscles retracting the ovipositor. Cerci single-jointed. Intersegmental membrane VIII-X often invaginated for a variable distance within segment VIII. Vulvar scale absent and anovaginal opening at tip of segment X. Vaginal apparatus located at the end of a very long vaginal vestibule with such fine membranous walls that they are virtually invisible, consequently appearing to be free inside abdomen. Last three segments retract during copulation, the vaginal vestibule turning inside out like the finger of a glove, and the vaginal apparatus protruding from the abdomen.

The base of segment VIII is in the form of a sclerotized collar. Distally, the segment is membranous. In some groups, the membranous part is invaginated within the sclerotized basal collar (fig. 27E). The posterior margin of the collar may be indented or expanded caudad as a pair of lobes (Nielsen 1980). Segment IX is unsclerotized and difficult to distinguish from the intersegmental membrane from segment VIII (Schmid 1970). The sternite of this segment is also membranous, with a sclerotized band that is prolonged into segment X.

Anterior apophyses arise from the antecostal suture of abdominal segment VIII and posterior apophyses project anteriorly from the posterior margin of abdominal segment IX.

Segment X is similar to IX, but longer. The tergite is sclerotized and bordered of a chitinous lateral edge. The sternite is very lightly sclerotized and has an internal apodeme projecting from segment IX (fig. 15E). The lateral wall of the segment X bears sclerotized rods (Matsuda 1976). When abdominal muscles attached to these segments contract, the terminal abdominal segments are invaginated.

The gonopore is located at the apex of the segment X, below segment XI. The anus opens into the vagina, so that the gonopore functions as a cloaca (Matsuda 1976). The dorsum of segment XI of the female bears a pair of unsegmented cerci (Matsuda 1976).

Internal structures of the females of *Rhyacophila*

The generalized internal anatomy of the reproductive system of female *Rhyacophila* is illustrated in figure 5. The sclerotized part of the genital chamber has been given several names by authors, including bursa copulatrix (Schmid 1970) and spermathecal sclerite (Nimmo 1971, 1977). Because the sclerotized parts of the genital chamber are actually separate sclerites, Prather (1998) and Prather and Morse (2001) used the terminology of Nielsen (1980) and referred to the complex as the vaginal apparatus. The shape of this apparatus is variable in *Rhyacophila*, and is species specific. The apparatus is comprised of three parts, basally is the rounded or cup-shaped processus spermathecae, followed by the intermediate process, and terminating in a longer, tapering proximal part (Nielsen 1980).

The distal end of the ductus bursae is a sclerotized tube that flattens as it opens underneath the processus spermathecae. The spermathecal duct opens onto the processus spermathecae. Sperm is directly transferred to the spermatheca in Trichoptera, rather than to the bursa copulatrix (Nielsen 1980).

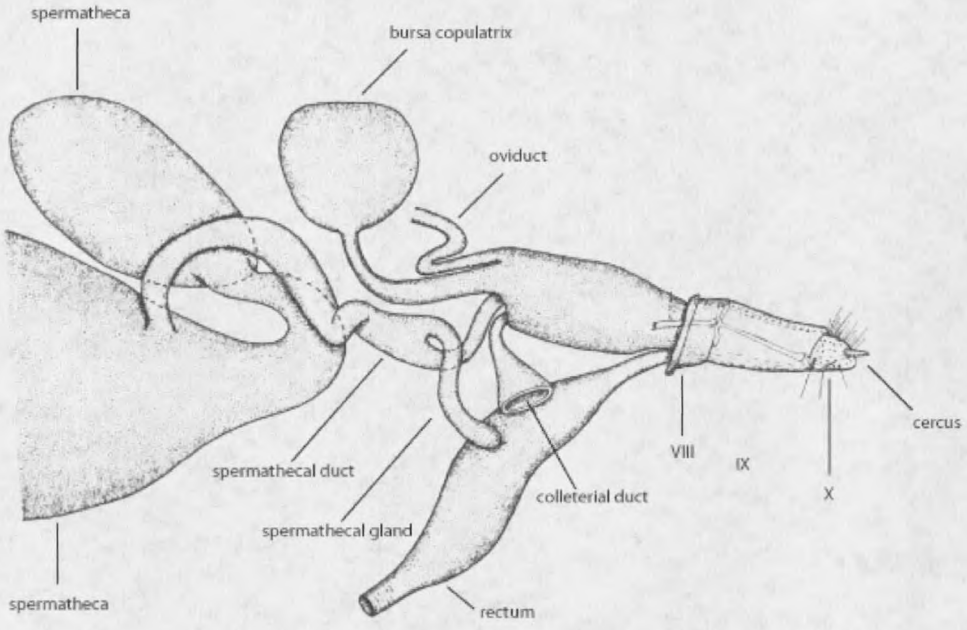

Figure 5: Generalized internal anatomy and abdominal segments VIII, IX and X of female *Rhyacophila* (after Nielsen 1980).

Behind the processus spermathecae is the opening of the colleterial duct which secretes a gelatinous mass that swells in water and protects the egg as well as gluing the eggs to the substrate (Hinton 1980). Following the opening of the colleterial duct is the intermediate process, which may have taxonomically important lateral ridges or lobes. The posterior process expands caudad from the intermediate process, and extending into the anterior part of segment IX.

During copulation, as the terminal abdominal segments are evaginated, the vaginal apparatus is exerted through the gonopore and holds the apex of the aedeagus during copulation (Schmid 1970, Matsuda 1976).

CHAPTER 3

MATERIALS

During this study, I examined 1678 specimens of the verrula- and alberta-groups of *Rhyacophila*. Of these specimens, there were 793 males, 270 females, 533 larvae, and 82 pupae. Specimens were either collected by myself or borrowed from museums. Voucher specimens from my personal collecting efforts were placed in the Montana State Entomology Collection. Throughout the course of my study, I had the opportunity to travel to several museums to search through undetermined material. Specimens from the following institutions and collections were examined. The curator responsible is listed in parentheses.

BCPM Royal British Columbia Museum, Victoria (David Blades).

CASC California Academy of Sciences, San Francisco (Norman Penny).

CNCI Canadian National Collection, Ottawa, Ontario (J. F. Landry).

DER David E. Ruiter personal collection, Englewood, Colorado.

EMEC Essig Museum of Entomology, Berkeley, California (Cheryl Barr).

FLBS Flathead Lake Biological Station/Global Climate Change Project, Polson, Montana (F. Richard Hauer).

JJGC J. Joseph Giersch personal collection.

MTEC Montana State Entomology Collection, Bozeman, Montana (Michael Ivie).

ROME Royal Ontario Museum, Toronto, Ontario (Glenn Wiggins).

OSAC Oregon State University, Corvallis, Oregon (Darlene Judd).

RASV Institute of Biology and Soil Sciences, Far Eastern Branch of the Russian Academy of Science, Far Eastern Branch, Vladivostok, Russia (Tatyana I. Arefina).

UASM University of Alberta, Edmonton, Alberta (Daniel Shepley).

CHAPTER 4

METHODS

This study was based on morphological characters of adult, larval, and pupal specimens, using the operational species concept of Whitehead (1972). Using this concept, unique morphological characters are hypothesized to be inherited genetically, delimiting species.

The focus of the field work for this study was *Rhyacophila* in high elevation streams in Montana. Collection sites were chosen according to accessibility. Collecting trips were made throughout the summers of 2000-2001 to snowmelt and spring-brook habitats located in Glacier National Park, Beartooth Plateau, and the Bitterroot, Gallatin, Crazy, Pioneer, and Tobacco Root Mountains. Location data were recorded with the use of a handheld GPS unit. Larvae were collected by agitating the stream bottom, and the resulting detritus was placed in a white enamel or plastic pan from which larvae were hand picked. Adults were collected by beating vegetation or by collecting at night on a white sheet illuminated with fluorescent black light. Larvae and adults were collected directly into 80% ethanol. Pupae, which included the last larval exuviae, were collected directly from rocks or bryophytes and placed into mosses and refrigerated in a cooler. Once in the laboratory, pupae were kept in a refrigerator under constant temperature and darkness until the genitalia of the pharate adults and darkened adult wing pads were visible, or the adults emerged. Larvae, adults, and some pupae with pharate adults were stored in 80% ethanol.

Adults were cleared in either heated lactic acid or potassium hydroxide. Lactic acid was preferred, as the sclerites tended to retain their color when using this method. Sclerites of the female genitalia were removed from the abdomen using micro-tools constructed from variously modified insect pins glued to wooden dowels. Some larvae were dissected and prepared for photography in glycerin. The pupal integument was peeled from metamorphotypes and mounted on a microscope slide in glycerin. Pupal mandibles were removed and cleared for photography in lactic acid.

Specimens were studied with a Wild M5A dissecting microscope or Olympus BX40 compound microscope. Measurements were made with a 100 increment scale. Images were captured with an Olympus DP11 digital camera mounted to either the dissecting or compound microscope. Images were enhanced and modified using AutoMontage © and Adobe PhotoShop ©. Care was taken to enhance or darken characters that were already on the images. Layout for plates was done in Adobe Illustrator ©. Distribution maps were created using iMap © for plotting distributions from specimens examined and from literature. Dubious records for larvae from the literature were omitted. PAUP* (Swofford 2000) was used to search for shortest trees, and characters were mapped onto the resulting trees using MacClade 4.0 running in Windows 98 using ARDI Executor Macintosh emulator software. The computer used for all graphics and phylogenetic analyses was a Dell Dimension series with 250MB RAM and 1GHz Pentium4 processor.

Characters were polarized using outgroup comparison outlined by Watrous and Wheeler (1981). Relationships were hypothesized based on synapomorphies and

parsimony. Cladistic principles outlined by Wiley (1981), Wiley et al. (1991) and Lipscomb (1998) were used to interpret the results of the analyses. Data on each label are followed by "/" (slash), each line within the label is separated by ";" (semicolon), the lending institution or individual is in parentheses.

CHAPTER 5

SYSTEMATICS OF THE GENUS *RHYACOPHILA*

Genus *Rhyacophila* Pictet

Rhyacophila Pictet, 1834: 67, type species: *Rhyacophila vulgaris* Pictet (selected by Ross, 1944: 32).

For a complete synonymy see Morse (1999).

CHAPTER 6

REVISION OF THE VERRULA-GROUP

History of the concept of the group

In the original description of *R. verrula*, Milne (1936) did not place *R. verrula* in a phylogenetic context, but described the presence of the closed m-cell formed by a crossvein between M_{1+2} and M_3. Although the closed m-cell in the forewing was recognized by several authors (Davis 1948, Nimmo 1971), it had not been used as a phylogenetic character. This crossvein has been reported in another genus of Rhyacophilidae, *Fansipangana*, but is reduced in other species groups of *Rhyacophila*. As *Fansipangana* has only recently come to my attention, I was not able to borrow material of this genus for use as an outgroup in my analysis of the verrula-group, and therefore coded the closed m-cell as derived for the group. Further investigations of the verrula-group may show it to be basal to the rest of *Rhyacophila*, and only the inclusion of *Fansipangana* in an analysis of *Rhyacophila* will help determine the polarization of this character.

On the basis of the male genitalia, Ross (1956) placed *R. verrula* in Branch 9 of his phylogeny on the basis of the articulation of the anal sclerite with the apical band. He also interpreted the trough-shaped ventral structure of the phallic apparatus as the fused parameres of the aedeagus. Schmid (1970) believed this sclerotized structure to be the ventral lobe of the phallic apparatus and placed *R. verrula* in the invaria-twig of the philopotamoides-branch. Botoșăneanu (1970) placed both *R. singularis* and *R. haddocki*

in the verrula-group. Denning and Schmid (1971) included a fourth species in the verrula-group, *R. potteri*, but expressed doubt that *R. haddocki* should be included. Denning (1975) included *R. leechi* as another species of the verrula-group. Nimmo (1977) described *R. autumnalis* as another member of the group. *Rhyacophila rickeri*, originally considered by Ross (1956) to belong to the sibirica-group, was later included in the verrula-group by Schmid (1981) based on the closed m-cell in the forewing.

Diagnosis of the philopotamoides-branch (translated from Schmid 1970):

Schmid (1970) placed *R. verrula* in the invaria-twig of the philopotamoides-branch. The diagnosis of the philopotamoides- branch follows (from Schmid 1970):

Segment IX with an apical dorsal lobe; segment X very large, higher than long and not laid out obliquely or vertically; cerci absent; anal sclerites paired; apical band small, strongly sclerotized and composed of three parts: two side arms in vertical position and perpendicular to tergal strap and a horizontal apical lobe, resulting from curve of median tongue; tergal strap obvious and well sclerotized; phallic apparatus complete, massive and not elongate.

Diagnosis of the invaria-twig (translated from Schmid 1970):

Schmid hypothesized that the invaria-twig is of Nearctic origin, secondarily dispersing to the Palearctic. The diagnosis of the invaria-twig follows (From Schmid 1970):

Segment IX lengthened and equipped with an apical dorsal lobe; segment X large, a little concave posteriorly and oblique in position; anal sclerites paired, large and with long root; apical band small, with the median tongue not well developed; tergal strap long and narrow; phallic apparatus with dorsal appendage present, endotheca large; aedeagus thick, ventral lobe split in two even and membranous parts; tendons of the phallotheca and of the inferior appendages very long, and not joined together to the tergal strap; harpago of the inferior appendages with only one zone of spinules.

New diagnosis of the verrula-group

Male: Dorsal appendage of phallic apparatus elongate; ventral lobe present, variously modified. Female: Basal third of segment VIII sclerotized, narrowed to posterior membrane. Larva: Head rounded. Mandibles with teeth on apical edge. Phytophagous. Pupa: Abdominal hook plates small, rounded; less than 30 spinules; posterior plates similar in shape to anterior plates; posterior plates absent from segment VI.

Species included in the verrula-group

R. chandleri Denning: new placement

R. haddocki Denning: placed by Botoșăneanu (1970)

R. leechi Denning: placed by Denning (1975)

R. potteri Denning in Denning and Schmid: placed by Denning in Denning and Schmid (1971), *R. autumnalis* Nimmo NEW SYNONYMY

R. rickeri Ross: placed by Schmid (1981)

R. singularis Botoşăneanu: placed by Botoşăneanu (1970)

R. verrula Milne: placed by Ross (1956)

Table 1. Species included in the *Rhyacophila* verrula-group, showing previously described, recently associated, and unknown life stages.

Species	male	female	larva	pupa
R. chandleri				
R. haddocki				
R. leechi				
R. potteri				
R. rickeri				
R. singularis				
R. verrula				

previously described
recent association
unknown

Biology summary

The unique morphology and phytophagous feeding habits of *R. verrula* was first described by Smith (1968), and a further description of the feeding ecology was published by Thut (1969). Levanidova (1980) described the morphology of *R. singularis*, which was similar to that of *R. verrula* in the hypognathous position of the head. She also noted the phytophagy of the species, and its association with bryophytes. I have found the larvae of *R. rickeri* and *R. potteri* to be morphologically similar to *R. verrula* and *R. singularis*, having a rounded head and prominent setae on the anterior margin of the pronotum. *R. rickeri* is closely associated with liverworts, and *R. potteri* with mosses, which are prominent in the gut contents and as construction material for the covering of the pupal cocoons.

Most species of the verrula-group are confined to cold alpine streams and springs, and therefore have limited distributions. The wide distribution of *R. verrula* may be due to a higher thermal tolerance than other species in the group.

Key for the identification of males of the verrula-group

1. Ventral lobe of phallic apparatus sclerotized, without dorsal spines (fig. 20D).....2

1' Ventral lobe of phallic apparatus membranous, with dorsal spines (fig. 12D).....4

2. Ventral lobe of phallic apparatus shaped like a trough, enclosing phallicata. Harpago entire dorsally (fig. 20B).....3

2' Ventral lobe not trough-shaped, reduced to acuminate lateral arms, not expanded below phallicata (fig. 8C). Harpago emarginate dorsally.....*R. haddocki* Denning

3. Dorso-lateral margins of segment IX produced as an expansion that smoothly curves caudad over segment X and is apically bifid (fig. 20B) [widespread through western North America].....*R. verrula* Milne

3' Dorso-lateral margins of segment IX produced as an expansion that projects straight caudad over segment X, apex flattened at a 90-degree angle (fig. 10C) [Southern Oregon and Northern California].....*R. leechi* Denning

4. Segment VIII with elongate, blade-like extensions (fig. 18B) [Asian Far East].....

.....*R. singularis* Botoșăneanu

4' Segment VIII without elongate, blade-like extensions.....5

5. Segment X broadly fused to segment IX. Phallicata nestled within dorsal lobe of phallic apparatus, with apex visible within as a dark, sclerotized spine (fig. 6E).....
.....*R. chandleri* Denning

5' Segments IX and X not fused. Phallicata separate from dorsal lobe of phallic apparatus.....6

6. Dorso-apical lobe of segment IX a wide and apically truncate plate. Segment X projected caudad as a dorsally folded plate. Ventral lobe of phallicata apically divided into two lobes bearing dark dorsal spines (fig. 12D).....
.....*R. potteri* Denning in Denning and Schmid

6'. Dorso-apical lobe of segment IX an apically blunt, short, triangular projection. Segment X short, complex, not a plate, roughly quadrate in lateral view. Ventral lobe of phallicata apically entire, dorsally concave (fig. 15D).....*R. rickeri* Ross

Key for the identification of females of the verrula-group

1. Posterior process of vaginal apparatus well sclerotized throughout, oblong; without basal wrinkles (fig. 15F).....*R. rickeri* Ross

1' Posterior process of vaginal apparatus sclerotized only in apical half, or not at all; basally with wrinkles.....2

2. Forewing with 3-r4 crossvein, discoidal cell closed(fig. 6A).....*R. chandleri* Denning

2' Forewing without 3-r4 crossvein, discoidal cell open (fig. 9A).....3

3. Posterior process of vaginal apparatus lightly sclerotized (fig. 10G).....4

3' Posterior process of vaginal apparatus darkly sclerotized (fig. 20G).....5

4. Posterior process of vaginal apparatus thin basally (fig. 8H).....*R. haddocki* Denning

4' Posterior process of vaginal apparatus basally wider (fig. 20G).....*R. verrula* Milne

5. Posterior process of vaginal apparatus basally triangular in cross section (fig. 12F)...

.....*R. potteri* Denning in Denning and Schmid

5' Posterior process of vaginal apparatus basally cylindrical in cross section.....6

6. Distribution limited to the Asian far-east.....*R. singularis* Botoşăneanu

6' Distribution limited to southern Oregon and northern California.....*R. leechi* Denning

Key for the identification of larvae of the verrula-group

The larvae of *R. haddocki*, *R. leechi*, and *R. chandleri* are unknown.

1. abdomen with fingerlike gill filaments (fig. 18K) [Asian far-east].....

.....*R. singularis* Botoşăneanu

1' abdomen without gill filaments.....2

2. Anterior margin of pronotum with scale-like setae (fig. 15J).....*R. rickeri* Ross

2' Anterior margin of pronotum with long, acute setae (fig. 20I).....3

3. Posterior tip of frontoclypeus with single muscle scar (fig. 12H). Anterior margin of pronotum with stout setae (fig. 12G). FC_3 seta on frontoclypeus long, 4/5 length of FC_2 seta. Pronotum with three sublateral setae midway along length, one at the border of the darkened margin and the other two farther inward (fig. 12G) .....

.....*R. potteri* Denning in Denning and Schmid

3' Posterior tip of frontoclypeus with a pair of muscle scars (fig. 20H). Anterior margin of pronotum with thin setae (fig. 20I). FC_3 seta on frontoclypeus shorter, 1/2 length of FC_2 seta. Pronotum with 2 sublateral setae midway along length, one at the border of the darkened margin and another other farther inward (fig. 20I).....*R. verrula* Milne

<u>*Rhyacophila chandleri* Denning</u>

Figure 6.

Rhyacophila chandleri Denning, 1956:74. Anderson, 1976: 33.

Diagnosis. Male: segments IX and X fused; phallic apparatus with dorsal process enclosing darkly sclerotized phallicata; forewing with closed discoidal cell formed from r3-r4 crossvein. Female: Distinguished from other members of verrula-group by closed cell formed from r3-r4 crossvein.

Description. Male. Forewing 10-11 mm, yellow, with lighter area between A and Cu_2 veins, with hyaline areas at fork of M, r-m cross vein, r3-r4 cross vein, and at apex of

Cu_2 at wing margin; stigma white; Cu_1 vein darkened; crossvein between M_{1+2} and M_3 forming closed m-cell; r3-r4 crossvein present, enclosing discoidal cell (fig. 6A). Head, antennae, abdomen, and thorax yellow. All setal warts densely covered with long, clear setae. Head with large median setal wart posterad of median ocellus posteriorly expanded laterally; large lateral ocelli with rounded setal warts laterally; well separated from oblong posterior setal warts; frons with pair of lateral setal warts. Apical segment of labial palp thick, somewhat spindle shaped, with concave internal surface (fig. 6B). Legs yellow, with yellow spurs; spur formula 3-4-4; protibial spurs shorter than on other tibiae; all tarsal claws equal in length and form. Segment VIII unmodified. Segment IX narrow laterally, inflected to receive coxopodite. Segment X broadly fused to segment IX; posterior margin emarginate, dorsally concave (fig. 6C) . Coxopodite short and wide, very tall at base, slightly narrowing apically. Harpago subequal in length to coxopodite, thinner, rounded apically. Dorsal appendage of phallic apparatus wide; projecting directly caudad; up-curved at apex; ventrally concave; wrapped around and fused to phallicata, with horizontal lateral wings subapically; apical margin rolled inward. Phallicata a dark, heavily sclerotized extrusible spine inside of dorsal appendage. Ventral lobe membranous at base, tapering to undivided apex, apically with dorsal patch of brown spines (figs. 6E and 6F).

Female. Forewing length 12mm, color and venation as in male. Similar to other species of the verrula-group. Body identical to that of male. Forewing with r3-r4 cross vein. Vaginal apparatus with processus spermathecae basally sclerotized, apically

emarginate; posterior process flexible, ribbed at midlength, tapering to an apical, sclerotized tube (figs. 6G and 6F).

Larva unknown.

Pupa unknown.

Distribution. Alpine areas of Southern Oregon and Northern California (fig. 7).

Type material studied. None. Holotype repository: CASC

Other material studied. OREGON: Deschutes County: 1 ♂- Tyee Cr., Devil's Lk.; 11 Aug, 82 R. W. (RWW)/2 ♂♂- Century Drive; Devil's Lk. VIII-19-85 BLT BW (RWW)/7 ♂♂- Century Dr.; Tyee Cr. at Devil's Lk.8-20-83 (RWW).
Douglas County: 1 ♀- Shadow Cr. trib of; S. Umpqua. 42° 59'N 122°51'W; V-26-86 (RWW).
Lane County: 1 ♂- Waldo Lk.; 7-23-69. BLT. Goeden (RWW)/1 ♂- Willamette Natl. For.; Rigdon Ranger District; Ddee Lake South end; Aug. 9, 1990 (RWW).

Discussion. Denning (1956) noted that *R. chandleri* did not resemble any other species of *Rhyacophila*, and Anderson (1976) listed this as an unplaced species. However, closer examination has revealed the presence of the closed m-cell of the forewing (fig. 6A) and similarities between the phallic apparatus of this species and others on the verrula-group, including the expanded dorsal appendage of the aedeagus (fig. 6E). *Rhyacophila chandleri* is a highly derived species in that the dorsal appendage of the phallic apparatus is entirely wrapped around the phallicata. The tip of the phallicata is visible as a dark sclerite within the dorsal appendage, and may be extruded from the apex. Besides the fusion of tergite IX to X, the absence of anal sclerites and unsclerotized

tergal strap are also autapomorphic. The membranous ventral lobe of the phallic apparatus, which is not apically divided as in *R. rickeri*, aligns it with other species in the verrula-group. Another autapomorphy exhibited by this species is the presence of the r3-r4 cross vein, enclosing the discoidal cell. This character has not been reported in other species of *Rhyacophila*, although it has been described as an autapomorphy of *Philocrena trialetica* (Kumanski 1981). As in *R. chandleri*, the phallicata of *P. trialetica* also appears to be a movable sclerite within the endotheca. The placement of *P. trialetica* in the verrula-group is not feasible, however, as it lacks the synapomorphies of the verrula-group such as the closed m-cell in the wing and the expanded dorsal appendage of the phallic apparatus.

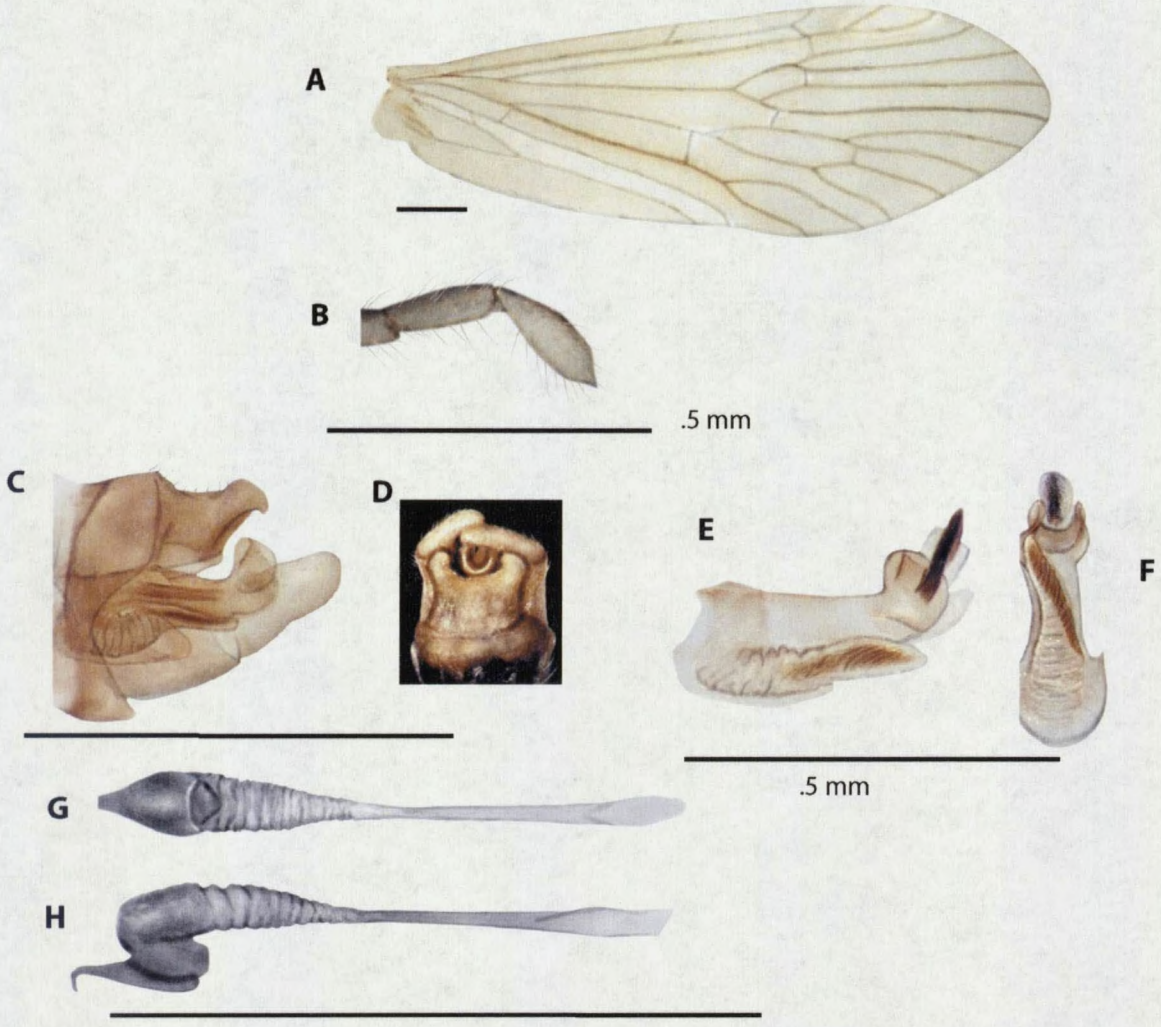

Figure 6: *Rhyacophila chandleri* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male terminal segment of labial palp, (C) male genitalia lateral, (D) male genitalia dorsal, (E) phallic apparatus lateral, (F) phallic apparatus dorsal, (G) female vaginal apparatus ventral, (H) vaginal apparatus, lateral.

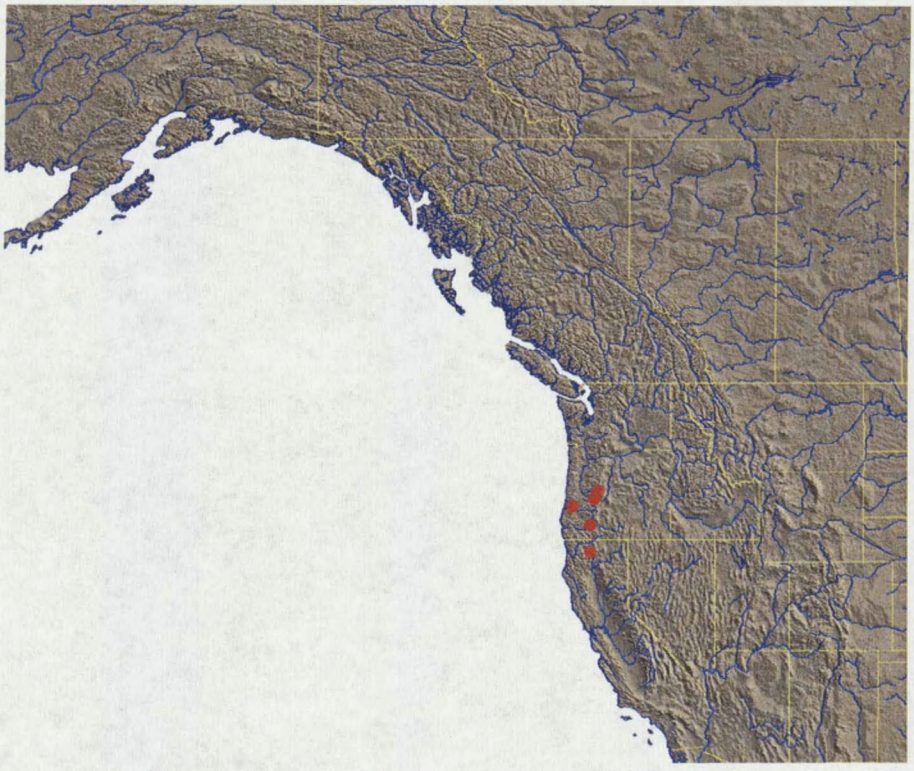

Figure 7: Distribution of *Rhyacophila chandleri.*

Rhyacophila haddocki Denning

Figure 8.

Rhyacophila haddocki Denning, 1968: 64. Anderson, 1976: 33. Oregon Natural Heritage Program, 2001: 28.

Diagnosis. Male: apical metatibial spur modified; segment VIII caudal expansion bilobed; segment IX with dorsal strap very thin, nearly incomplete, without apico-dorsal or apico-lateral lobes; segment X apically bifid, hanging over prominent apical band; harpago dorsally emarginate. Female: processus spermathecae basally rounded, apically emarginate; posterior process thin, unsclerotized.

Description. Male. Forewings 11 mm long; yellow with light brown patterns, pattern in central area of wing as bands within cells, patterning concentrated to trailing margin of wing; crossvein between M_{1+2} and M_3 forming closed m-cell (fig. 8A). Head and antennae yellow; single rounded setal wart posterad of median ocellus; small, round setal wart posterad of each lateral ocellus, separated from larger, round posterior wart by bump. Maxillary palps subequal in length to protibiae. Thorax and abdomen yellow. Legs yellow, spurs and spines brown; tarsal formula 3-4-4; subapical spur of protibia well developed; meso- and metatibial spurs longer than protibial spurs; inner apical meta-tibial spur modified as heavily sclerotized, triangular plate with an apical spine that bends back along the apex of the plate, tuft of short, silky setae arising from concave surface of plate opposite spine (fig. 8E). Tarsal claws on all legs equal in length and form. Segment V with carina dropping ventrad from scent gland opening, then smoothly curving caudad (fig. 8G). Segment VIII with dorso-caudad expansion as pair of short rounded lobes, separated by shallow emargination (fig. 8F). IX wide ventrally and laterally, tergum narrowed to very thin dorsal band, almost not continuous dorsally. X extended caudad as plate, semi-membranous mesally, lateral lobes gradually convergent, distal margin truncate and emarginate, bearing few short, whitish setae. Apical band prominent, ventrally concave, projects caudad ventral to tergite X, may be mistaken for ventral lobe of X (fig. 8D). Anal sclerite small, borne on ventral surface of apical band.
Tergal strap membranous. Coxopodite short, quadrate, somewhat broadened apically. Harpago wide, length .8 times that of coxopodite, base .7 times height of coxopodite; dorsal edge less than half as along as ventral edge, dorso-caudal edge smooth, concavely

emarginate. Phallic apparatus with dorsal appendage thin, barely sinuate, apically upcurved, dorsally concave. Endotheca sclerotized. Ventral lobe reduced to pair of thin, acuminate lateral arms on either side of endotheca (fig. 8C). Phallicata wide basally, decreasing in width along length, curved dorsad beyond mid portion, apex curved back caudad.

Female. Head, thorax, and base of abdomen as in male. Processus spermathecae basally rounded, apically emarginate; posterior process thin, unsclerotized (fig. 8H).

Larva. The larva of *R. haddocki* is unknown. However, due to the close relationship of this species to *R. verrula* and *R. leechi*, the larva will likely be very similar to, if not indistinguishable from that of *R. verrula*.

Distribution. Until recently, this species was only known from the type locality, Gravel Creek, more commonly known as Parker Creek, on Mary's Peak, in Benton County, Oregon. I have recently received a report of a male and female from Curry County Elk River Fish Hatchery, Siskiyou National Forest, 2 June 1991 by Baumann and Stark. [D. Ruiter, personal communication] (fig. 9).

Type material studied. ♂ HOLOTYPE, ♀ ALLOTYPE- Gravel Creek, Mary's Peak; Benton County, Oregon; 30 July 1966, J. Haddock (CASC).

Other material studied. OREGON: Benton County: 1 ♂, 1 ♀- M.P. Parker Cr.; at Pk C.G. 8-9-83 B.W. (RWW).

Discussion. Denning (1968) was not able to place *R. haddocki* into any known species groups, and Anderson (1976) listed this as an unplaced species. Botoşăneanu (1970) considered this species to be in the verrula-group, but in the description of *R.*

potteri, Denning in Denning and Schmid (1971) had reservations about including the species in this group.

Segment X of *R. haddocki* is in the form of a dorso-ventrally flattened plate. The apical band is prominent, projecting beneath segment X, with the anal sclerite lying in the dorsal surface. Denning (1968) interpreted this to be the ventral lobe of segment X, but this structure is undoubtedly homologous with the apical band of other species of the verrula-group.

Based on the presence of a modified inner metatibial spur of the male, the expanded dorsum of tergite VIII, and the long, partially sclerotized endotheca, this species forms a complex with *R. verrula* and *R. leechi*. The purpose of the modified spur is unknown, although similar structures have been seen in other taxa of Trichoptera, and may be involved with spreading pheromones from the segment V abdominal scent glands. As in *R. verrula* and *R. leechi*, the dorsum of segment IX slopes anterad, although it is not secondarily expanded as an apico-lateral lobe as in *R. verrula* and *R. leechi*. The structure of the phallic apparatus of *R. haddocki* is puzzling. While the phallicata has an acute apex, like other species in the verrula-group, it is sinuous along its length. Of particular interest are the acuminate lateral projections arising from either side of the endotheca, which Denning (1968) referred to as the lateral arms. These thin, heavily sclerotized structures are suggestive of parameres. However, as parameres are absent in other species if the verrula-group, they are rather likely the remnants of the sclerotized ventral lobe.

R. haddocki has previously been only collected from Parker Creek on Mary's Peak, near Corvallis, Oregon. At an elevation of 1249 meters, Mary's Peak is the highest point in the Coastal Range of Oregon, and is the headwaters of the Willamette and Alsea River systems. The summit is in the subalpine zone, dominated by an old growth forest of noble fir, *Abies procera,* and is well known as yielding several rare or poorly known genera of Trichoptera (Anderson 1976). A recent record of a single male/female pair has come to my attention by way of David Ruiter (personal communication), collected by Baumann and Stark from the Siskiyou National Forest, Curry County, Oregon. According to Dr. Richard Baumann (personal communication), the collecting locality is a large, wet seep, which also yielded several species of Plecoptera adults that are restricted to seeps and springs.

This species has been given a state and global biodiversity rank of 1 (critically imperiled because of extreme rarity or especially vulnerable to extinction or extirpation) by the Oregon Natural Heritage Program (2001).

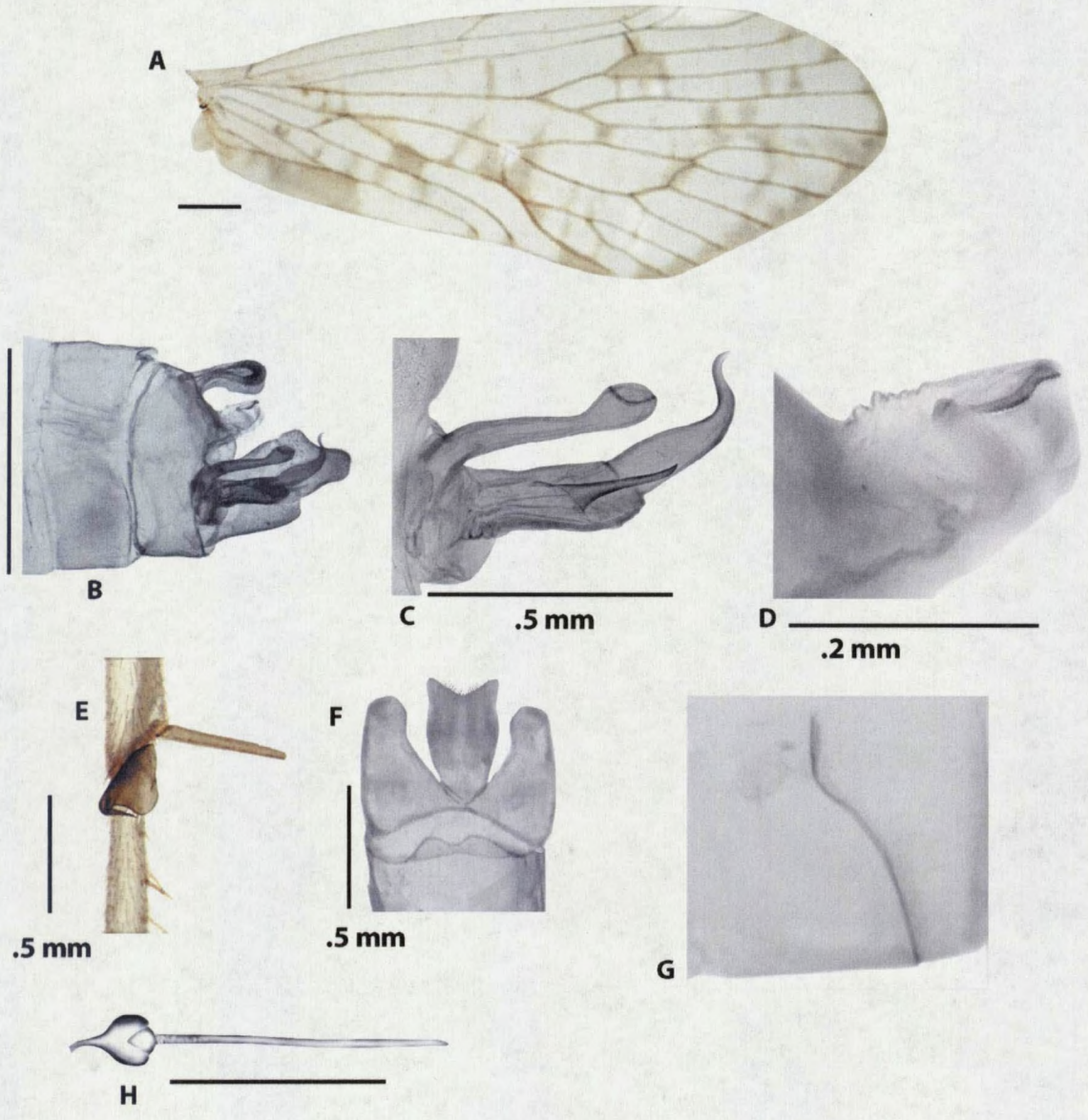

Figure 8: *Rhyacophila haddocki* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male genitalia, lateral, (C) male phallic apparatus, lateral, (D) male apical band and anal sclerite, (E) modified meta-tibial spur, (F) male segments VIII, IX and X, dorsal (G) lateral carina leading from scent gland of female abdominal segment V, (H) vaginal apparatus, ventral.

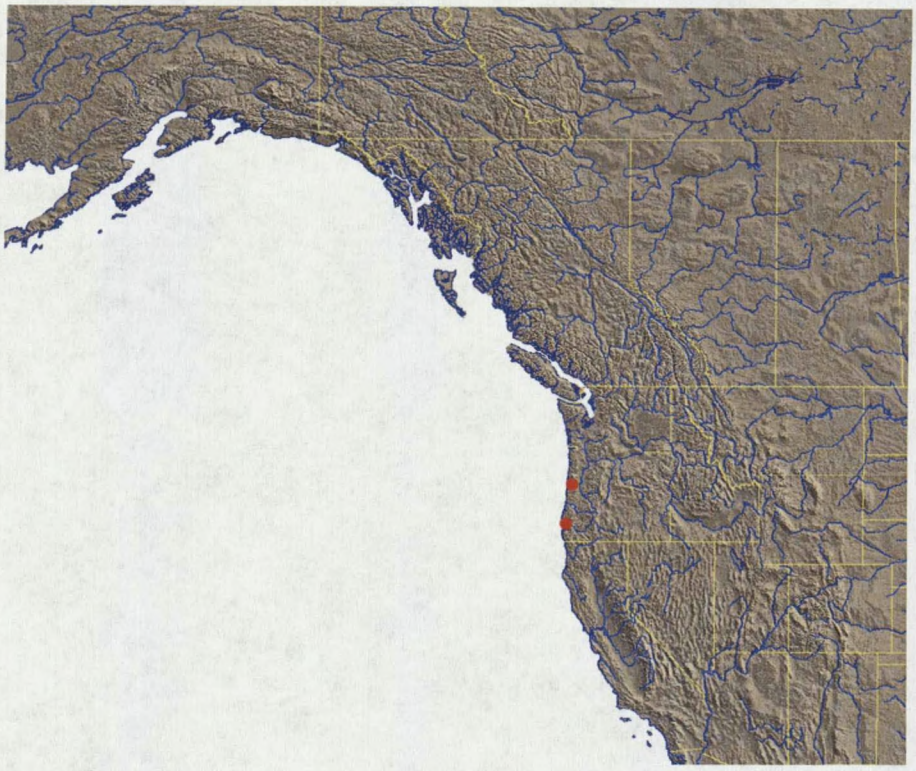

Figure 9: Distribution of *Rhyacophila haddocki*.

Rhyacophila leechi Denning

Figure 10.

Rhyacophila leechi Denning, 1975: 954. Oregon Natural Heritage Program, 2001: 28.

Diagnosis. Male: distinguished from *R. verrula* by expanded dorso-lateral margins of segment IX, apex curved downward at acute angle, rather than smoothly curving as in *R. verrula*. Female: superficially resembles *R. verrula,* but with minor modifications of longer, more narrow processus spermatheca, and longer vertical portion of the carina leading from scent gland opening on segment V.

Description. Male. Forewings 11-12 mm, yellow, with bands of brown in apical ¾ of wing, mottled at apex; crossvein between M_{1+2} and M_3 forming closed m-cell (fig.

10A). Head yellow, pair rounded setal warts posterad of median ocellus; small rounded setal wart posterad of each lateral ocellus; large oblong setal wart on posterior margin of head; narrow, vertical setal wart with single row of setae ventro-posterad of eye. Maxillary palps subequal in length to protibiae. Pronotum with yellow submedian warts. Antennae yellow. Thorax yellow; edges of pleural sclerites not noticeably darker. Legs yellow, with yellowish-brown spines and spurs; tibial spur formula 3-4-4, subapical protibial spur reduced; protibial spurs smaller than on meso- or metatibial spurs; apex of inner apical metatibial spur modified and shorter than outer apical spur, curved downward at 90 degree angle, with heavily sclerotized, acute spine flanked by bilobed, fringed inner flap (fig. 10B). All tarsal claws equal in length and form. Mesonotum yellow, median wart with antero-lateral arms extending anterad on mesonotum. Metanotum yellow. Abdomen yellow; segment V with lateral carina leading ventrad from scent gland opening, vertical in dorsal section, tapering to smooth curve (fig. 10F). Segment VIII with modified dorso-posterior margin, as pair of lateral lobes each with smaller inner lobe, flanking the sides of deep mesal incision (fig. 10D). Segment IX without apico-dorsal lobe; instead with narrow, short dorsal strap ventrad of which postero-lateral edges produced as pair of large, slightly arched lobes fused at midlength; subacute, bifurcate distal margin, caudally concave; each arched lobe with blunt, ventral process, wider laterally than ventrally in lateral view, with dorsal excavation leading toward dorsal strap before curving back out to ventral lobe of postero-lateral process (fig. 10C). Segment X small, dorsally convex saddle-shaped sclerite; proximo-dorsal edge articulating with ventral lobes of postero-lateral processes. Anal sclerite small, without

long root, covered with minute spicules, fitting into ventral concavity of segment X. Tergal strap lightly sclerotized. Coxopodite curved dorso-caudad. Harpago 1/3 length of coxopodite; thinner basally; parallel sided along most of length; apex broadly rounded. Phallic apparatus similar to *R. verrula*; with long, digiform, dorsally arched dorsal appendage arising from endotheca, distally coming into contact with the anal sclerites, distally widened with concave, upturned apex. Phallicata arising on dorsal surface of membranous endotheca, thin tube-shaped distally; ventral lobe (fig. 10E) modified, sclerotized with lateral walls fused, flattened ventrally, with lateral carina on each ventro-lateral edge, apex quadrate in cross section.

Female. General form identical to male. Sub-apical protibial spur present, but smaller than on other legs. Segment VIII long and tapered, basal portion sclerotized, more membranous distally, annular dilation at extremity of segment, segment X with dorsal sclerotized plate covering distal 2/3 of segment. Vaginal apparatus spermathecae simple, lacks secondary dorsal curve of *R. verrula*; processus spermathecae emarginate distally, with lateral edges expanded slightly. Posterior process with wrinkled surface on basal half, tapering to long thin tube, sclerotized at apex (fig. 10G).

Larva. Unknown.

Pupa. Unknown.

Distribution. Coastal ranges of Southern Oregon and Northern California (fig. 11).

Type material studied. ♂ HOLOTYPE, ♀ALLOTYPE- Siskiyou County, California, road to Taylor Lake; 5750', Salmon Mountains, Etna Road; 19 August 1972, Hugh B. Leech (CASC).

Other material studied. CALIFORNIA: Del Norte County: 1 ♂- Patricks Crk Rd; 2.4 \mi Hwy 199; June 6, 1993; D.J. Burdick (CASC)/ 1 ♂- So. Frk. Smith Ri.; Rd. 427 4.2 mi.; from start; June16, 1993 (CASC)/ 1 ♂, 1 ♀- So. Frk. Smith Ri.; 4.2 mi on Rd. 427; 1st order steam; 16 June 1993 (CASC).

Plumas County: 1 ♂- 1 mi S. Meadow; Valley 14 Sept. 1983; G. Ulrich (CASC)/ 1 ♂- Meadow Valley; 9 Sept. 1983; coll. G. Ulrich (CASC).

Siskiyou County: 1 ♂- 3 mi. E.; Weed Sept 26, 1975; D.G. Denning (CASC)/ 1 ♂- Seiad Valley; 3-6 Nov, 1986 Fulton (CASC)/ 1 ♀- 17; air km SW Callahan; Trail Ck. Cmpgrd.; VII-27-1982; blacklight; J. Benedictis; & J. Powell; collectors (EMEC)/ 1 ♀- VII-2-84 site 1; Lauck. no locale data; available (RWW).

OREGON: Jackson County: 3 ♂♂- Oct. 9, 1991; ? shoat trib of; Jenny Cr., 6 mi. S.; Pinehurst RWW (RWW).

Lane County: 1 ♀- HJA Admin site; Lookout Cr. 44 13'N 122 20'W; 440m UV light RWW 6-18-86 (RWW)/ 1 ♂- ibid., 6-3-86 (RWW)/ 1 ♂- ibid., 8-12-86 (RWW)/ 1 ♂- ibid., VI-22-87 (RWW)/ 1 ♂- Roaring R.; VII-24-86 BLT Courtney (RWW)/ 2 ♂♂- Wilamette Natl. For.; Rigdon Ranger District, 1991 UV light; June 23-Aug 15, RWW det. (RWW).

Discussion. Very little has been published on *R. leechi*, and few records exist. This species resembles *R. verrula* in the reduction of the apico-dorsal lobe and the

expanded dorso-lateral margins of segment IX, the small segment X, and the sclerotized ventral lobe of the phallic apparatus (figs. 8C and 8E). The ventral lobe is flattened at the apex, rather than being sharply keeled as in *R. verrula* (figs. 12B and 12D). The shape of the dorso-lateral lobe is also distinctive. The inner apical metatibial spur of the male (fig. 10B) is shared with *R. verrula* (fig. 20E) and *R. haddocki* (fig. 8E), as well as the overall form of these species. The larva of *R. leechi* is unknown, but because of the close relationship of this species to *R. verrula*, the larva is likely to be identical to that of *R. verrula*. It is likely that this species is confined to smaller, headwater streams, or even springs.

This species has been given a global and state rank of 3 (rare, uncommon or threatened, but not immediately imperiled) by the Oregon Natural History Program (2001).

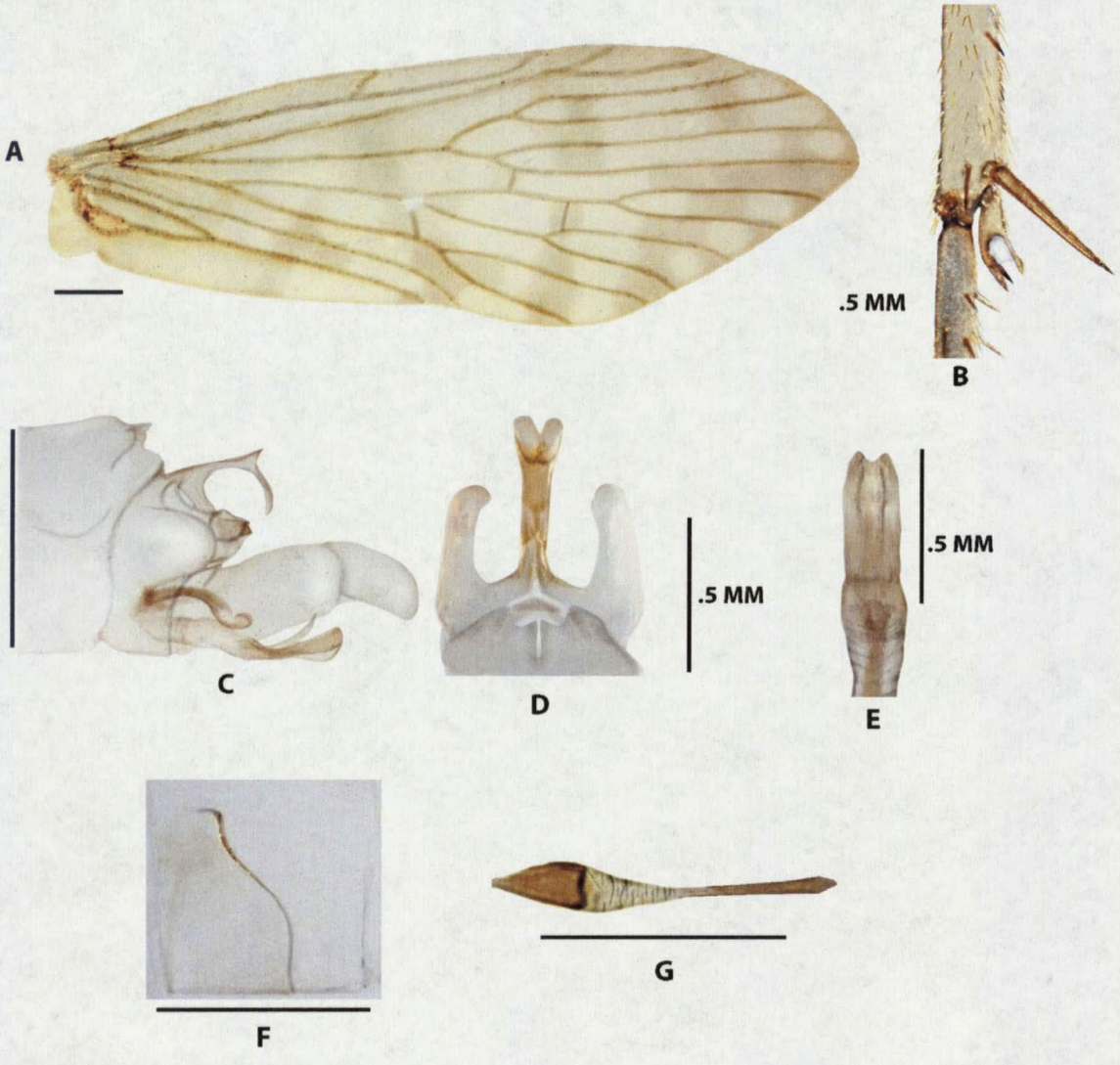

Figure 10: *Rhyacophila leechi* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) modified meta-tibial spur, (C) male genitalia, lateral, (D) male genitalia, dorsal, (E) ventral lobe of phallic apparatus, ventral, (F) male genitalia dorsal, (G) lateral carina leading from scent gland of female abdominal segment V, (H) vaginal apparatus, dorsal.

Figure 11: Distribution of *Rhyacophila leechi*.

Rhyacophila potteri Denning in Denning and Schmid

Figure 12.

Rhyacophila potteri Denning in Denning and Schmid, 1971: 1556. Wold, 1974: 118.

Rhyacophila autumnalis Nimmo, 1977: 30. Schmid, 1981: 39. (NEW SYNONYMY)

Diagnosis. Male: segment IX with well developed, truncate, apico-dorsal lobe; dorsally with depression forming shallow trough. Segment X horizontal, dorso-ventrally flattened, lateral edges folded dorsad. Phallic apparatus with long, acuminate phallicata; ventral lobe membranous, apically divided into two lobes bearing dorsal spines. Female: processus spermathecae apically concave, posterior process basally triangular in cross-section, apex laterally flattened. Larva: posterior tip of frontoclypeus with single muscle

scar. Anterior margin of pronotum with stout setae. FC3 seta on frontoclypeus long, 4/5 length of FC2 seta. Pronotum with three sublateral setae midway along length, one at the border of the darkened margin and the other two farther inward.

Description. Male. Forewing length 9.5-10.5 mm; light brown with darker bands and irrorate pattern; crossvein between M_{1+2} and M_3 forming closed m-cell (fig. 12A). Head brown dorsally, lighter posterad of setal warts, laterad of median ocelli and ventrad of median ocellus; setal wart posterad of median ocellus; large trilobed setal wart posterad of median ocellus, median lobe closely appressed to rounded lateral warts; small rounded setal wart posterad of each lateral ocellus. Posterior setal wart horizontally oblong. Antennae brown, each flagellomere lighter basally and apically. Maxillary palps yellow, subequal in length to protibiae; tip of apical segment dark brown. Thorax yellowish brown, lateral margins of pleural sclerites lighter. Legs yellowish brown; coxae with anterior face darker, covered by setae surrounded by lighter circles; irregular lighter patch dorsally on femur and apical half of tibia and of each tarsal segment (fig. 12E); spurs and spines yellowish brown; tibial spur formula 3-4-4, proleg spurs shorter than on other legs. Tarsal claws of all legs similar in size and shape. Sternites and pleurites of abdomen yellow; tergites darker; with long dorsal setae in dorsal row across each tergite. Apico-dorsal margin of segment VIII unmodified. Segment IX tergum wide; narrowed to receive segment X and again to receive coxopodite; distal 2/3 of dorsum with depression forming shallow trough continuing on to dorso-caudally projecting flattened lobe, apically truncate in dorsal view (fig. 12C). X complexly broad, folded, roughly oblong plate; with pointed lateral lobes separated from the main body of the segment by carinae;

posterior portion dorsally convex with mesal circular incision at apex; spines ventrally; projecting beyond segment IX (fig. 12B). Tergal strap sclerotized and fused to segment X. Anal sclerite small, without deep root, located at apex of apical band. Phallic apparatus with long, sinuate dorsal process arising from endotheca; base of phallicata flattened with lateral lobes, distal portion tubular, acuminate; ventral lobe membranous, extensile, apex divided into two elongate lobes each bearing dorsal patch of dark spines (fig. 12D).

Female. Wings, head, thorax, and base of abdomen as in male. Segment VIII long, tapered, basal portion sclerotized, more membranous distally, annular dilation at extremity of segment. Segment X with dorsal sclerotized plate covering distal 2/3 of segment. Processus spermathecae of vaginal apparatus chalice-shaped, apically concave; posterior process with massive basal half, ribbed horizontally, triangular in cross-section, tapering to well sclerotized, laterally flattened tube at apex (fig. 12F).

Larva. Mature larva approximately 20 mm in length. Head rounded, nearly spherical; widest just anterad of midlength (fig. 12H); dark muscle scars in longitudinal rows along parietal sclerites, two rows dorsally, five rows laterally, muscle scars larger and darker than those of *R. verrula* (fig. 20H), leaving less background color in spaces between. Frontoclypeus short, little more than half length of head capsule; with darkened muscle scars, three large scars posterad of the widest part of the sclerite, two laterally, one medial scar composed of two scars fused together; frontoclypeal seta FC_1 minute, clear, curved inward; FC_2 long, subequal to width of frontoclypeus; FC_3 clear, longer than that of *R. verrula*, 4/5 length of FC_2. Long setae around eye, on anterior margin of

pronotum, anterior and lateral margins of frontoclypeus, and posteriorly above genae. Maxillary palpus short; all segments subequal. Submentum reduced to pair of sclerites each at base of submental setae and small median sclerite. Mentum undivided. Mandibles short, stout and pyramidform; left mandible with three apical teeth; right mandible short two apical teeth, single small mesal tooth, pencillus basally. Pronotum light brown, with darkened muscle scars; anterior margin with line of 15-20 long, robust setae (fig. 12G), setae shorter and more robust than those of *R. verrula* (fig. 20I), longest setae subequal in length to mesal length of pronotum; three sublateral setae midway along length, one at border of darkened margin, two farther mediad; anterolateral corners with rounded notch bearing three setae, two long, subequal in length, third seta shorter (about ½ as long). Forelegs broadened. Abdomen without gills or protuberances. Anal proleg short, with long scabrous setae; lateral sclerite of anal proleg with darkened muscle scars; sclerite at the base of seta PRb4 prominent, floating in membrane posterad of basoventral hook, projecting inward as spine, resembling a secondary baso-ventral hook, bearing stout, spine-like PRb_4 seta; baso-ventral hook prominent, though not as much as *R. verrula* (fig. 20J), dark, projecting from basal membrane; apico-lateral spur absent from lateral sclerite of anal proleg; anal claw with seta 8 borne on prominent tooth-like projection.

Pupa. Length of male 9 mm; female 10.5 mm. Wing sheaths reach segment VI of male, segment IV of female. Antennae reach beyond genitalia of male, segment VI in female; scape with 3-4 black setae. Head with eight long, black dorsal setae; one submedian seta on each side posterad of median ocellus, one posterad of each lateral ocellus, postero-lateral pair on each side. Frons with row of three submedian setae on

either side; clypeus narrowly apically rounded, three setae on each side; labrum with five antero-lateral setae on each side; one seta on anterior margin of eye; one short genal seta posterad of ventral articulation of mandible. Mandibles short, stout; length of mandible apex to inner margin 1.3 times basal width of mandible; each with two basal setae, one clear, dorsad of dark brown seta; right mandible with two median teeth and approximately nine denticles; left mandible with single median tooth, and approximately twelve denticles decreasing in size toward apex (fig. 12I). Pronotum with five dorsal setae on each side. Each side of mesonotum and metanotum with anterior seta and dorsal seta laterad of scutellum. Abdomen with dorsal presegmental hook plates on segments III to VII, postsegmental on segments III to V, plate spinule formula III: 7+18; IV: 7+24; V: 20+23; VI: 15; VII: 12 (fig. 12J). Abdominal segments I-VIII with one dark dorsal seta at Sa_1 and Sa_2, three to four setae on pleurites I-VII, one seta at ventral Sa_2 on segments I-VIII. Legs with five long black setae on anterior face of each coxa, one apically and distally on each femur. Mesotibiae without swimming setae.

Distribution. In addition to the type locality, field parties from the Royal Ontario Museum have collected this species from the Lolo Pass, Lost Trail Pass, and Skalkaho Pass areas of Idaho and Montana. In addition to these localities, I have collected metamorphotypes and adults from the Pioneer Mountains of Montana, and larval sclerites from an empty cocoon from the Tobacco Root Mountains of Montana. It is likely that the range of this species extends even farther North along the Montana border (fig. 13).

Type material studied. ♂ HOLOTYPE- Swamp Creek, Elk Summit Road; Idaho County, Idaho; 3 Aug. 1960, D. S. Potter (CASC).

Other material studied. ALBERTA: 1 ♂- Rowe Bk, 6350, Wat. Nat.; Pk, Alberta. 12/9/75. D.B. Donald *R. autumnalis* HOLOTYPE CNCI No. 15162 (CNCI)/ 1 ♂- Ruby Bk, 6750', Wat. Nat.; Pk, Alberta. 24/8/75.; D.B. Donald; *R. autumnalis* PARATYPE; CNCI No. 15162 (UASM)/ 2 ♂♂- Rowe Bk, 6350, Wat. Nat.; Pk, Alberta. 12/9/75. D.B. Donald (CNCI).

IDAHO: Idaho County: 1 ♂- Big Creek, N. Savage; Pass, Elk Summit Road 10-IX-71; D. S. Potter, R. A. Haick (CASC)/ 2 ♂♂- small run crossing; Rt. 12, 11 mi. s.w. Lolo Pass, 25 JUN 1968; Wiggins, Yamamoto, Smith (ROME)/ 2 ♂♂- IX-10-71; Savage Pass Seep; Elk Summit Road; D.S. Potter, R.A. Haick (CASC).

MONTANA: Beaverhead County: 1 l, 4 ♂♂, 1 ♀, 8 pupae- Beaverhead Deerlodge FR 192.2; Mule Cr. Tributary; 45.4189°N, 112.9360°W, 2417 m; 10 VIII 2001; J. Giersch (JJGC)/ larval sclerites- Beaverhead/Deerlodge FR 192.2; Mule Cr. Tributary; 45.4189°N, 112.9360°W, 2417 m; 30 VIII 2001; J. Giersch (JJGC).

Flathead County: 1 ♀- Cattle Queen Cr. @ Mineral trail; 48.8201°N, 113.822°W; 13 IX 1996(FLBS)/ 1 ♂- Mineral Cr. headwaters-W. fork above confluence; 48.8414°N, 113.836°W; 28 VIII 1997(FLBS)/ 2 ♂♂- Mineral Cr. headwaters @ confluence of E. and W. forks; 48.8406°N, 113.835°W; 28 VIII 1997(FLBS).

Granite County: 1 ♀- Small stream on FR 1352; N. of Skalkaho Pass; 46.2661°N, 113.7656°W, 2255 m; 26 VII 2001; J. Giersch (JJGC)/ 1 ♂ metamorphotype pupa- Crooked Cr.; 2 km N Skalkaho Pass; 46.2661°N, 113.7656°W, 2255 m; 26 VII 2001; J. Giersch (JJGC).

Madison County: larval sclerites-: above Branham Lakes; S. Fork Indian Creek Headwaters; 45.5244°N, 112.0179°W, 2906 m; 02 IX 2001; J. Giersch (JJGC)
Missoula County: 1 l- spring runs cross-;ing Rt. 12 at Lolo Pass, elev.; 5187'; 25 JUN 1968; Wigginis, Yamamoto, Smith (ROME).

Ravalli County: 1 l- creek; 2.5 mi. e. Daly Cr. Rd.; Flowing into Daly Cr., Rt; 38, s. Grantsdale. 11 AUG.; 1981. G.B. Wiggins (ROME)/ 1 ♂- strm.; at Rt.38, 2-1/2 mi.e.; Daly Cr. Rd., e. Grants-;dale. 12 AUG 1981.; G.B. Wiggins (ROME)/ 1 ♂- Skalkaho Falls on Rt.; 38e. Grantsdale. 4 Aug.; 1981. G.B. Wiggins (ROME)/ 1 ♂- ibid., 11 AUG; 1981. G.B. Wiggins (ROME)/ 10 l- FR 1352 sidestream; .7 km N of Skalkaho Pass; 46.2525°N, 113.7713°W, 2264 m; 13 VII 2001; J. Giersch (JJGC)/ 2 l- ibid., 26 VII 2001; J. Giersch (JJGC)/ 2 ♂♂- Skalkaho Falls on Rt.; 38 e. Grantsdale. 12 AUG; 1981. G.B. Wiggins (ROME)/ 3 l- stream crossing; Rt. 93, 1.2 mi. N. Lost Trail; Pass, June 26, 1968, Wiggins; Yamamoto, Smith (ROME).

Discussion. *Rhyacophila potteri* was included in the verrula-group by Denning and Schmid (1971), although they noted differences in the form of sclerite IX, the aedeagus, and the absence of modifications on tergum VIII.

The phallic apparatus of *R. potteri* most closely resembles that of *R. singularis* in the presence of the ventral lobe that is divided at the apex, the prominent apico-dorsal lobe on segment IX, and the shape of segment X. *Rhyacophila potteri*, however, lacks the modified margin of segment VIII.

Comparison of specimens of *R. potteri* from near the type locality with type material of *R. autumnalis* has led me to decide that *R. autumnalis* is a junior synonym of

R. potteri. Nimmo (1977) distinguished *R. autumnalis* from *R. potteri* by the acute rather than blunt apex of the harpago, as can be seen in the illustrations for the description of *R. potteri* (Denning in Denning and Schmid 1971). Because the harpago curves mesad apically, the shape changes depending on how the specimen is lying. Therefore, a harpago that appears to be blunt may actually be quite acute if the specimen is rolled. *Rhyacophila autumnalis* was described from Waterton Lakes National Park, and *R. potteri* from the Bitterroot Mountains of Idaho. Further collecting, as well as the discovery of more museum specimens indicate that the distribution of *R. potteri* is more extensive than previously thought, extending at least as far east as the Tobacco Root Mountains of Montana. It is likely that *R. potteri* has a continuous distribution along the Montana-Idaho border north to British Columbia and Alberta.

I have collected *R. potteri* at four localities in Montana, all of which are small streams or seeps with abundant mosses. Larval-adult associations were first made from pupae reared from a small cobble bottomed stream draining a spring-fed marsh that runs below a roadcut in the Mule Creek drainage of the Pioneer Mountains (fig. 14). The moss *Amblystegium riparium* is abundant along the bottom and margins of the stream, and pupae were collected from within the moss mats, with the mosses tightly wrapped around the cocoons.

A small, moss-covered stream north of Skalkaho Pass also yielded larvae and pupae, and I have also identified larval sclerites from a vacated pupal cocoon collected from an alpine spring in the Tobacco Root Mountains of Montana. Adults have been

collected in the subalpine zone of the upper Mineral Creek drainage of Glacier National Park, and Waterton National Park in Alberta.

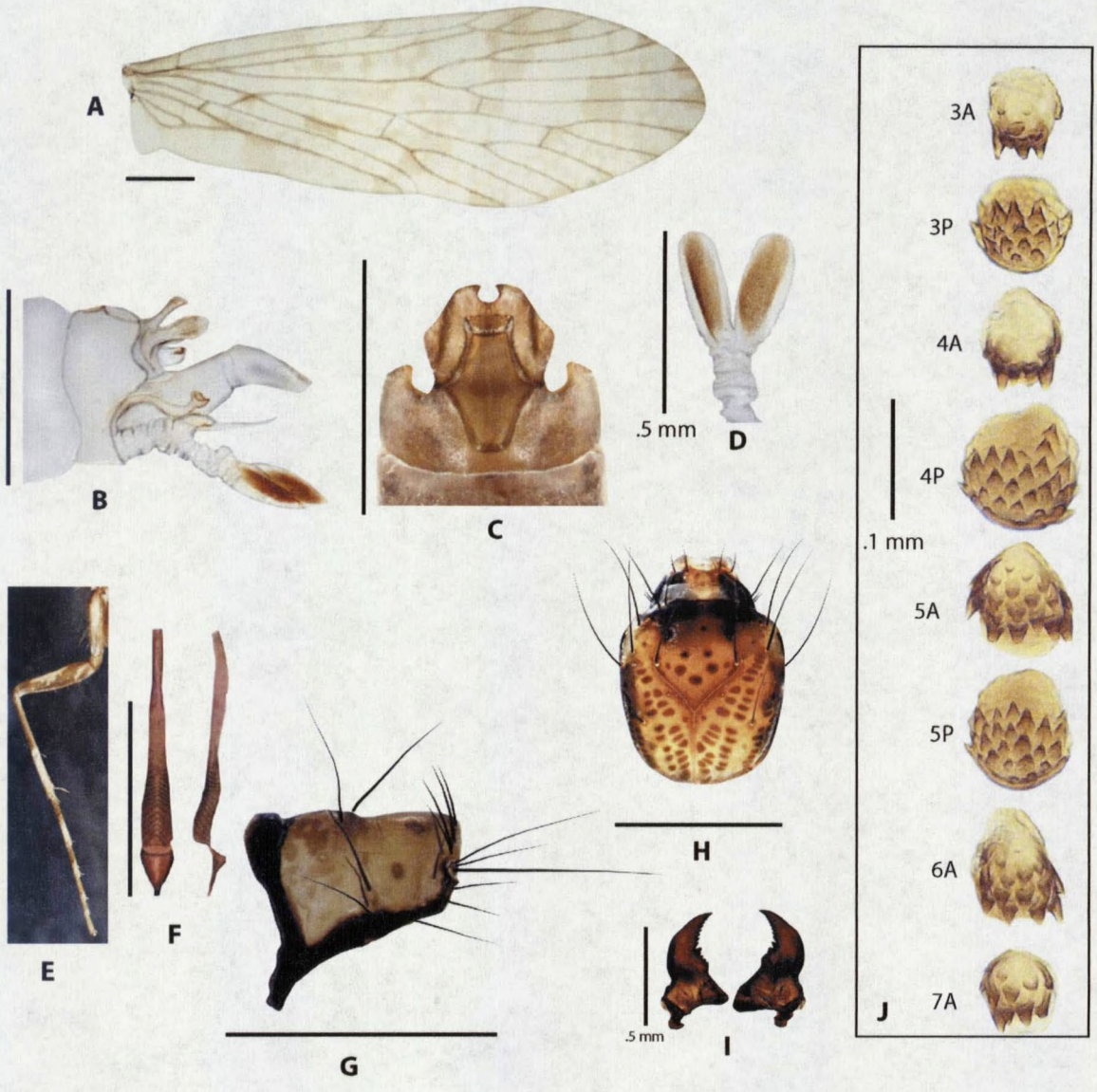

Figure 12: *Rhyacophila potteri* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male genitalia, lateral, (C) male genitalia, dorsal, (D) apex of ventral lobe of male phallic apparatus, (E) male metathoracic leg, (F) female vaginal apparatus ventral and lateral, (G) larval pronotum, lateral, (H) larval head, dorsal, (I) pupal mandibles, (J) dorsal hook plates of pupa.

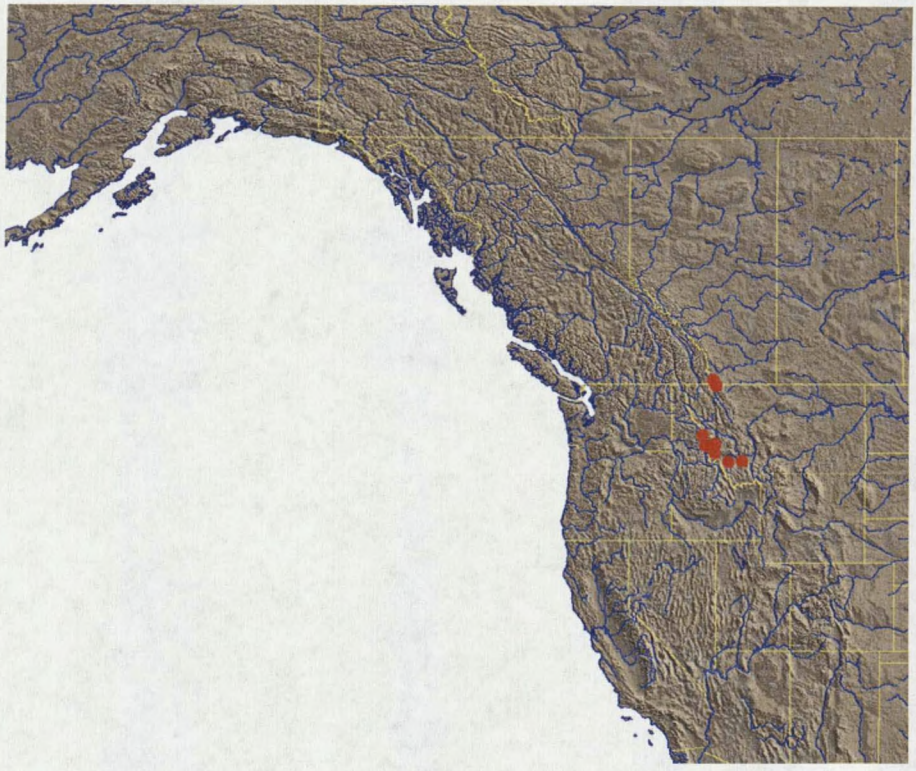

Figure 13: Distribution of *Rhyacophila potteri*.

Figure 14: Small spring-fed stream in the Mule Creek drainage of the Pioneer Mountains, Montana. *Rhyacophila potteri* pupae were collected from the thick mats of the moss *Amblystegium riparium* at the margins of the stream.

Rhyacophila rickeri Ross

Figure 15.

Rhyacophila rickeri Ross, 1956: 95. Nimmo, 1971: 28. Ellis, 1978: 204. Schmid, 1981: 39. Roemhild, 1982: 10. Vineyard, 1981: 99. Vineyard, 1982: 74. Schmid, 1993: 161.

Diagnosis. Male: segment IX with short, triangular apico-dorsal lobe, segment X short, complex, ventral lobe of phallic apparatus entire, covered with apical spines. Female: vaginal apparatus short, heavily sclerotized. Larvae: anterior margin of thorax with short, scale-like marginal setae.

Description: Male. Forewing 11-12 mm, yellow with darker irrorate pattern; crossvein between M_{1+2} and M_3 forming closed m-cell (fig. 15A). Head with dark brown area dorsally, extending as lobe posterad of lateral ocelli (fig. 15B); lighter posterad of setal warts, laterad of median ocelli and ventrad of median ocellus; setal wart posterad of median ocellus; large trilobed setal wart posterad of median ocellus, median lobe closely appressed to rounded lateral warts; small rounded setal wart posterad of each lateral ocellus. Posterior setal wart horizontally oblong. Vertex light brown, with darker setal warts and ventral margin along clypeus. Antennae light brown, each flagellomere darker medially. Pronotum brown. Thorax yellowish-brown, pleural margins lighter. Legs yellowish-brown, coxae covered by setae surrounded by lighter circles, darker coloration as irregular medial band on femora and apical portions of tibiae and tarsomeres; spurs and spines brown, spur formula 3-4-4, protibial spurs shorter than on other legs; tarsal claws equal in size and form on all legs. Abdomen light brown, lighter laterally. Segment

VIII dorsally with short, wide, entire, posterior extension (fig. 15C). Segment IX annular, widest dorsally, posterior margin slightly concave to receive coxopodite; ventrally thin; dorsally with blunt apicodorsal projection extending over tergite X, triangular and posteriorly rounded in dorsal view; base of projection set off from rest of the dorsum by furrow. Segment X short, situated horizontally, roughly quadrate in lateral view, with two horizontal lobes on each side of midline in dorsal view, outer lobes longer than middle lobes. Tergal strap darkened, well sclerotized. Anal sclerite well sclerotized, with two ventral points covered with spicules. Apical band well sclerotized laterally. Coxopodite directed dorso-posteriorly. Harpago narrower than coxopodite, tapering to rounded apex, about ¾ length of coxopodite, offset from harpago at an angle. Phallic apparatus with elongate, dorsoventrally flattened dorsal projection, sigmoid in shape, curved upward at tip with apical concavity covered with spicules, equally broad basally and apically, narrowing to half width at midlength. Phallicata long, thin, tube with flared, trilobed base; parameres absent; ventral lobe expanded as extensile, membranous lobe with apical portion concave and covered with dorsal patch of spines, somewhat asymmetrical and wrapping around the tip of the phallicata when ventral lobe is not expanded (fig. 15D).

Female. Coloration and form of wings, head, thorax, and base of abdomen as in male. Basal third of segment VIII sclerotized, narrowed to posterior membrane (fig. 15E). Vaginal apparatus sigmoid in lateral view; processus spermathecae dorsally rounded, roughly triangular, basally rounded and widened at intermediate process; posterior process long, ovoid, basally constricted, widened medially, narrowed distally, lateral edges rolled inward forming median channel (fig. 15F).

Larva. Length of mature larva approximately 18 mm. Head dark brown, nearly black in life, lighter coloring around eyes; somewhat dorsoventrally flattened, not as rounded ventrally as *R. verrula*; widest at midlength; muscle scars on head capsule slightly raised above the surface, furrowed between scars giving wrinkled appearance; P_3 seta on head may be flattened at tip (figs. 10G and 10H). Frontoclypeus with darkened coloring covering portion anterad of tentorial pits and associated parietal areas around base of mandible; frontoclypeal seta FC_1 minute, clear, curved inward, FC_2 long, subequal to width of frontoclypeus, FC_3 clear, longer than that of *R. verrula*, ½ length of FC_2. Pronotum with two sublateral setae midway along length, one at the border of darkened margin and one farther inward; 15 to 20 short, stout, scale-like setae, tips, wide, flattened, less than 1/3 length of mesal length of pronotum (figs. 10J and 10K). Anal proleg similar to *R. verrula,* short, broad, with short, dark basoventral hook; sclerite on ventral membrane with long medially directed spine and bearing stout PRb_4 seta; anal claw with seta 8 borne on prominent tooth-like projection.

Pupa. Length of male 11 mm; length of female 12 mm. Wing sheaths reach to segment V of male, segment IV of female. Antennae reach beyond genitalia of male, segment VI in female; scape with two apical black setae, one thin, clear basal seta. Head with eight long, black dorsal setae; one submedian seta on each side posterad of median ocellus, one posterad of each lateral ocellus, and postero-lateral pair on each side. Frons with row of two submedian setae on either side; clypeus apically membranous, truncate, with three antero-lateral setae on each side, median seta minute, clear; labrum with five antero-lateral setae on each side; one seta on the anterior margin of eye; one short genal

seta posterad of ventral articulation of mandible. Mandibles short, stout; length of mandible apex to inner margin 1.5 times basal width of mandible; each with two basal setae, one clear, dorsad of dark brown seta; right mandible with two median teeth and approximately eleven denticles; left mandible with single median tooth and approximately fourteen denticles decreasing in size toward apex (fig. 15L). Pronotum with five dorsal setae on each side. Each side of mesonotum and metanotum with an anterior seta and dorsal seta laterad of scutellum. Abdomen with dorsal presegmental hook plates on segments III to VI, postsegmental on segments III to V, presegmental plate in segment III small, vestigial; plate spinule formula III: 2+16; IV: 13+20; V: 20+20; VI: 15 (fig. 10M). Abdominal segments I-VIII with one dark dorsal seta at Sa_1 and Sa_2, three to four setae on pleurites I-VII, one seta at ventral Sa_2 on segments I-VIII. Legs with five long black setae on anterior face of each coxa, one apically and distally on each femur. Mesotibiae without swimming setae.

Distribution. This species occurs in gravelly, high alpine streams in isolated ranges Glacier National Park, Montana, Alberta, British Columbia, Mount Hood and Sisters region of Oregon, and Mount Rainier, Washington. (fig. 16).

Type material studied. None. Type Repository: Illinois Natural History Survey Insect Collection, Champaign, Illinois.

Other material studied. ALBERTA: 1 ♀- Lake Agnes at creek above Lake Louise; Hab: moraine, 630pm; 11/9/66, A. Nimmo (UASM)/ 1 l- 18.5 mi. n.L.; Louise cutoff on rd.; to Jasper, 5750' elev.; 28 jun 1967. J.&R. Wold (ROME)/ 1 ♂- Jasper Nat. Park; Mt. Edith; 3-X-1964; A.P. Nimmo (CNCI)/ 1 ♂- Loc: Alpine Meadow Trail, Mt. Edith

Cavell, J.N.P.; Dat. 7/10/89.Col. A.P. Nimmo (UASM)/ 1 ♂- Path to Edith Cavell Alpine; Meadows, J.N.P.; hab. snow; 7/10/67, A. NIMMO (CNCI)/ 5 l- Loc. Entry Creek; 30 July, 1979 Coll. Maldenhauer (UASM).

BRITISH COLUMBIA: 1 l- B.C.: Alaska Hwy., km; 1183, sm. trib. of Swift; R. 59° 55'Nx131.30'W; 13 JUN 1980. #800025. ROOM Fld. Pty. (ROME).

ALASKA: 1 l- 1 Sept. 71; above falls to first flat; Sashin Cr.;Little Port Walker (CASC)/ 1 l- Cooper R.; 4 mi. S. Haley Cr.; 21 AUG 1967.; J. Lohrenze. (ROME)/ 1 l- Kenai; Penn., Torrential; Mtn., trib. to Lower; Russian L. 8 JUL; 1969. E.L. Charnov (ROME)/ 1 l- Glacier Bay Nat Mon.; 6 Miles N. Lituya Bay; 910-980m 14 Aug. 79; D.H. Kavanaugh coll.; Stop 79-19 (CASC)/ 12 l- Aniakchak Natl Mon; Alas Peninsula 56°56'N; 158°6'W 300-400m elev; Surprise Lake & tribs; VIII-30-88; Inlet streams (RWW).

MONTANA: Flathead County: 1 ♀- 29IX1998; Logan Cr. by H20 tanks to spring; Logan Pass; Glacier National Park, MT (FLBS)/ 1 ♀- 970924; Logan Cr. @ Source pond, Logan Pass; 1745 hrs; Glacier National Park (FLBS)/ 1 ♀- ibid., 24 IX 1997(FLBS)/ 1 ♀- Logan Cr. near water tank- Logan Pass; 48.697°N, 113.725°W; 29 IX 1998(FLBS)/ 1 l- Logan Cr. springhead; Glacier National Park; 48.6985°N, 113.7307°W, 2118 m; 10 VI 2000; J. Giersch (JJGC)/ 1 l- ibid., 29 IX 1998(FLBS)/ 1 l, 1 m metamorphotype pupa- Logan Cr. at H20 Falls; NW of H20 tank, Logan Pass; 48.6964°N, 113.7258°W, 2031 m; 02 VIII 2000; J. Giersch (JJGC)/ 1 ♀, 2 ♂ metamorphotype pupae- ibid., 17 VIII 2001; J. Giersch (JJGC)/ 2 l- Logan Creek at Logan Pass; near water tanks; Glacier National Park; 10 VII 1998 J. Giersch (FLBS)/ 2 l-

ibid., 22 IX 1998(FLBS)/ 2♂♂, 3♀♀- Logan Cr. near water tank- Logan Pass; 48.697°N, 113.725°W; 22 IX 1998(FLBS)/ 3 l- 24 VI 98; Logan Cr. @ cement; diversion for H20 tank inlet; Logan Pass; Glacier National Park (FLBS).

Glacier County 1 l- Bullhead Lake inlet strm; E. side Swiftcurrent Pass, GNP; 48.7803°N, 113.7422°W, 1656 m; 05 VIII 2000; J. Giersch (JJGC)/ 1 l- Reynolds Cr.; Logan Pass, GNP; 48.6884°N, 113.7227°W, 2058 m; 04 VIII 2000; J. Giersch (JJGC)/ 1 larval sclerites- ibid., 17 VIII 2001; J. Giersch (JJGC)/ 4 l- ibid., 17 VIII 2001; J. Giersch (JJGC)/ 1 ♂- Reynolds High Site- Logan Pass; 48.6874°N, 113.732°W; 10 IX 1997 (FLBS)/ 17 l- Lunch Cr. below H2O falls; Above Going to the Sun Rd.; 48.7007°N, 113.7023°W, 1991 m; 16 VIII 2001; J. Giersch (JJGC)/ 2 l- Reynolds Cr. Lower H2O falls; Logan Pass, GNP; 48.6966°N, 113.7252°W, 2014 m; 24 VII 2000; J. Giersch (JJGC).

OREGON: Clackamas County: 2 ♂♂- Mt. Hood, strm.; crossing rd. 3.3 mi. below; Timberline Lodge; Sept 28-29, 1966; Wiggins, Yamamoto, Odum (ROME)/ 1 l- ibid., RWW; 8-25-88 (RWW)/ 1 l- Mt. Hood strm.; x-ing rd.3.3 mi. below; Timberline Lodge.; 20 APR 1964.; G.B. Wiggins, R.S. Scott (ROME)/ 1 l- ibid., 13 JUL 1963; G.B. Wigginis (ROME)/ 1 l, 1 ♀ metamorphotype pupa- Mt Hood; Strms below Timberline; Lodge 4200-5200'; 45 17'N 121 43'W RWW; 8-25-88 (RWW).

Deschutes County: 1 ♀- Todd Lk.; inlet springhead. ca 6000'; 9-28-83 pupa reared (RWW)/ 1 l- Tyee Cr.; Springhead. 9-28-83 (RWW)/ 17 l- ibid., VIII-20-85 BW (RWW)/ 1 ♂- Woodland; spring trib Todd Lk. 9-29-83 (RWW)/ 2 l- Century Dr.; Goose Cr. headwaters sprgs; 8-20-83. BW (RWW)/ 3 l- S. Sisters; Goose Cr. ~ 1/4 mi. up

moraine; Lk. trail. 5500-6000'. BW; Aug 14, 1982 (RWW)/ 2 ♂♂- Sisters Wilderness; South Sisters, Moraine; L., 6400'. 6400'. 24 SEPT; 1981. B. Wisseman. (ROME).

Hood River County: 2 l- Mt. Hood; Mitchell Cr. nr. Meadows; ski area. 5000-5200'; VIII-25-89 RWW (RWW).

WASHINGTON: Pierce County: 1 l- WA: Mt. Rainier Natl. Park; Edith Cr. 5670' MORA; VII-25-86 (RWW).

Discussion. Ross (1956) originally placed *R. rickeri* in the sibirica-group on the basis of the form of the membranous ventral lobe of the aedeagus. Schmid (1970) agreed with Ross' placement, but considered *R. rickeri* to be the most basal species of the group based on characters that he considered plesiomorphic in the sibirica-group. These characters include the large apical band, short tergal strap, long dorsal appendage of the phallic apparatus, and the membranous, undifferentiated apex of the ventral lobe. However, Schmid (1981) later placed *R. rickeri* in the verrula-group based on closer examination of the aedeagus, as well as the presence of the closed median cell in the forewing.

The ventral lobe of the phallic apparatus is membranous as in *R. singularis*, *R. potteri*, and *R. chandleri*, but the apex is entire and dorsally covered with a field of spines as in *R. chandleri*.

Records from Aniakchak National Monument, Alaska show this species occurring at much lower elevation than at lower latitudes, at 400 meters elevation. Data from these records show the ecosystem to be typical for specimens collected from other localities.. Adults of this species have been collected in July from high gradient first through fourth

order streams on Baranof Island, Alaska (Ellis 1978). Nimmo (1971) reported this species emerging in October near very small brooks flowing from moraines at high altitude (2,200 m), occasionally being collected directly from the snow. I have collected this species regularly from very cold, high alpine streams at Logan Pass in Glacier National Park. Much like those of *R. potteri*, pupae are found directly within mats of a leafy liverwort, *Scapania undulata*, often on the underside of rock overhangs in waterfalls (fig. 17) [J. Giersch., personal observation].

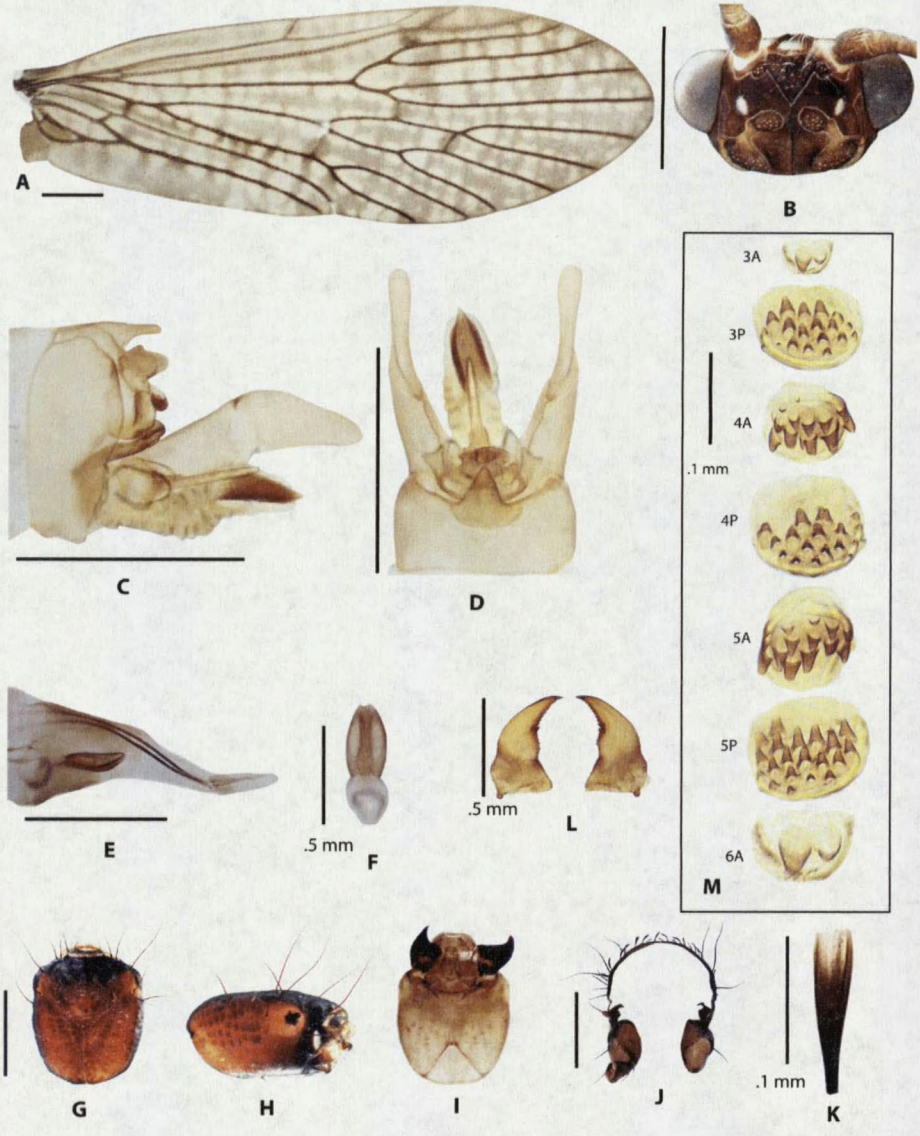

Figure 15: *Rhyacophila rickeri* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male head, dorsal, (C) male genitalia, lateral, (D) male genitalia, dorsal, (E) female terminal segments of abdomen, lateral, (F) female vaginal apparatus, ventral, (G) larval head, dorsal, (H) larval head, lateral, (I) larval head, ventral, (J) pronotum, anterior view (K) seta from anterior margin of pronotum, (L) pupal mandibles, (M) dorsal hook plates of pupa.

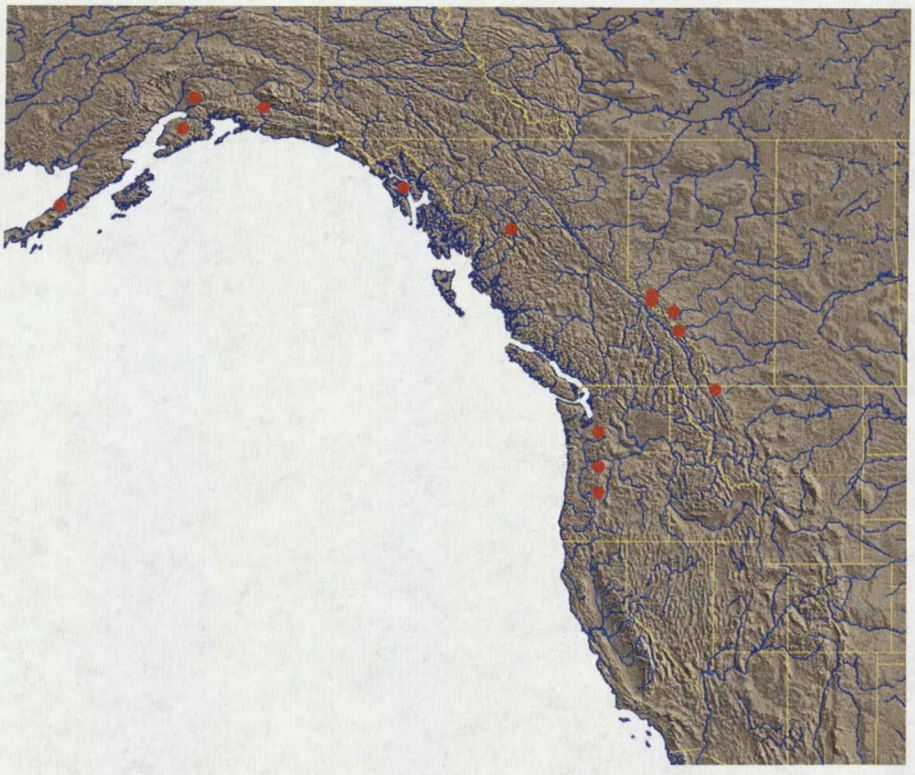

Figure 16: Distribution of *Rhyacophila rickeri*.

Figure 17: Waterfall on Logan Creek, at Logan Pass, Glacier National Park, Montana. *Rhyacophila rickeri* pupae were collected from mats of the leafy liverwort, *Scapania undulata,* on the undersides of rock layers in the falls.

Rhyacophila singularis Botoşăneanu

Figure 18.

Rhyacophila singularis Botoşăneanu, 1970: 281. Levanidova, 1980: 67. Levanidova, 1980: 171. Levanidova, 1986: 7. Ko and Peck, 1988: 9. Levanidova et al., 1995: 4. Arefina, 1997:26

Diagnosis. Male: segment VIII with long, blade-like lateral extensions; segment IX apico-dorsal lobe with pair of apical, closely appressed bulbous lobes covered by minute spicules; phallic apparatus ventral lobe membranous, extensile, apically divided into pair of lobes, with dark, dorsal spines. Female: processus spermathecae of vaginal apparatus apically with V-shaped emargination; posterior process tapering to long, lightly sclerotized apex. Larva: head rounded; small gills on thorax and abdomen.

Description. Male. Forewing 13-14 mm; yellow, patches of brown forming banded patterns on apical half; crossvein between M_{1+2} and M_3 forming closed m-cell (fig. 18A). Head brown, setal warts yellow; frons with triangular brown patch between lighter colored lateral warts; single large median setal wart posterad of median ocellus; smaller, longitudinal setal wart posterad of each lateral ocellus, connected to larger, rounded wart posterad; thin vertical wart with single row of setae following posterior margin of eye. Maxillary palps elongate, subequal in length of protibiae. Pronotum yellow with submedian warts. Antennae brownish yellow. Thorax yellow, edges of pleural sclerites darker. Legs yellow, spurs and spines brown; tibial spurs 3-4-4; apical protibial spurs smaller than meso- or metatibial spurs; anterior tarsal claw of proleg larger than posterior claw, wide at base (fig. 18E); meso- and metathoracic tarsal claws equal in

length and form. Mesonotum brown, lighter median wart having antero-lateral branches reaching anterad. Metanotum brown. Segment VIII modified, composed of three main parts; medially with well sclerotized, tri-lobed stalk composed of two lateral, rounded, concave lobes covered with fine tubercles, flanking median lobe forming dorso-ventral carina, giving appearance of a triangular point in dorsal view (fig. 18C); flanking median projection is pair of large, long, blade-like, apically rounded extensions, expanded prominently above tergite IX. Segment IX wide, slightly narrowed near insertion of segment X and coxopodite (fig. 18B); in dorsal view with prominent apico-dorsal lobe caudally bearing pair of medially fused minutely tuberculate bulges (fig. 18C); apico-dorsal lobe resembles tuberculate club in lateral aspect, extending over tergite X. Segment X broad, complexly folded, roughly oblong plate; with pointed lateral lobes separated from main body of segment by carinae; posterior portion dorsally convex with mesal circular incision at apex; spines ventrally; projecting beyond segment IX. Tergal strap lightly sclerotized. Anal sclerite small, without deep root, located at apex of apical band. Coxopodite with dorsal edge almost straight, ventral edge ascending, half as wide apically as basally. Harpago subequal in length to coxopodite, without apical emargination, long, lobate, apically rounded, angled ventrad. Dorsal appendage long, sinuate, apically wide, concave, arising from endotheca; basally wrapped around base of phallic apparatus. Phallicata thin, acuminate; arising ventrally from bulbous base ventrad of wide, membranous bilobed plate. Ventral lobe extensible, membranous, tube; pair of bifid lobes bearing dark spines apically (fig. 18D).

Female. Forewing 15 mm, coloration and venation identical to male. Coloration of head, thorax, and abdomen as in male. Tarsal claws equal in size and length, equal to claws on all tibiae. Segment V with light carina leading ventrad from scent gland opening (fig. 18F). Processus spermathecae of vaginal apparatus with apical V-shaped emargination; posterior process tapering to long, lightly sclerotized tip (fig. 18G).

Larva. Length of mature larva approximately 13 mm. Head brown, rounded, somewhat dorso-ventrally flattened; widest across eyes; dark muscle scars in longitudinal rows along parietal sclerites, two rows dorsally, five rows laterally (fig. 18I). Frontoclypeus short, little more than half length of head capsule; with darkened muscle scars, three large scars posterad of widest part of sclerite, two laterally, medial scar composed of three scars fused together; frontoclypeal seta FC_1 minute, clear, curved inward, seta FC_2 long, longer than width of frontoclypeus, FC_3 clear, half the length of FC_2. Long setae around eye and posteriorly above genae. Maxillary palpus short. Submentum reduced to pair of sclerites each at base of submental setae and one horizontal median sclerite. Mentum undivided. Mandibles short, stout and pyramidform; left mandible with three apical teeth; right mandible short, two apical teeth, single small mesal tooth, pencillus at base. Pronotum dark brown, with darkened muscle scars; anterior margin with line of 15-20 setae, longest setae half length of pronotum mesal length; two sublateral setae midway along length, one at border of darkened margin, one farther mesad; three setae in rounded notch at anterolateral corners of pronotum, two long, subequal in length one shorter (about 1/4 as long) seta. Forelegs broadened. Thorax and abdomen with short gills (fig. 18K); segment II of thorax with one gill near Sa_3, two

others posterad; segment III with one gill posterad of Sa_3, one farther posterad. Abdominal segment I with single gill anterad and another posterad of Sa_2; two gills on pleurite, anterior gill in more dorsal position than posterior gill; segments II-VIII with gills as on segment I, additionally with one posterad of Sa3 seta, another more posterad . Anal proleg short with long setae (fig. 18J); lateral sclerite of anal proleg with darkened muscle scars; sclerite at the base of seta PRb_4 small, floating in the membrane posterad of the basoventral hook, bearing stout PRb_4 seta. Baso-ventral hook prominent, from basal membrane; apico-lateral spur absent from lateral sclerite of anal proleg anal claw with seta 8 borne on prominent tooth-like projection.

Pupa. Unknown.

Distribution. South of Khabarovsk region of Russia (Levanidova et al. 1995), North Hamgyong Province, North Korea (Botoşăneanu 1970), Mt. Deogyusan National Park, South Korea (Ko and Peck, 1988) (fig. 19).

Type material studied. None. Holotype repository: Zoological Institute of the Polish Academy of Sciences, Warsaw.

Other material studied. RUSSIA: 1 ♀- Primorye Territory,; Kedrovaya R.; basin. 13.06.1973; Leg. Budnikova (RASV)/ 1 ♂, 1 ♀- Primorye Reservation; "Kedrovaja Pad", Kedrovaja; River, June 13, 1973.; Leg. Levanidova (CNCI)/ 2 l- Primorye Territory; Goaraysky Stream; Kedrovaya River; basin. 9.11.1975; Leg. Nikolagva (RASV).

Discussion. *Rhyacophila singularis* has been collected from North Korea (Botoşăneanu 1970), South Korea (Ko and Peck 1988), and the Russian Far East (Levanidova 1980, 1982, 1986). Botoşăneanu (1970) included *R. singularis* in the

verrula-group, noting the modified tergite VIII. Botoşăneanu considered the complex form of this tergite to be the most advanced specialization in the group, but considered structure of the aedeagus to be plesiomorphic. The membranous ventral lobe is the basal condition of the verrula-group aligning *R. singularis* with *R. rickeri*, and *R. chandleri*, and *R. potteri*. The apically bilobed ventral lobe of the phallic apparatus and the shape of segment X is shared with *R. potteri*. The highly modified dorsum of segment VIII, with long expanded lateral lobes and trifid median projection is retained, although reduced in the *R. verrula*, *R. leechi*, *R. rickeri*, and *R. haddocki*, but lost in the other species of the group.

Levanidova (1980) described the morphology of *R. singularis*. She noted its phytophagous feeding habits of the species, and its association with bryophytes.

Dr. Tatyana Arefina (personal communication) reports that *R. singularis* is a rare species in southern Primorye and has been collected in only two mountain streams.

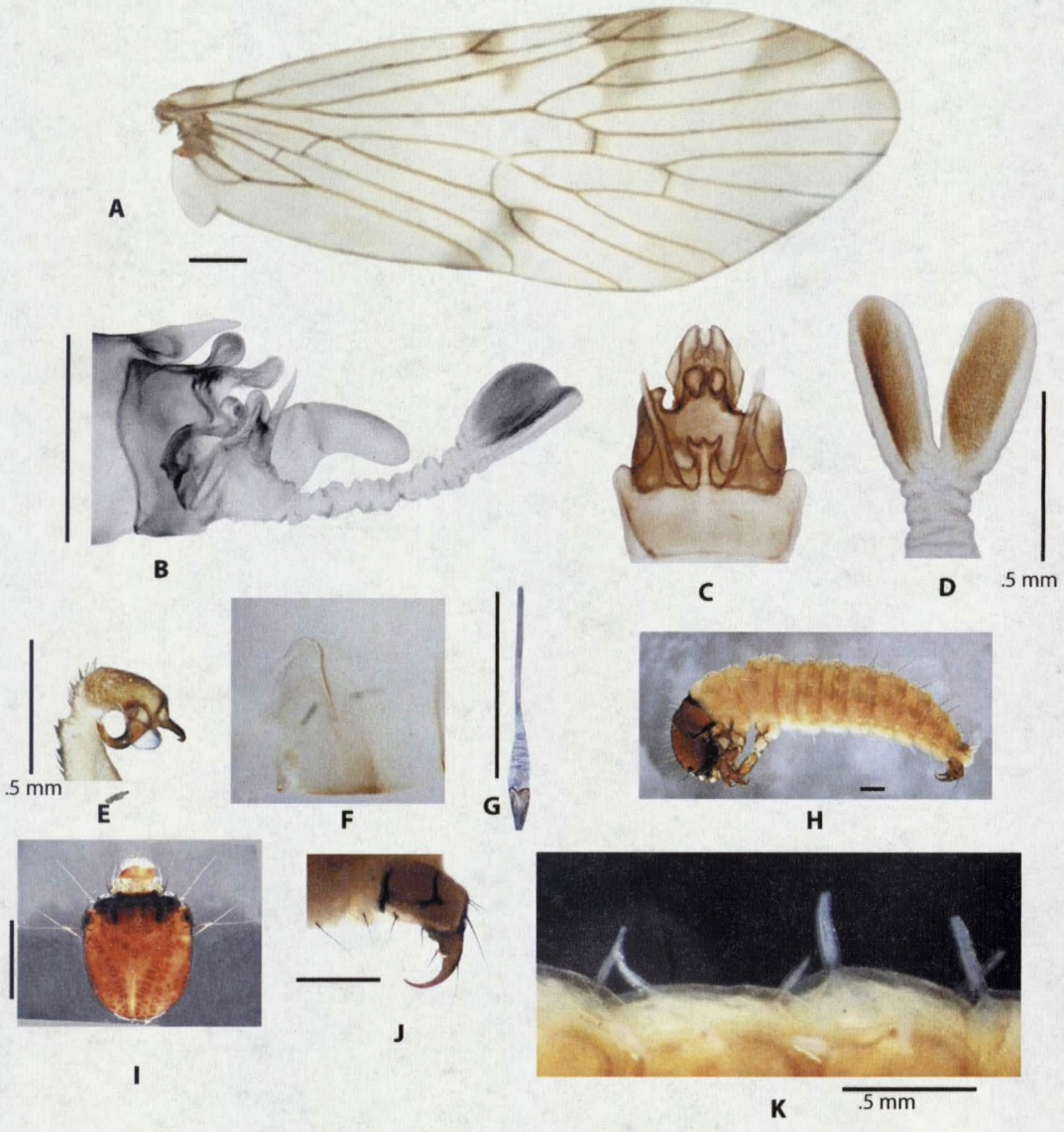

Figure 18: *Rhyacophila singularis* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male genitalia, lateral, (C) male genitalia, dorsal, (D) apex of ventral lobe of male phallic apparatus, (E) male protarsal claws, (F) lateral carina leading from scent gland of female abdominal segment V, (G) vaginal apparatus, ventral, (H) larva, lateral, (I) larval head, dorsal, (J) larval anal proleg, lateral (K) larval abdominal gills.

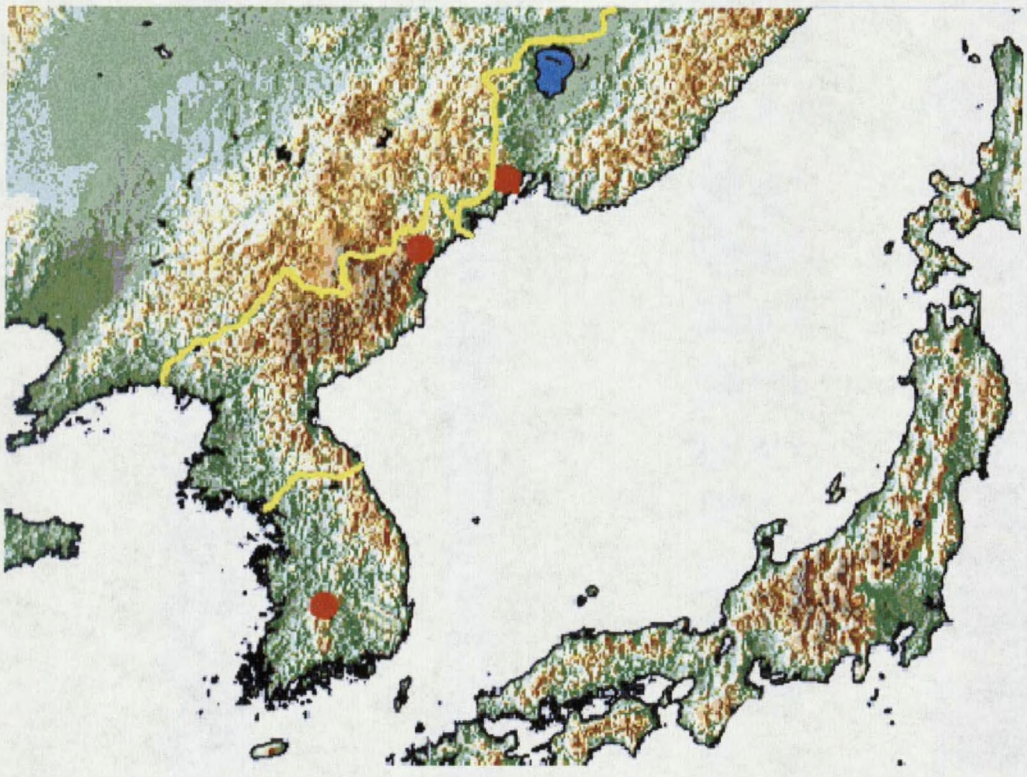

Figure 19: Distribution of *Rhyacophila singularis*.

Rhyacophila verrula Milne

Figure 20.

Rhyacophila verrula Milne, 1936: 90. Knowlton and Harmston, 1938: 286. Ross, 1944: 291. Davis, 1948: 28. Denning, 1948a: 102. Denning, 1948b: 22. Ross and Spencer, 1952: 45. Schmid and Guppy, 1952: 41. Ross, 1956: 108. Schmid, 1958: 12. Fischer, 1960: 151. Denning, 1963:245. Smith, 1968: 671. Thut, 1969: 894. Schmid, 1970: 65. Nimmo, 1971: 34. Newell and Potter, 1973: 14. Wold, 1974: 118. Allan, 1975: 1044. Denning, 1975: 954. Anderson, 1976: 28. Ellis, 1978: 204. Short et al., 1978: 13. Newell and Minshall, 1979: 40. Short and Ward, 1980: 26. Schmid, 1981: 40. Roemhild, 1982: 10. Vineyard, 1982: 74. Anderson et al.,

1984: 14. Ruiter and Lavigne, 1985: 88. Herrmann et. al., 1986: 449. Ward, 1986: 191. Erman and Erman, 1990: 10. Gustafson, 1990: 99. Williams, 1991: 112.

Rhyacophila oregonensis Ling, 1938: 62. Ross, 1944: 291.

Diagnosis. Male: dorso-lateral lobes of segment IX curved caudad, medially fused, apically bifid; subapical foretibial spur absent; inner apical spur of hind tibia modified. Female: base of segment VIII sclerotized, tapering to membranous apex; processus spermathecae rounded emargination distally; posterior process thinning apically to membranous tube. Larva: Posterior tip of frontoclypeus with pair of muscle scars. Anterior margin of pronotum with thin setae; FC_3 seta on frontoclypeus 1/2 length of FC_2 seta; pronotum with 2 sublateral setae midway along length, one at border of darkened margin and one other farther inward.

Description. Male. Forewing 11-15 mm; yellow, with bands of brown in apical ¾ of wing; crossvein between M_{1+2} and M_3 forming closed m-cell (fig. 20A). Head yellow, brown dorsally (fig. 20F), pair of triangular rounded setal warts posterad of median ocellus; small rounded setal wart posterad of each lateral ocellus; large oblong setal wart on posterior margin of head; narrow, vertical setal wart with single row of setae ventro-posterad of eye. Maxillary palps subequal in length to protibiae. Antennae brownish-yellow. Legs yellow, with yellowish-brown spines and spurs; tibial spur formula 2-4-4, subapical protibial spur absent; protibial spur smaller than meso- or metatibial spurs; inner apical meta-tibial spur modified, heavily sclerotized; distal portion thin, concave, bearing dense marginal fringe and acute spine in concave portion (fig. 20E). All tarsal claws equal in length and form. Thorax yellow laterally, dark highlights on pleura.

Mesonotum yellowish-brown dorsally, median wart with antero-lateral arms extending anterad on mesonotum. Metanotum yellowish-brown dorsally. Abdomen yellow; segment V with lateral carina leading ventrad from scent gland opening, tapering ventrad as smooth curve. Segment VIII with expanded dorso-median, apically slightly bifid lobe, flanked by a flap-like lateral lobe on each side (fig. 20C). Segment IX with narrow, short dorsal strap ventrad of which postero-dorsal edges produced as pair of large, evenly arched lobes fused medially and parted at apex; each lobe with blunt, ventral process, followed by a deep ventral incision, followed by a broad lobe, then narrowing toward venter (fig. 20B). Segment X small, dorsally convex saddle-shaped sclerite with proximo-dorsal edge articulating with ventral lobes of latero-dorsal process. Anal sclerite small, without long root; covered with minute spicules; fitting into ventral concavity of segment X. Tergal strap lightly sclerotized. Coxopodite held dorso-caudad; parallel sided. Harpago 1/3 length of coxopodite; not as wide basally; concave mesally with apical zone of spicules; apically rounded or blunt point. Phallic apparatus with long, digiform, sigmoid dorsal appendage arising from endotheca, distally coming into contact with anal sclerites; distally widened with concave apex. Phallicata arising on dorsal surface of membranous endotheca; thin tube-shaped distally; ventral lobe modified, sclerotized, apex triangular in cross section (fig. 20D).

Female. Forewings as in male; length 10-14 mm. Coloration of head, thorax, and abdomen as in male. Segment V with carina leading ventrad from scent gland opening evenly curved. Segment VIII long and tapered; basal portion sclerotized; more membranous distally; annular dilation at extremity of segment. Segment X with dorsal

sclerotized plate covering distal 2/3 of segment. Vaginal apparatus with processus spermathecae emarginate distally; lateral edges expanded slightly. Posterior process wrinkled on basal half; tapering to long thin tube at apex, lightly sclerotized (fig. 20G).

Larva. Mature larva approximately 20 mm in length. Head rounded, nearly spherical; widest at midlength; head capsule with dark muscle scars in longitudinal rows along parietal sclerites; two rows dorsally; five rows laterally (fig. 20H). Frontoclypeus short, little more than half length of head capsule; with darkened muscle scars, most posterior of which are distinctly separate; darkened coloring covering anterior margin of frontoclypeus, covering lateral margins to tentorial pits associated parietal areas around base of mandible. Frontoclypeal seta FC_1 minute, clear, curved inward; FC_2 long, subequal to width of frontoclypeus; FC_3 clear, ½ length of FC_2. Long setae around eye, anterior and lateral margins of the frontoclypeus, and posteriorly above genae. Maxillary palpus short; all segments subequal in length. Submentum reduced to pair of sclerites each at base of submental setae; median sclerite may be present in earlier instars. Mentum undivided. Mandibles short, stout and pyramidform; left mandible with three apical teeth; right mandible short with two apical teeth, single small mesal tooth with basal pencillus. Pronotum light brown with darkened muscle scars; line of 15-20 long, thin setae along anterior margin of pronotum (fig. 20I); most posterior setae longest, subequal in length of mesal length of pronotum; directed dorsally. Anterolateral corners of pronotum with rounded notch with three setae, two long, subequal in length and one shorter (about 3/5 as long) seta; 2 sublateral setae midway along length, one at border of darkened margin and one farther mesad. Forelegs broadened. Abdomen without gills or

protuberances. Anal proleg short with long scabrous setae; sclerite at base of seta PRb_4 prominent, floating in membrane posterad of basoventral hook, projecting inward as spine, giving appearance of secondary baso-ventral hook (fig. 20J), bearing stout, spine-like PRb_4 seta; baso-ventral hook prominent, dark, projecting well from basal membrane. Apico-lateral spur absent from lateral sclerite of anal proleg. Anal claw with seta 8 borne on prominent tooth-like projection.

Pupa. Length of male 10.5 mm. Length of female 12 mm. Wing sheaths reach to apex of segment IV. Antennae reach abdominal segment IX in male, segment VIII in female; scape with 3-4 black setae. Head with eight long, black dorsal setae; one submedian seta on each side posterad of median ocellus, one posterad of each lateral ocellus, and a postero-lateral pair on each side. Frons with row of three submedian setae on either side; clypeus margin narrowly rounded, three setae on each side, lateral most clear; labrum with five clear antero-lateral setae on each side; one seta on anterior margin of eye; one genal seta posterad of ventral articulation of mandible. Mandibles long and curved (fig. 20K); length of mandible apex to inner margin 2.5 times basal width of mandible; each with two basal setae, one clear, dorsad of dark brown seta; right mandible with two median teeth and approximately thirteen denticles; left mandible with single median tooth, approximately fifteen denticles decreasing in size toward apex. Pronotum with five dorsal setae on each side. Each side of mesonotum and metanotum with anterior seta and dorsal seta laterad of scutellum. Abdomen with presegmental dorsal hook plates on segments III-VI, postsegmental hook plates on segments III-V; plate spinule formula III: 4+13; IV: 10+21; V: 13+18; VI: 13 (fig. 12L). Segments I-VIII with one dark dorsal

setae at Sa_1 and Sa_2, three to four setae on pleurites I-VII, one seta at ventral Sa_2 on segments I-VIII. Legs with five long black setae on anterior face of each coxa, one apically and distally on each femur. Mesotibiae with long, silky fringe of swimming setae on the basal four segments.

Distribution. This species has a very wide distribution throughout western North America, occurring from Alaska, Yukon Territory, British Colombia, Alberta, Washington, Oregon, California, Idaho, Montana, Wyoming, Colorado, and Utah (fig. 21).

Type material studied. 1 ♂ PARATYPE- Hope Mts.; B.C. 28 VIII 1931; A.N. Gartrell (CNCI).

Other material studied. ALBERTA: 1 ♀-Portal Ck., Hwy. 93a, J.N.P.; 11/9/68, A. Nimmo (UASM)/ 1 ♀-Rapid Creek Gap, T. C. Hwy. 'Bridge'. 630 PM; A. Nimmo, 25/9/66 (UASM)/ 1 ♀-Red Earth Ck. B.N.P., T.C. Hwy.; Bridge, 930AM; 4/10/66, A. Nimmo (UASM)/ 1 l- Banff, roadside; spring on rd. to Sundance; Canyon, June 22, 1962; G.B. Wiggins et al. (ROME)/ 1 l- South Cr. at; forestry trunk rd. nr.; Nordegg, ca. 52°30'Nx; 116° 10'W. 18 JUL 1963; A.P. Nimmo (ROME)/ 1 ♂-4000'; 22-VIII-1955; W. Muckel (CNCI)/ 1 ♂-Forestry Trunk Rd. X; Ram R. 52°05'N 115°50'W; 1575m, IX-23-87 G.W.C (RWW)/ 17 l- stream crossing; Rt. 1A, 9.2 mi. S. Johnston Canyon; Cpgrd., Banff Nat.; Pk. , 29-31 July, 1969; #690266, ROME Field Party (ROME)/ 5 ♂-Red Earth Ck. B.N.P., T.C. Hwy., B.N.P 10AM; 25/8/67, A. Nimmo (UASM)/ 6 l- Loc. Dyson Creek; May 22, 1980 Coll. V. Gotceitas (UASM).

BRITISH COLUMBIA: 1 ♀-Columbia tribs of; Canoe R. Yellowhead; Hwy. 5 mi. S. Albreda; J. Furnish. IX-16-86 (RWW)/ 1 l- Goldwater R. at; Goldwater Cpgrd., Victoria; Vancouver Isl. 27-28 JUN; 1969 #690134 ROME Fld. Pty. (ROME)/ 1 ♂-Hope Mts.; B.C. 28 VIII 1931; A.N. Gartrell (CNCI)/ 1 ♂-Wellington; 12-X-1949; Richard Guppy (CNCI)/ 1 ♂, 1 ♀-Yoho Nat.; Park Kickinghorse Camp; grounds 4100' Oct. 5, 1963; G. E. Ball (UASM)/ 7 ♂-ibid., 5/Oct/63, A. Nimmo (UASM)/ 12 l- sm. stream crossing; T.C. Hwy., ca. 12.1 mi. e. western boundary Glacier; Nat. Pk., 26 July 1969; #690252, ROME Field Party (ROME)/ 2 l- B.C. : spr. run & pools; at Rt. 3, ca. 5.6 mi. W.; Fernie, 24 JUL 1970; #700434 ROM Fld. Pty. (ROME)/ 3 ♀♀-Robson Ck., Mt. Robson Pk., B.C.; 1-5PM; 8/10/67, A. Nimmo (UASM).CALIFORNIA: El Dorado County: 1 l- Rt. 89, sm strm; top Luther Pass 7500'; VIII-5-85 BW (RWW).

CALIFORNIA: Fresno County: 1 l- Rancheria Crk.; 2690m; 11 July 84; coll. J. MacDonald (CASC)/ 1 ♂-Mill Creek; T14S R27E; SE 12 Sequoia; Lake Oct. 12, 1981; coll. R. Gill (CASC)/ 1 ♂-Mill Flat Creek; at Sequoia L.; Oct 2, 1981; coll: R. Gill (CASC)/ 1 ♂-Short Hair Cr.; Court Right Lake; Oct 24, 1981; coll. R.F. Gill (CASC)/ 2 ♂♂-Bear Creek; Maxson Rd.; Oct. 24, 1981; col. R. F. Gill (CASC).

Humboldt County: 4 l- E. of Fish; L. IV-II-81 B. Lauck (RWW).

Madera County: 1 ♂-Cascadel Woods; 4-13 Sept 1983; D.J. Burdick coll (CASC)/1 ♂-ibid., 27 Sept-10 Oct 83 (CASC)/ 10 ♂♂-ibid., X/11-17 83 (CASC)/ 6 ♂♂-ibid., 13-20 Nov 83 (CASC)/1 ♂-Sugar Pine; 1-X-93 M. Hannet (CASC)/1 ♂-Central Camp; IX/28-X/9/83; J. Larson (CASC)/1 ♂-ibid., X/9-X/21/83; coll. B. Larson (CASC)/ 5 ♂♂-ibid., IX/28-X/9/83; J. Larson (CASC)/2 ♂♂-T68 R23 E25; Lewis Cr.; X/9/83-X/19/83; coll.

B. Zane (CASC)/ 1 ♂-ibid., IX/23-X/1/83 (CASC)/ 1 ♂-ibid., 20-28 Oct 83; coll. B. Zane (CASC)/ 1 ♂-ibid., 1-8 Oct. 83; B. Zane (CASC)/1 ♂, 1 ♀-Sugar Pine; 21 Oct, 1991; Mark Hannel (CASC)/1 ♂, 1 ♀-T7S R23E; SE27: Whsky Falls; Oct. 25, 1981; coll, R.F. Gill (CASC).

Placer County: 1 ♂-Creek at Pine Crest Rd.; 25 Aug 1973 Denning (CASC).

Shasta County: 1 ♂-Burney Fall; Shasta Co. Cal. Elev 2,800; d29 m6 y1947 H.P. Chandler (CASC)/ 1 ♂, 1 ♀-Creek nr. Castle Crags; State Park; 18 Oct. 1973; D.G. Denning (CASC)/ 15 ♂♂, 2 ♀♀-Old Station, Hat Cr. (ROME)/ 2 ♀♀-Hatchet Cr. at; Rt. 299 10-15-76 C. Lauck (RWW).

Sierra County: 2 l- Howard Ck. at N. Frk.; Yuba River 6 June '76; R.S. Miller colr. (MTEC).

Siskiyou County: 1 ♂-1 Mi. E. Mt. Shasta; City, elev. 4000'; X-1-1996, J.A. Powell, BL trap (EMEC)/ 3 l- Hwy.; 99, City Pk of Mt. Shasta; Headwaters Sacramento; Riv., 3500' elev., 18 June 1967; J. Wold (RWW).

Tehama County: 1 l- Spring run in Gurnsey; Cr. Cpgrd., Rt. 89, S. of; Childs Meadows; June 19, 1967, T. Yamamoto (ROME)/ 16 l, 1 ♀-Spring along Highway #89; east of Mill Creek; coll: D.E. Ruiter 23 Jan 85 (DER)/ 1 l-: Co. ENE of Goat; Hill 39°50'N 122°43'W; V-7-85: ca 5000' Courtney; Trickle; BW 87 (RWW).

Tulare County: 1 ♂-Sequoia Natl. Prk; Dorst Crk. Cmpg; 20 Sept 84; D.J. Burdick coll.(CASC).

Tuolumne County: 1 ♂-Blue Canyon; Sonora Pass; VIII-30-60; C.A.Toschi collector (EMEC).

COLORADO: Larimer County: 12 ♂♂-Stream out of Agnes Lake; near Cameron Pass, Colo; Aug 10, 1955 (CASC).

Routt County: 1 ♂-Steamboat; Springs; IX-20-41; O. Bryant (EMEC).

San Juan County: 1 l- Mill Cr.; Colo. Hwy 550; 37.6785°N, 107.7953°W, 2974 m; 16 V 1995; J. Giersch (JJGC).

IDAHO: Bear Lake County: 1 ♂, 1 ♀-St. Charles Crk.; 7 mi. W. St. Charles; 13 Sept; 86 (CASC)/ 4 l- St. Charles Creek.12 Mi. W.; St. Charles. 42°07'N; 111° 25'W; 12 July 1985 (ROME).

Boise County: 2 l- Mores Cr.; at mi. 10 cprgd.; Boise Nat. For. 4 MAY; 1981. #813123b. 10 Mile Cr. C.R. Parker (ROME).

Custer County: 1 l- Jordan Creek, trib.; Yankee Fk. Salmon R., HECLA Mining; Det. Aquatic Biology Associates, Inc.; All sites March 1996 (RWW)/ 1 ♂, 2 ♀♀-Jordan Cr Trib; Yankee Fk Salmon R; 44 26'N 114 44'W 2160m; Sunbeam Mines: RWW; 10-55-87 (RWW)/ 2 ♂♂-ibid., VIII-3-87 (RWW).

Idaho County: 1 l- Holly Crk. at Rt. 12; N.E. Lowell; 24 June 1968, Wiggins, Yamamoto, Odum (ROME)/ 1 ♂-Swamp Cr. at; Elk Summit Rd.; 46.3973°N, 114.6188°W, 1707 m; 16 VIII 2000; J. Giersch (JJGC)/ 2 ♂♂, 1 ♀ metamorphotype pupae- E. of Lolo Pass, forest rd.; Mi 5, Above Brushy Fork Cr.; 46.6248°N, 114.4954°W, 1692 m; 25 VII 2001; J. Giersch (JJGC)/ 4 ♀♀-ibid., 25 VII 2001; J. Giersch (JJGC)/ wings- Brushy Fork Bridge; SE of Lolo Pass; 46.6200°N, 114.4757°W, 1598 m; 25 VIII 2001; J. Giersch (JJGC).

Shoshone County: 3 l- spring runs along rd.; between Thompson Pass &; Wallace. 27 JUL 1981.;G.B. Wiggins. (ROME)/ 1 ♂, 6 ♀♀-Black Prince Crk.; 941001 (JJGC).

MONTANA: Beaverhead County: 10 l- Price Cr. below Guy Mine; Comet Ridge Rd., Pioneer Mtns.; 45.4658°N, 113.0668°W, 2501 m; 09 VIII 2001; J. Giersch (JJGC).

Carbon County: larval sclerites- Rock Cr.; blw Glacier Lk Trailhead; 45.0024°N, 109.5139°W, 2711 m; 11 VIII 2000; J. Giersch (JJGC).

Flathead County: 1 ♀-above Oberlin Falls, below rd.; Logan Pass, GNP; 48.6994°N, 113.7225°W, 1934 m; 22 IX 1998; J. Giersch (JJGC)/ 1 ♂-Bow Cr.; 1 Oct 81 Weaver (CASC)/ 1 ♂-Cattle Queen Cr. @ Mineral trail; 48.8201°N, 113.822°W; 27 VIII 1996(FLBS)/ 14 ♂-ibid., 27 IX 1996(FLBS)/ 1 ♂-Dolly Varden Cr.; 5 Oct 81 Weaver; coll. Phil Torchio (CASC)/ 1 ♂-Fish Creek @ Amphitheater; 48.549°N, 113.983°W; 22 VIII 1996(FLBS)/ 3 ♂♂, 1 ♀-ibid., 6 IX 1997(FLBS)/ 1 ♀-Logan Cr below road, above Oberlin Falls; 48.6995°N, 113.723°W; 24 IX 1997(FLBS)/ 5 ♀♀-Logan Cr. @ Logan Pass; 48.6969°N, 113.727°W; 1 VIII 1996(FLBS)/ 5 ♂♂-Logan Cr. @ Springhead; 48.6985°N, 113.732°W; 24 IX 1997(FLBS)/ 3 ♂♂-Logan Cr. near water tank- Logan Pass; 48.697°N, 113.725°W; 29 IX 1998(FLBS)/ 6 ♂♂, 7 ♀♀-ibid., 22 IX 1998(FLBS)/ 1 ♂-McDonald Cr. above Lake @ Bridge; 48.6386°N, 113.856°W; 1 X 1995(FLBS)/ 1 ♂-ibid., 14 IX 1996(FLBS)/ 5 ♂♂-ibid., 12 X 1995(FLBS)/ 3 ♂♂-ibid., 23 X 1996(FLBS)/ 1 ♀-ibid., 24 X 1996(FLBS)/ 17 ♂♂-ibid., 28 IX 1996(FLBS)/ 4 ♂♂-ibid., 29 IX 1996(FLBS)/ 3 ♂♂, 1 ♀-ibid., 29 VIII 1997(FLBS)/ 1 ♂-ibid., 6 IX 1997(FLBS)/ 14 ♂♂-ibid., 10 IX 1997(FLBS)/ 5 ♂♂, 2 ♀♀-ibid., 14 IX 1997(FLBS)/ 12♂♂-ibid., 23 IX 1997(FLBS)/ 1 ♀-ibid., 24 IX 1997(FLBS)/ 8 ♂♂-ibid., 26 IX 1997(FLBS)/ 1 ♀-

ibid., 16 X 1997(FLBS)/ 1 ♀-Mineral Cr. Above Floodplain; 48.7861°N, 113.805°W; 22 IX 1996(FLBS)/ 1 ♀-Mineral Creek @ gorge; 48.8067°N, 113.818°W; 13 IX 1996(FLBS)/ 3 ♂♂-Mineral Creek @ suspension bridge; 48.7582°N, 113.82°W; 22 IX 1995(FLBS)/ 20 ♂♂-ibid., 22 X 1996(FLBS)/ 11 ♂♂-bid., 24 X 1995(FLBS)/ 5 ♂♂-bid., 25 IX 1996(FLBS)/ 4 ♂♂-bid., 25 IX 1996(FLBS)/ 3 ♂♂, 2 ♀♀-bid., IX 1996(FLBS)/ 1 ♂-bid., 21 X 1997(FLBS)/ 1 ♂-Morrison CR in Logdgepole; 18 Sept 81; Weaver (MTEC)/ 1 ♀-bid., 9-1-82 (MTEC)/ 1 ♂-Packer's Roost Springbrook; 48.7449°N, 113.778°W; 25 IX 1996(FLBS)/ 1 ♀-bid., 9 X 1996(FLBS)/ 2 l- Rand Crk. @ Ashley L.; 7-14-74 (MTEC)/ 4 ♂♂-Trail CR Mid FK; Flathead R 10-9-82 (MTEC).

Gallatin County: 1 ♀-1.5 mi. W. Hyalite Res.; 11 SEPTEMBER 1995; R.S. Miller colr. (MTEC)/ 16 ♂♂, 2 ♀♀-Blackmore Cr. trap; July 88-June 1989; D.L. Gustafson (MTEC)/ 3 l- Blackmore Cr. at culvert; 1km. SW of Hyalite Res.; 45.4792°N, 110.9822°W, 642 m; 08 VII 2000; J. Giersch (JJGC)/ 6 l- ibid., 18 V 2000; J. Giersch (JJGC)/ 3 ♂♂-Little Teepee Ck; 16 Oct 77 (MTEC)/ 4 ♂♂-WFK of SFK of; Sourdough Cr; 25 Oct 1978 (MTEC).

Glacier County: 2 ♂♂-50 Mtn. area-stream near large boulders along Highline tr.; 48.8596°N, 113.867°W; 1 X 1997(FLBS)/ 8 l- E. side Swiftcurrent Pass; 300m from top, GNP; 48.7799°N, 113.7608°W, 2136 m; 05 VIII 2000; J. Giersch (JJGC)/ 17 l- Glacier Nat.; Pk., Park Cr. 14 JUL; 1969 J.M. Stauffer (ROME)/ 29 ♂♂-Kootenai Creek @ packers' camp below 50 mtn.; 48.8544°N, 113.899°W; 30 IX 1997(FLBS)/ 1 ♂-Lower Reynolds Cr@ Gorge- Logan Pass; 48.6924°N, 113.713°W; 16 X 1997(FLBS)/ 39 l- Lunch Cr. below H2O falls; Above Going to the Sun Rd.; 48.7007°N, 113.7023°W, 1991

m; 16 VIII 2001; J. Giersch (JJGC)/ 1 l- Lunch Cr. West Branch; above Going to the Sun Rd. Glacier Nat. Park; 48.7019°N 113.7032°W; 23 VIII 2000, J. Giersch (JJGC)/ 4 l- ibid., 2 VIII 2001; J. Giersch (JJGC)/ 1 ♀-Reynolds Cr. @ waterfall-Logan Pass; 48.6873°N, 113.727°W; 10 IX 1997(FLBS)/ 2 p- Seep on cliff Going to the Sun Rd.; 48.6988°N, 113.7050°W, 1930 m; 100m W. of Lunch Cr., GNP; 22 VIII 2000; J. Giersch (JJGC).

Granite County: 6 l- Skalkaho Hwy; Sand Basin Rd. fork; 46.2122°N, 113.6992°W, 1951 m; 10 VII 2001; J. Giersch (JJGC).

Lake County: 1 ♀-XI-22-69; Yellow Bay Creek; Flathead Lake; D.S. Potter (MTEC)/ 1 l- Yellow Bay; Park, Flathead L., sm.strm. 19 JUL; 1965. D. Lehmkuhl (ROME)/ 5 l- spring;run crossing For. Rd.; 129, 2 mi. N. Porcupine; Cr. Rd., S. Swan L. 2 AUG; 1981. G.B. Wiggins. (ROME).

Lincoln County: 1 l- near Troy; ASARCO Mining for Parametrix, Inc.; Stanley Creek; Aquatic Biology Associates, Inc.; 8-14-97 (RWW)/ 3 l- Near Troy; ASARCO Mining for Parametrix, Inc.; Fairway and Stanley Creeks; Aquatic Biology Associates, Inc.; 4-2-96 (RWW)/ 5 l- spring at Ross Cr.; Giant Cedars, Cabinet; Mts., s. Libby, 26 JUL; 1981. G.B. Wiggins (ROME).

Madison County: 1 ♀, 5 ♂♂ metamorphotype pupae- above Branham Lakes; S. Fork Indian Creek Headwaters; 45.5244°N, 112.0179°W, 2906 m; 02 IX 2001; J. Giersch (JJGC)/ 1 l- W. of Branham Lakes; S. Fork Indian Creek Headwaters; 45.5244°N, 112.0179°W, 2906 m; 02 IX 2001; J. Giersch (JJGC)/ 7 ♀♀-Louise Lake Outlet;

Deerlodge National Forest; 45.5971°N; 112.0463°W; 2677m; 16IX 2000; J. Giersch (JJGC).

Missoula County: 1 l- MT Hwy 12; 2.5 km N. of Lolo Pass; 46.6537°N, 114.5816°W, 1524 m; 25 VII 2001; J. Giersch (JJGC)/ 3 l- spring runs cross-;ing Rt. 12 at Lolo Pass, elev.; 5187', Missoula Co.,; 25 JUN 1968; Wiggins, Yamamoto, Smith (ROME).

Park County: 1 l- Druckmiller Lake; Outlet; 46.0320°N, 110.3066°W, 2764 m; 02 VIII 2001; J. Giersch (JJGC)/ 1 l- E. fork Hyalite Cr.; Hyalite Rec. area; 45.4386°N°N, 110.9086°W, 2374 m; 10 VI 2001; J. Giersch (JJGC).

Ravalli County: 1 l- MT. Hwy. 93; 1.6 km. N. Lost Trail Pass; 45.7049°N, 113.9339°W, 2090 m; 08 IX 2001; J. Giersch (JJGC).

NEVADA: Washoe County: 1 ♂-unnamed spr. W. of Hwy; 431 N. of L Tahoe flying nr. spr. in afternoon; X-5-96 M. Meyers coll. (EMEC)/ 2 ♂♂-ibid., X-17-99 Myers (EMEC).

OREGON: Benton County: 1 ♀-N. Fork Rock Cr.; Mary's Peak; Sept. 25, 1966; Wiggins, Yamamoto, Odum (ROME)/ 1 l- 0.6; mi. from Mary's; Peak Rd. #1296; 2440' elev.; 7 MAY 1969.J. Wold (ROME)/ 1 l- 1 mi.; off Mary's Peak Rd.; on Rd. #129616 JUN; 1968. J.&R. Wold (ROME)/ 1 l- top; of Mary's Peak,; Parker Cr. 14 JUN; 1968. J. Wold (ROME)/ 1 ♂-Parker Cr., Mary's; Peak; Sept. 24, 1966; Wiggins, Yamamoto, Odum (ROME)/ 2 l - Mary's Pk.; The Seep: Parker Cr.; 11-15-83 83; Berlese. (RWW)/ 2 l- Mary's Peak; N. Fork Rock Cr., Apr. 13, 1964; Wiggins and Scott (ROME)/ 2 l- temp. stream below; Parker Crk. on Mary's; Pk. Rd., Aug. 7, 1968; Elwin Evans, coll (RWW)/ 2 pupae- 7.1 mi. from; end pavement (old Hwy. 34); on Mary's Pk. Rd., May 7, 1969; temp stream below Parker; Falls, 2, 830' elev., 47° F; Jan Wold, Coll. (RWW)/ 4 ♂♂, 2

♀♀-Mary's Pk. campground; Parker Cr. BLT: Oct 14, 1982 (RWW)/ 6 l- Parker Falls, Mary's; Pk. Rd., Mar 12, 1963; N.H. Anderson coll. (RWW)/ 5 ♂♂, 2 ♀♀-Parker Cr. Falls; Sept 12, 1964; T.G. Marsh & C. Baker (RWW).

Clackamas County: 1 ♀-Timberline Lodge; 23-VI-1965; F. Schmid (CNCI)/ 1 l- Mt. Hood National Forest; Bull Run R., City of Portland watershed; det. Aquatic Biology Associates, Inc.; 9-16-96 (RWW)/ 1 l- Mt. Hood, 1 mi. up rd.; to timberline Lodge 45°F, June 12, 1969; Jan Wold, coll. (RWW)/ 1 ♂-Trib. Still Cr., nr. Timber; line Lodge, Mt Hood VIII-10-55 S.G. Jewett, Jr. (CASC)/ 28 l- Mt Hood, streams; crossing road to Timberline; Lodge near Government; Camp, June 12, 1967; T. Yamamoto (ROME)/ 4 l- Mt. Hood, streams; crossing rd. to Timberline; Lodge, April 18, 1964; G.B. Wiggins & R.S. Scott (ROME/ 1 l- Mt. Hood, South Fk.; Iron Crk., at Rt. 35 nr.; Government Camp; Sept. 29, 1966; Wiggins, Yamamoto, Odum (ROME).

Deschutes County: 1 ♀-Century Dr.; Devil's Lk. VII-19-85 BLT BW (RWW)/1 ♀-So. Sisters; Fall Cr. ~5500' 9-18-82 (RWW)/1 l- Century Dr.; Devil's Lk. Tyee Cr. Spring; head Aug 12, 1982 R.W. (RWW).

6 l- mouth of; Tyee Cr. at Devil's Lk.; 9-29-83 BW (RWW)/2 l- So. Sisters; Goose Cr. Headwaters. 5500'; 9-18-82 (RWW)/1 l- Tumalo; Cr. at Co. Rd. 4601 bridge, 10; mi. w. of Bend. Deschutes Natl.; For. 44°02'N x 121°16'W, 4800 ft.; Kick sample. 12-13 JUL 1991; WK Gall. ROME 912412 (ROME)/1 ♂ metamorphotype pupa- Quinn; River nr. Crane Prairie Reserv.; July 8, 1969, Jan Wold (RWW)/5 ♂♂, 1 ♀-Squaw Cr.; nr. falls 44°10'N 121°40'W; VIII-9-86 4450' Courtney (RWW).

Douglas County: 1 ♂-Mouth of Muir Cr.; trib of Rogue R.; VI-17-49. Jewett (RWW)/ 2 ♀♀-Silent Cr., Diamond; VIII-25-47; S. G. Jewett, Jr. (RWW)/ 3 p- Umpqua Nat. Forest; Headwat. Bulldog Cr. 3800-5000' elev; Coll; R.W. Wisseman, June 19, 1998; Site 10 3900' (RWW).

Grant County: 6 l- Grasshopper CK; Riffle Qual; 6-14-82 (RWW).

Hood River County: 1 l- nr; Bennett Pass, N. Fk.; Iro Crk., 4400' elev.; July 11, 1968; N. H. Anderson coll. (RWW)/ 1 l- 12; mi. S of Hood R., waterfall; N of bridge over E. fk. of; Hood R.3.VII.85 #850158; ROME Fld. Pty. (ROME).

Jackson County: 1 ♀-Union Creek; 7-VI-1965; F. Schmid (CNCI).

Jefferson County: 2 ♂♂-Metolius R.; X-4-51; S.G. Jewett, Jr. (CASC).

Josephine County: 1 l- 1.2 mi. below Oreg. Caves; Nat. Mon.: Lake Crk.; 3,650 ft. elev.; Aug. 5, 1967; J.&R. Wold (RWW).

Klamath County: 1 ♂-Crater Lake Natl. Park; Sphagnum Bog VII-31-64; J. Schuh + J. Duertrees (CASC)/ 1 ♂-Annie Springs; 7-VI-1965; F. Schmid (CNCI)/ 1 ♂, 2 ♀♀-Crater Lk. Natl. Pk.; Vidae Falls; 9-12-68; J. Schuh, R. Brown (CASC)/ 1 ♂, 2 ♀♀-22 mi. NE Bly; 1 mi. W. of Daisy Creek Camp; 9-VII-64; R. Scott, R. Rieder & Joe Schuh (CASC)/ 2 ♂♂-Boundary Spring 12-IX-68; R. Brown & J. Schuh (CASC)/ 5 l, 1 p- Crater Lake National Park; Sun & Lost Creeks, Bull Trout Project; Det. Aquatic Biology Associates, Inc.; Sun Cr. all sites Aug-Sept, 1994 (RWW)/ 9 l- ibid., 8-1-96 (RWW)/ 1 ♂-12 mi. NE Bly Long; Cr. 5200'. IX-24-67; Evans and Schuh (RWW).

Lake County: 1 ♂-Bridge Cr.; 26506 EPA. 8-84. BW (RWW).

Lane County: 1 ♂-Hack Cr. (clearcut); H.J. Andrews Epx. Fr.; 11 mi. N.E. Blue River; Grofius 10.6.71 (RWW)/ 2 ♀♀-HJA Admin Site; Lookout Cr. 44 13'N 122 20'W; 440m UV light RWW 7-7-86 (RWW)/ 1 ♂-HJA Headwat xing; McRae Cr. on 1506 359.; 4019' 7-13-78 (RWW)/ 1 ♀-HJA Mack Cr. O.G.; VIII-24-87 BLT. JFK (RWW)/ 1 ♀-HJA. 11 Mi. NE; Blue R. 10-16-78. Cooper (RWW)/ 7 ♂♂-HJA Admin Site; Lookout Cr. 44 13'N 122 20'W; 440m UV light Aug-Nov 1987 (RWW)/ 1 ♂-Lookout Cr, HJA; Oct 19, 89. N.H.A (RWW)/ 1 ♀-Mack Cr. (Old Growth); H.J. Andrews For.; 11 mi. N.E. Blue River; Grafius 9-14-71 (RWW)/ 2 ♂♂-ibid., 10-2-71 (RWW)/ 10 l- Mt. St. Helens Clearwater; +Elk Cr. Meyerhoff sites; May-June 86 (RWW)/ 4 ♂♂-Ollallie Cr. Camp, Mc;Kenzie R. Or. VII-15-52; S.G. Jewett, Jr. (CASC)/ 1 ♀-Quartz Cr.; 5 km NE Blue River 490m; Date: IX-10-86; Trap: Alder Canopy Fog (RWW)/ 3 ♂♂-Willamette Natl. For.; Rigdon Ranger District, 1991 UV Light; June 23-Aug 15, RWW det. (RWW).

Linn County: 1 ♀-Breitenbush; Oct.20, 1968 Evans (RWW)/ 1 ♂, 1 ♀-N. Fk.; Santiam Riv., Parish; Lake Rd. Sept 5, 1968; E. Evans, coll. (RWW)/ 1 ♂, 1 ♀-Upper; Soda Creek, Trib of S. Santiam R. XI-10-84; JKF (RWW)/ 1 p- 5.8 mi. NW; Quartzville Rd. on Yellowstone; Rd., vic. Green Peter Reservoir; Aug 6, 1970, Jan Wold & N. H. Anderson (RWW).

Marion County: 1 ♂-Clackamas R. @ F.S. Rd 46 xing 44° 54'N 121° 53'W 720m; 23-24.V.87 Blacklight trap; G.W. Courtney (RWW).

Union County: 2 l- 6 mi.; N.W. Elgin, 4000' elev.; July 9, 1968, Phillips Cr.; N.H. Anderson coll. (RWW).

Wallowa County: 1 ♀-Wallowa Lk.; St. Park. Sept.1, 1962. BLT; D.L. Mays (RWW)/ 9 l- Wallowa; Lk. State Pk., sm. picnic; area stream, May 30, 1970; Elwin Evans & Mike Tew (RWW).

Wasco County: 1 ♂-White AR. below; Barlow Cr. 9-25-84; Scacia (RWW).

UTAH: Cache County: 4 ♂♂, 1 ♀-Spring Hollow; Logan Canyon; 10 Oct 1974; George Knowlton (CASC).

WASHINGTON: Cowlitz County: 2 ♂♂-Weyerhaeuser artificial; stream, 3 mi. N. Lk. Merrill; Kalama R. Drainage; June 18, 1968, N.H. Anderson (RWW).

Lewis County: 1 ♀-Summit Cr. at; C.Grd., 46°42'N 121°32'W; 2350' VIII-26-86 BLT; Courtney (RWW)/ 1 l- Mt. Rainier Natl. Park; Paradise R. Can. Wye; VIII-13-86 Furnish (RWW)/ 1 l- 1.8 MI.E.; Stevens Crk.Bridge on; Stevens Canyon Rd., Mt.; Rainier Nat. Park; July 28, 1969, J.&R. Wold (RWW).

Pierce County: 5 l- Longmire, Mt.; Rainier Nat. Pk.; seepage streams crossing West; Side Rd., 2500'; 13 June 1969, #690074; ROME Field Party (ROME)/ 1 ♂-Mt. Rainier; Nat Park, White; River Camp, 22-VIII-66; D.C.& R.A. Reatz coll. (EMEC).

Skamania County: 1 ♂-Mt St. Helens; UPCW 8-2-85 (RWW)/ 1 ♀-Mt. St. Helens; Clearwater R. Log Camp 2450'; VIII-12-85 J. Bigleow (RWW)/ 1 ♂-Mt. St. Helens; Clearwater Cr. Meyerhoff; VIII-1-86 (RWW)/ 1 ♂-ibid., VIII-22-86 BLT Meyerhoff (RWW)/ 12 ♂♂, 7 ♀♀-ibid., IX-4-86; BLT: Meyerhoff (RWW)/ 4 ♂♂, 1 ♀-ibid., X-13-86; BLT: Meyerhoff (RWW)/ 2 ♂♂-Mt. St.; Helens BLT Elk Cr.; VIII-2-86 Meyerhoff (RWW)/ 5 ♀♀-ibid., IX-20-86 BLT: Meyerhoff (RWW)/ 6 ♂♂-ibid., VIII-23-86; BLT:

Meyerhoff (RWW)/ 2 ♂♂, 2 ♀♀-Mt. St. Helens; Elk Cr. Emergence; VIII-23-86 Meyerhoff (RWW).

Spokane County: 2 l- small streams at Big Spring; picnic ground on Mount Spokane; D.E. Ruiter, 9 June 1996 (DER).

Yakima County: 1 ♂, 1 ♀-Mase Cr.; IX-11-80 NHA (RWW).

WYOMING: Albany County: 3 ♂♂, 1 ♀-Lake Marie, Snowy Range mtns.; near Centennial; Aug 31, 1947 D.G. Denning (CASC).

Carbon County: 3 ♂♂-Snowy Range Mtns.; Sept 25, 1947; D. Denning (CASC).

Park County: 1 l- btwn Snow L. and Wall L.; Beartooth Plateau; 44.9856°N, -109.5549°W, 3166 m; 18 VII 2001; J. Giersch (JJGC)/ 1 ♂-Tower Cr. Yellowstone; Nat. Park; VIII-; 23-55 K.M. Fender (CASC)/ 13 l- BTH spur rd. above chain lakes; E. of Top of World Store; 44.9231°N, -109.5245°W, 2937 m; 17 VII 2001; J. Giersch (JJGC)/ 7 l- Frozen Lake inlet; Beartooth Plateau; 44.9623°N, -109.4892°W, 3109 m; 13 VIII 2001; J. Giersch (JJGC).

Discussion. Ross (1956) considered *Rhyacophila verrula* to be a very unusual species, based on the fusion of the apical band, tergal strap, and the anal sclerite. Because the anal sclerite is articulated with the apical band, rather than with the tenth tergite, Ross (1956) placed *R. verrula* in Branch 9 of his phylogeny. He also interpreted the trough-shaped ventral structure of the phallic apparatus as the fused parameres of the aedeagus. Rather than being the fused parameres, Schmid (1970) believed this sclerotized structure to be the ventral lobe of the phallic apparatus. Because of the presence of this structure, as well as the dorsal appendage of the phallic apparatus, Schmid considered this species

to belong to the invaria-branch. The secondary loss of the apico-dorsal lobe of segment IX, and the modified meta-tibial spur align this species with *R. leechi* and *R. haddocki.* The expanded dorso-lateral lobes of segment IX, small segment X, and the sclerotized ventral lobe of the phallic apparatus make *R. verrula* the sister species of *R. leechi.* These apomorphies suggest the derived condition of *R. verrula.*

Smith (1968) first described the larva of this species, showing it to have a unique morphology. The rounded, nearly spherical head, stout mandibles, and sclerite on the basoventral membrane of the anal proleg are unique in the genus *Rhyacophila.*

The wide distribution suggests a wide ecological tolerance of this species, as it populates a wider variety of running waters than other species in the verrula-group, in a wider altitudinal range. Thut (1969) reported *Rhyacophila verrula* in relatively rapid currents in the study streams, at 1.4-1.75 ft/sec. Nimmo (1971) collected *Rhyacophila verrula* from "larger, swift, deep boulder strewn mountain creeks, and occasionally from smaller, shallower pebbly creeks".

Gustafson (1990) reported *R. verrula* in highest abundance in mountain spring creeks, and also common in "warmer, more productive mountain streams; colder, less productive mountain streams; and the coldest, high mountain streams".

Of the seven species of *Rhyacophila* studied by Thut (1969), *Rhyacophila verrula* was the most abundant, with a maximum abundance of over 1000 individuals/m2. This high concentration of larvae made for a considerable contribution to the total biomass, as well as making this species an important food source for other *Rhyacophila* species in the stream.

Rhyacophila verrula is generally considered to be univoltine. Gustafson (1990) reported instars of this species throughout the year, with late instar larvae present in the winter with most adults emerging in the fall. Nimmo (1971) reported an extended flight period, from May to October, with a peak emergence from August to September. In the Oregon Cascades, Anderson et al. reported September through November emergence (1984).

14 August- 25 September emergence in Wyoming (Ruiter and Lavigne 1985)

The phytophagous feeding habits of *R. verrula* are uncommon in the genus. Smith (1968) reported gut contents to include the green alga *Prasiola sp.*, watercress, and other unidentifiable plant material. Thut (1969) also reported the food of *Rhyacophila verrula* was found to be almost entirely of plant origin, mostly from bryophytes. *Rhyacophila verrula* as 20.3% diatoms, 63.7% mosses, 10.4% filamentous algae, 3.7% detritus, and 1.9% animal parts. Thut (1969) reported that the food resources of this species change throughout the year. Epilithic diatoms, which were more abundant during the winter and early spring than in the summer, were most abundant in the guts of fourth and fifth instar larvae. Mosses made up the bulk of the diet during the winter. Thut attributed this to the fact that mosses are the most abundant food source for this species during the winter, as they are able to thrive during low light levels. Gustafson (1990) also found bryophytes to be the primary food source of *R. verrula*, the abundance of which was reflected in the abundance of bryophytes at certain sites. Though closely associated with mosses, Gustafson (1990) attributed the absence of *R. verrula* from a mossy, confined stretch of the Gallatin River to thermal or streamflow fluctuations.

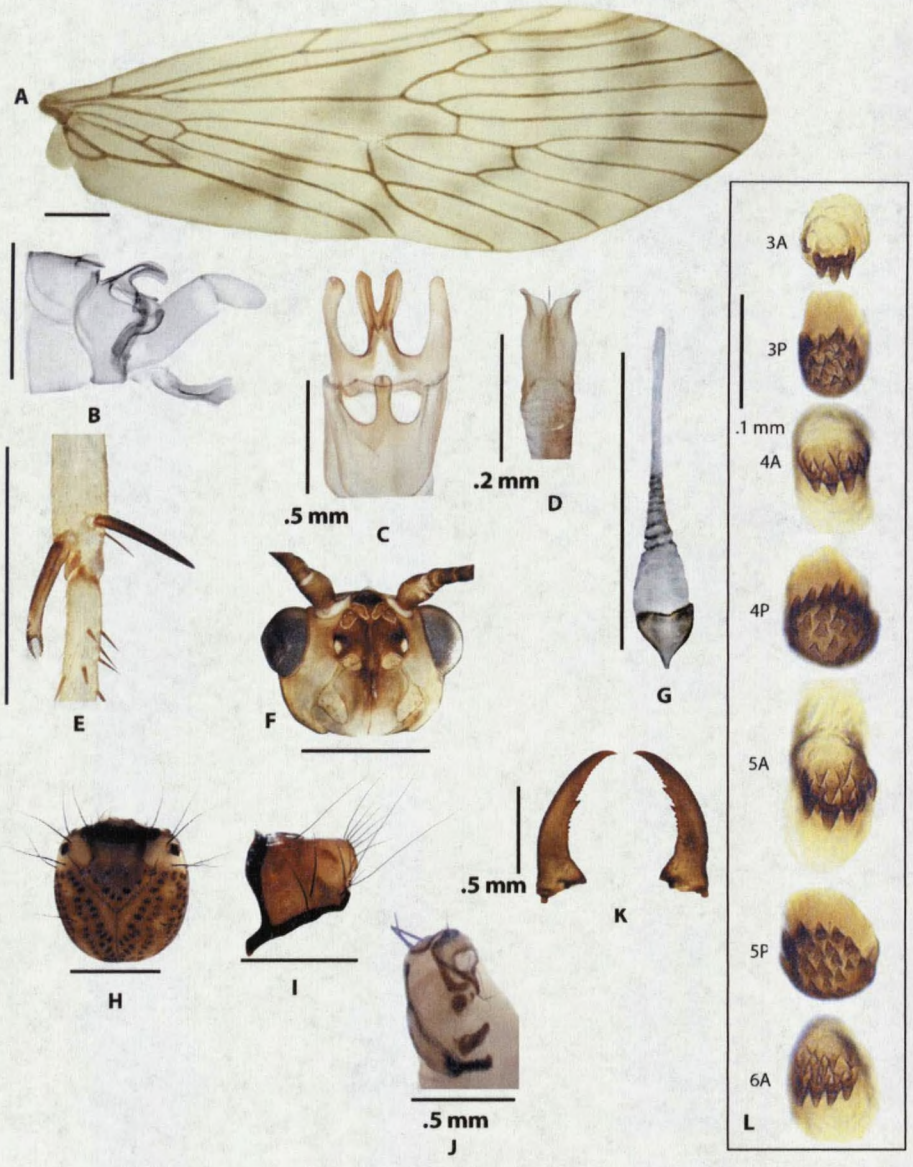

Figure 20: *Rhyacophila verrula* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male genitalia, lateral, (C) male segments VIII and IX, dorsal , (D) ventral lobe of phallic apparatus, ventral, male genitalia, dorsal, (E) modified meta-tibial spur, (F) male head, dorsal (G) vaginal apparatus, ventral, (H) larval head, dorsal, (I) larval pronotum, lateral, (J) larval anal proleg, ventral, (K) pupal mandibles, (L) dorsal hook plates of pupa.

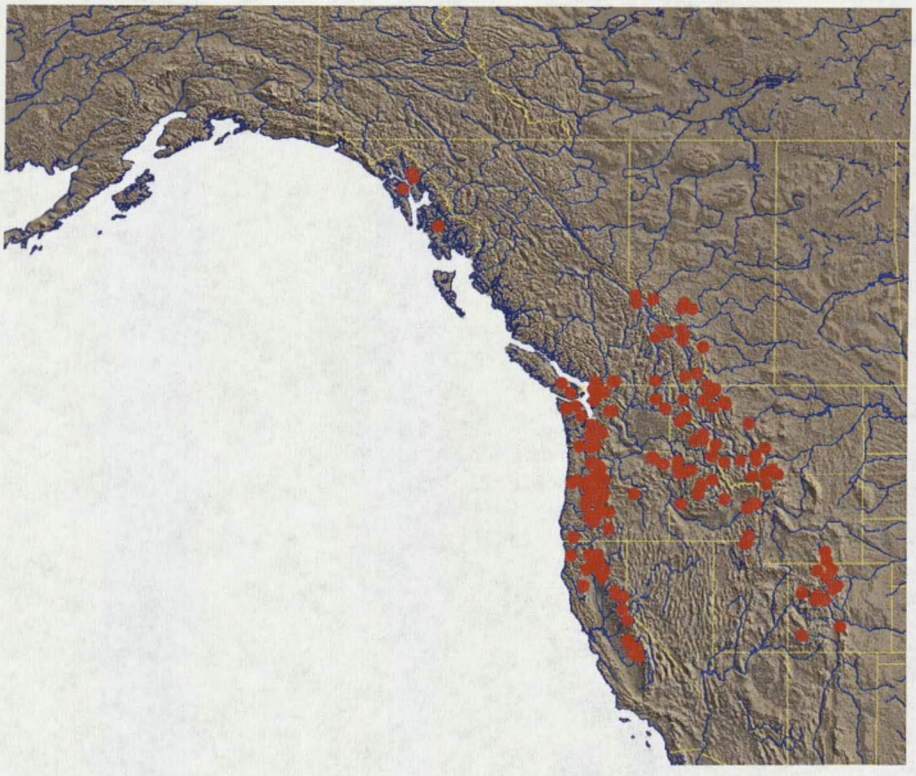

Figure 21: Distribution of *Rhyacophila verrula*.

CHAPTER 7

PHYLOGENETIC ANALYSIS OF THE VERRULA-GROUP

To determine a hypothesis of the relationship between the species of the verrula-group, a cladistic analysis was done using outgroup species in which male, female, larval, and pupal material was available. *Rhyacophila coloradensis*, *R. blarina* and *R. angelita* were used as outgroup taxa. The sibirica-group is hypothesized to be the sister taxon of the verrula-group (Schmid 1970). 44 characters representing 98 character states were used in the analysis and construction of cladograms.

Characters, states, and definitions are as follows:

Character 1. - male protarsal claws: in *R. singularis*, the anterior tarsal claw of proleg is larger than the posterior claw (fig. 18E).

(0) even:

(1) uneven.

Character 2. - inner apical tibial spur: the inner apical tibial spur of most *Rhyacophila* is unmodified, resembling other tibial spurs. In *R. verrula*, *R. leechi*, and *R. haddocki* is this character is secondarily modified in various ways (state 1).

(0) unmodified;

(1) modified.

Character 3. - male protibial subapical spur:

(0) present;

(1) reduced;

(2) absent.

While the spurs on the prothoracic legs of *Rhyacophila* tend to be smaller than the spurs on the other legs, the subapical spur may be reduced (state 1), or entirely absent (state 2), as in *R. verrula*.

Character 4. – forewing closed m-cell:

(0) absent;

(1) present.

Members of the verrula-group have a Closed m-cell in the forewing, resulting from a crossvein between M_{1+2} and M_3 (state 1).

Character 5. - Forewing r3-r4 crossvein:

(0) absent;

(1) present.

The forewing of *R. chandleri* has a r3-r4 crossvein enclosing the discoidal cell (state 1). This is autapomorphic for the species.

Character 6. - apical segment of labial palp:

(0) elongate;

(1) shortened.

The apical segment of *R. chandleri* is shortened compared to other species (fig. 6B) and somewhat concave. This character is autapomorphic for the species.

Character 7. - VIII dorsum: this character refers to whether or not the dorsum of segment VIII is expanded over the base of segment IX:

(0) not expanded, the posterior margin of tergum VIII is entire, and even across the dorsal width;

(1) expanded as a single or several lobes over segment IX (fig. 10D).

Character 8. - IX apico-dorsal lobe:

(0) present, expanded dorsally as a lobe over segment X (fig. 12B);

(1) absent, lobe is secondarily reduced (fig. 8B);

(2) expanded laterally (figs. 12B and 12C).

This character is ordered using Wagner parsimony because the presence of an apico-dorsal lobe is a synapomorphy for the invaria-twig, and is secondarily lost in some species. State 2 requires the intermediate state 1 as an intermediate state from state 0.

Character 9. - segment IX dorsal strap: the dorsum of segment IX may be wide (state 0) or narrow (state 1):

(0) wide (fig. 15C);

(1) narrow (fig. 8B).

Character 10. - IX apico-dorsal lobe apical incision.

(0) absent; apico-dorsal lobe not incised apically (fig. 12C);

(1) present; apico-dorsal lobe incised apically (fig. 18C).

Character 11. - segment X shape:

(0) plate; segment X is wide, more or less quadrate (fig. 18C);

(1) saddle; reduced to a small, ventrally concave plate covering the apical band (fig. 20B);

(2) middle points, lateral points; complexly shaped with a pair of medial points flanked by wider lobes (fig. 15D);

(3) with long dorsal extension; roughly C-shaped, with ventral ant lateral caudad extensions.

Character 12.- X plate shape:

(0) not folded (fig. 8B);

(1) folded (fig. 12C).

when segment X is shaped like plate, it may have secondary folds, having a W shape in caudal aspect.

Character 13. - X basal articulation:

(0) wide; basal articulation with segment IX wide, up-down movement restricted (fig. 15C);

(1) narrow; basal articulation narrow, dorsal, segment is more freely mobile in its up-down movement, covering the apical band (fig. 20B).

Character 14. - anal sclerites:

(0) present (fig. 8D);

(1) absent (fig. 6C);

Wagner parsimony was used, as the presence of anal sclerites is plesiomorphic for *Rhyacophila.*

Character 15. - anal sclerites fusion:

(0) separate;

(1) fused (fig.7D).

The anal sclerites may be entirely separate into two sclerites (state 1) or fused, at least at the base into a single sclerite (state 2).

Character 16. - anal sclerite root:

(0) absent;

(1) present.

In several groups beside the verrula-group, the anal sclerite has a variously shaped sclerotized base extending into segment X.

Character 17. - anal sclerite multi lobed:

(0) no (fig. 8D);

(1) yes (fig. 15D).

This character addresses whether or not the anal sclerites are simple or have bumps or lobes.

Character 18. - tergal strap: as the plesiomorphic condition of the philopotamoides-branch is a sclerotized tergal strap, this character is ordered.

(0) sclerotized (fig. 18B);

(1) unsclerotized (fig. 6C).

Character 19. - dorsal plate above phallicata:

(0) absent (fig. 8C);

(1) present (fig. 12B).

This character addresses the presence or absence of a flattened, sclerotized plate at the base of the phallicata.

Character 20. - harpago shape:

(0) concave (fig. 8B);

(1) tapered (fig. 15C);

(2) truncate.

This character relates to the shape of the harpago, depending on whether it is concave postero-dorsally (state 0), tapering to a blunt or rounded apex (state 1), or truncate and flattened at the apex (state 2).

Character 21. - dorsal appendage:

(0) absent;

(1) present (fig. 15C).

The dorsal appendage, when present, arises from the endotheca, as a sclerotized bump or an elongate process.

Character 22. - dorsal appendage length:

(0) short;

(1) long (fig. 15C).

The dorsal process, may be short and broadly attached to the endotheca (state 0), or elongate and entirely separate from the base of the phallicata.

Character 23. - dorsal appendage wrapped around phallicata:

(0) no (fig. 15C);

(1) yes (fig. 6C).

This is the autapomorphic condition of *R. chandleri*, in which the dorsal process of the phallic apparatus is expanded to the point of entirely encasing the phallicata.

Character 24. – parameres:

(0) present;

(1) absent (fig. 12B).

Character 25. - ventral lobe separation:

(0) separate from base;

(1) separate at apex (fig. 12D);

(2) not separated (fig. 15D).

The ventral lobe, when present may be entirely separate from the base at the endotheca (state 0) and present as a pair of membranous arms, present as a lobe that is separated apically as a pair of lobes (state 1), or entire along its length (state 2).

Character 26. - ventral lobe condition:

(0) membranous (fig. 15D);

(1) sclerotized (fig. 20D);

(2) reduced to lateral points (fig. 8C).

The ventral lobe can be entirely membranous (state 0), sclerotized as in *R. verrula* and *R. leechi* (state 1), or as in the autapomorphic condition of *R. haddocki*, reduced to a pair of sclerotized lateral points (state 2).

Character 27. - ventral lobe apical spines:

(0) absent (fig. 20B);

(1) present (fig. 18D).

An apical field of small, dark spines may be present on the dorsal surface of the ventral lobe.

Female characters:

Character 28. – female membrane VIII-XI:

(0) not invaginated (fig. 15E);

(1) invaginated.

This character refers to whether or not the membranous apical portion of segment VIII and base of IX is invaginated into the sclerotized basal collar of segment VIII, with the apical margin of the collar extending beyond.

Character 29. - posterior process base:

(0) not ribbed (fig. 15F);

(1) ribbed (fig. 20G).

The base of the posterior process of the vaginal apparatus may have a series of perpendicular ribs or folds, allowing for a certain degree of flexibility of the sclerite.

Character 30. - posterior process shape:

(0) short, truncate;

(1) long, tapering;

(2) short, rounded.

Larval characters:

Character 31. - larval frontoclypeus length in relation to entire head length

(0) more than half;

(1) less than half.

This character addresses the overall shape of the head capsule of larval *Rhyacophila*. When the frontoclypeus is more than half the length of the entire head capsule (state 0), the head capsule is rounded, as in members of the verrula-group, and is held in a

hypognathous position. The prognathous position of the head is reflected in species in which the frontoclypeus is less than half the length of the entire head capsule (state 1).

Character 32. - mandible teeth:

(0) on edge:

(1) on apex.

In most species of *Rhyacophila*, the teeth of the mandibles are concentrated on the dorsal or ventral cutting edges of the mandibles. In the verrula-group, the teeth of the mandibles are concentrated on the flat apex of the mandibles (state 1), and are suggestive of phytophagous feeding habits.

Character 33. - abdomen with gills:

(0) no;

(1) yes.

Character 34. - proleg lateral spur:

(0) absent;

(1) present.

This spur arises from the lateral sclerite of the anal proleg.

Character 35. - anal proleg claw ventral teeth:

(0) absent;

(1) present.

Character 36. - anterior pronontal setae:

(0) short;

(1) long, straight (fig.12I);

(2) scale-like (fig. 15J).

The anterior pronontal setae are particularly well developed in the verrula-group (state 1), and in the case of *R. rickeri*, they are modified as flattened setae resembling scales.

Character 37. – prementum:

(0) mid sclerite holds setae;

(1) mid sclerite does not hold setae;

(2) mid sclerite absent.

This character refers to the degree of reduction of the premental sclerite. This sclerite may be a rectangular, encompassing a seta on either side (state 0), reduced so that it is separate from each seta (state 1), or entirely absent with the only sclerites present at the base of the setae.

Character 38. - PRb4 sclerite:

(0) small;

(1) large (fig. 20J).

The sclerite at the base of the PRb4 seta on the ventral surface of the anal proleg may be well developed in some species, superficially resembling a secondary ventral hook.

Pupal characters:

Character 39. - pupal swimming setae:

(0) absent;

(1) present.

The tarsi of the mesothoracic legs of *Rhyacophila* pupae may have a fringe of long, silky seta used by the pupa to swim to the surface prior to molting (state 1). This character is absent in species that pupate directly within mosses (state 0).

Character 40. - 3P pupal plate: the posterior hook plate on abdominal segment III is absent in some species (state 1) As this is a reduction in the plesiomorphic state of a set of complete plates, this character is ordered.

(0) present;

(1) absent.

Character 41. - 6p pupal plate: the posterior hook plate on abdominal segment VI is absent in some species (state 1) As this is a reduction in the plesiomorphic state of a set of complete plates, this character is ordered.

(0) present;

(1) absent (fig. 20L).

Character 42. - 7a pupal plate: the anterior hook plate on abdominal segment VII is absent in some species (state 1) As this is a reduction in the plesiomorphic state of a set of complete plates, this character is ordered.

(0) present (fig. 12J);

(1) absent (fig. 15M).

Character 43. - 7p pupal plate: the posterior hook plate on abdominal segment VII is absent in some species (state 1) As this is a reduction in the plesiomorphic state of a set of complete plates, this character is ordered.

(0) present

(1) absent

Character 44. - 8a pupal plate: the anterior hook plate on abdominal segment VIII is absent in some species (state 1) As this is a reduction in the plesiomorphic state of a set of complete plates, this character is ordered.

(0) present

(1) absent

The character matrix is shown in Table 2.

Table 2. Character matrix used in the phylogenetic analysis of the *Rhyacophila* verrula-group.

Taxon\Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
R. chandleri	0	0	0	1	1	1	0	0	0	0	0	0	0	0	-	-	-	0	0	1	1	1
R. haddocki	0	1	0	1	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	1	1
R. leechi	0	1	1	1	0	0	1	2	1	1	1	-	1	1	1	0	0	1	0	1	1	1
R. potteri	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1
R. rickeri	0	0	0	1	0	0	1	0	0	0	2	-	0	1	1	0	1	1	1	1	1	1
R. singularis	1	0	0	1	0	0	1	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1
R. verrula	0	1	2	1	0	0	1	2	1	1	1	-	1	1	1	0	0	1	0	1	1	1
R. angelita	0	0	0	0	0	0	0	1	0	0	3	-	0	1	0	1	1	1	1	1	1	0
R. blarina	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0
R. coloradensis	?	0	0	0	0	0	0	1	0	0	2	0	0	1	1	1	1	1	1	2	0	-

Table 2. continued.

Taxon\Character	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
R. chandleri	1	1	2	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
R. haddocki	0	1	0	2	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
R. leechi	0	1	2	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
R. potteri	0	1	1	0	1	0	1	1	1	1	0	0	0	1	1	1	0	0	1	0	1	1
R. rickeri	0	1	2	0	1	0	0	2	1	1	0	0	0	2	1	1	0	0	1	1	1	1
R. singularis	0	1	1	0	1	0	1	1	1	1	1	0	0	1	1	0	?	?	?	?	?	?
R. verrula	0	1	2	1	0	0	1	1	1	1	0	0	0	1	2	1	1	0	1	1	1	1
R. angelita	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
R. blarina	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1
R. coloradensis	-	0	0	0	0	1	0	2	0	0	1	0	1	0	0	1	1	0	1	0	1	1

Characters 3,7,8,14,18,25,26,32,37,40,41,42,43, and 44 were ordered using Wagner parsimony for the reason explained in the description of each character. The rest of the characters were unordered, using Fitch parsimony (Wiley 1981; Wiley et al. 1991; Madison and Madison 2000; and Lipscomb 1998). The exhaustive option of PAUP* was used to search for the most parsimonious trees.

Results: Two trees were found using the exhaustive option of PAUP*, with the shortest tree requiring 71 steps, a Consistency Index (CI) of .70, a Retention Index of (RI) .73, and a Rescaled Consistency Index (RC) of .52. The tree was rooted and characters were traced in MacClade© 4.0.

Discussion of the verrula-group. The hypothetical phylogeny of the verrula-group is seen in figure 22. As in other groups of the invaria-twig, the dorsal appendage of the phallic apparatus is present (character 19, state 1). However, this character is much more pronounced in the verrula-group than in other species groups (character 22, state 1).

The verrula-group is monophyletic (fig. 22) based on the synapomorphic condition of an elongate dorsal appendage of the phallic apparatus (character 22, state 1) and the presence of a closed m-cell in the forewing (character 4, state 1). The plesiomorphic condition of this group is the membranous (character 26, state 0) undivided (character 25, state 2).

There are three groupings within the verrula-group, including the autapomorphic *R. chandleri*, the rickeri-subgroup, and the verrula-subgroup (fig. 22).

Rhyacophila chandleri is an isolated species based on three autapomorphies. The presence of the closed discoidal cell in the forewing (character 5, state 1), the short

terminal segment of the labial palp (character 6, state 1), and the dorsal appendage of the phallic apparatus which wraps around the phallicata (character 23, state 1). The absence of the apico-dorsal lobe (character 10, state 0) is either the plesiomorphic condition, or is secondarily lost due to the fusion of segments IX and X, and is likely a secondary modification of this sclerite.

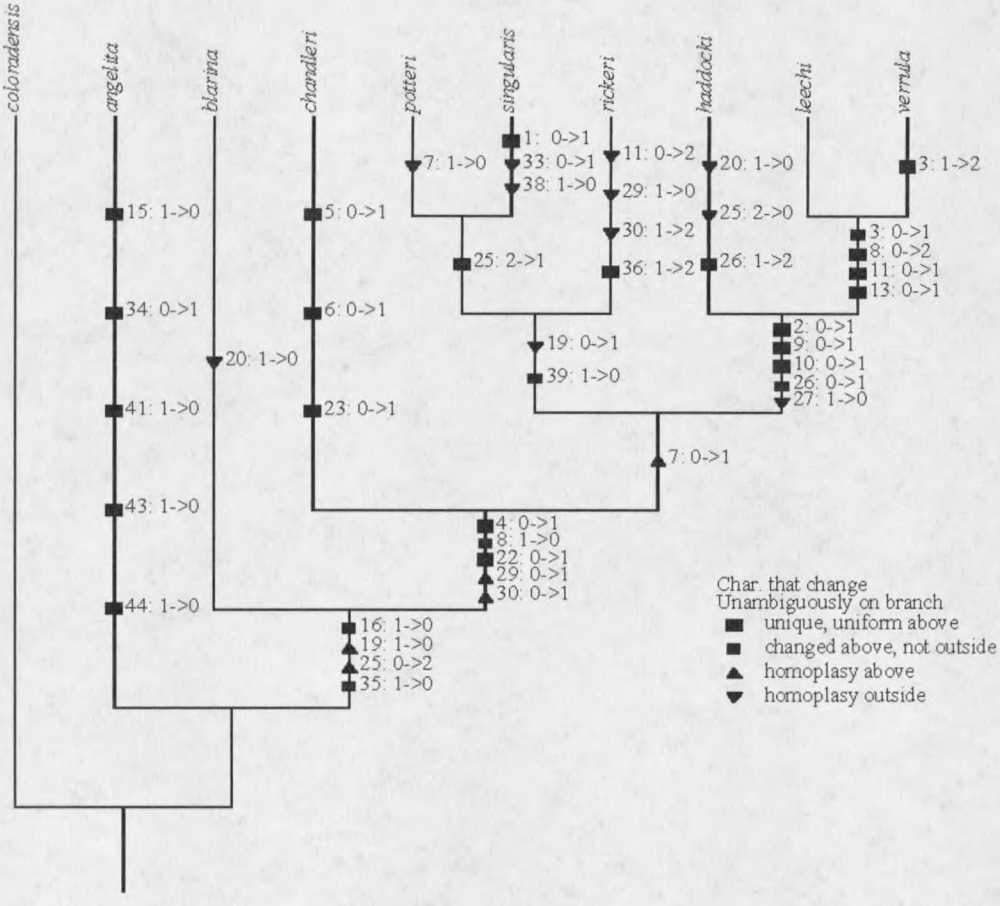

Figure 22: Cladogram showing the relationship hypothesis and monophyly of the verrula-group (only unambiguous changes shown).

The rickeri-subgroup is comprised of *R. rickeri*, *R. potteri*, and *R. singularis* (fig. 22). Synapomorphies for this subgroup are the presence of a dorsal plate at the base of

the phallicata (character 19, state 1) and the absence of mesotibial swimming setae of the pupae. In these three species, the plesiomorphic condition of the membranous ventral lobe of the phallic apparatus is retained (character 26, state 0).

Rhyacophila rickeri is basal to the rickeri-subgroup. The complex shape of tergite X (character 36, state 2), heavily sclerotized shape of the vaginal apparatus (character 30, state 2), the inflexible base of the posterior process of this structure (character 29, state 2), and the scale-like setae on the anterior margin (character 36, state 2) set this species apart from the rest of the rickeri-subgroup.

Rhyacophila potteri and *R. singularis* are sister species based on the separated apex of the ventral lobe of the phallic apparatus (character 25, state 1), with each lobe having a zone of dark spines. In contrast, the ventral lobe is apically entire in *R. rickeri* and *R. chandleri*, asymmetrically wrapping around the phallic apparatus (character 25, state 2).

The prominent apico-dorsal lobe of tergite IX also aligns *R. singularis* and *R. potteri* (character 8, state 0). This lobe is reduced to a blunt point in *R. rickeri.*

In *R. singularis* and *R. potteri*, tergite X is a complexly folded, caudally projecting plate. This segment is also in the form of a plate in *R. chandleri* and *R. haddocki*, although it lacks the folded appearance in these species.

Rhyacophila haddocki, R. leechi, and *R. verrula* form the verrula-subgroup (fig. 22) based on the modified inner apical spur of the metathoracic leg of the male (character 2, state 1), narrow tergal strap (character 9, state 1), and sclerotized ventral lobe of the phallic apparatus (character 26, state 1).

In the verrula-subgroup, the dorso-lateral edges of segment IX are sloped anterad, and the apico-dorsal lobe has been secondarily lost. In *R. verrula* and *R. leechi*, the lateral edges of the tergite are projected ventrad, then curving up into a caudad projection (character 8, state 2). This projection in *R. verrula* and *R. leechi* can be seen as a fusion of both sides of these lateral projections. Dorsally, segment IX is a thin strap, and a membranous area can be seen anterad of the fusion of the lateral lobes (character 9, state 1).

Rhyacophila leechi and *R. verrula* are sister species, aligned by the expanded lateral lobes of segment IX (character 8, state 2). In stark contrast to other species in the verrula-group, tergite X of *R. verrula* and *R. leechi* is reduced to a small, ventrally concave sclerite, covering the anal sclerites like a saddle (character 11, state 1), and the single articulation of this sclerite enabling it to move freely up and down (character 13, state 1). In addition, the subapical protibial spur of the male is reduced (character 3, state 1), being entirely absent in *R. verrula* (character 3, state 2).

The reduced condition of the ventral lobe to lateral points of *R. haddocki* is autapomorphic (character 26, state 2). The apico-dorsal lobe of *R. haddocki* is entirely reduced, and there are no lateral edges of the segment to take the place of the missing lobe, as there are in *R. verrula* and *R. leechi*. The dorso-lateral lobes of segment IX have either not been formed, or this incision was deep enough to entirely cut off the lobes in *R. haddocki*. The dorsal strap of tergite IX is very narrow, appearing to be incomplete dorsally.

Rhyacophila verrula, *R. leechi*, and *R. haddocki* form a complex of species in the verrula-group, suggesting that they evolved from an isolated ancestor from the rest of the group. The secondary loss of the apico-dorsal lobe (followed by the expansion of the dorso-lateral margins of the sclerite in *R. leechi* and *R. verrula*), modified hind tibial spur of the male, and the sclerotized endotheca are apomorphic. The modified inner metatibial spur expressed in males of *R. haddocki*, *R. verrula* and *R. leechi* resembles a similar character in some species of the family Glossosomatidae. This structure may be associated with spreading sex pheromones from the glands on segment V onto the abdomen.

The larval submentum of *R. verrula*, reduced to a pair of small lateral sclerites (character 37, state 2) is further evidence of the derived condition of this species complex. The phallic apparatus of *R. verrula*, *R. leechi*, and *R. haddocki* is also distinctive. These species lack the highly extensible endotheca seen in other members of the group, though it is basally membranous to some extent. The arms of the ventral lobe are sclerotized in *R. verrula* and *R. leechi* forming a trough that cradles the phallicata. Ross (1956) interpreted this as the fused parameres, but Schmid (1970) believed that this was the ventral lobe.

Although the knowledge of the larvae of the verrula-group is incomplete, the larvae of the associated species show distinct morphology. This includes the generally hypognathous position of the head, the shortened frontoclypeus, and the short, blunt mandibles with apical teeth rather than on the blade. This distinctive morphology reflects the phytophagous feeding habits of the group. The obligate phytophagy of the verrula-

group is unique in the genus. Smith (1968) and Thut (1969) reported that bryophytes comprise a large percentage of the food ingested by *Rhyacophila verrula*. Gut contents of *R. potteri* and *R. rickeri* that I examined were composed entirely of non-vascular plant fragments (J. Giersch personal observation). Although other species of *Rhyacophila* have been reported to be phytophagous (Botoşăneanu 1957), in no other known group is this mode of feeding exclusive to the entire lineage. I hypothesize that the verrula-group initially evolved to exploit non-vascular plants, with basal species such as *R. singularis*, *R. rickeri* and *R. potteri* having retained the association with these plants to the point of pupating directly within moss or liverwort mats. This food source may have allowed for an ecological advantage for this group, leading to speciation.

There are several reasons why phytophagy would be advantageous for the verrula-group. Mosses and liverworts play an important role in streams, offering protection, food, and substrate to aquatic macroinvertebrates. Due to decreased water velocity within bryophyte mats, they are areas of high particulate matter accumulation. This filtered organic matter can serve as a valuable food source. Bryophytes also tend to have higher invertebrate densities than the surrounding stream, particularly of species or instars small enough to move throughout the dense moss substrate (Suren 1991 and Winterbourn and Ryan 1994).

The affinity of phytophagous *Rhyacophila* species, such as *R. rickeri*, for alpine stream habitats may be due to the abundance of mosses and liverworts in these habitats. Autotrophic production is important in alpine streams, and is largely accomplished by bryophytes in the absence of higher aquatic plants (Ward 1994). The isolation of species

such as *R. potteri* to springs is related to the stability of these habitats, as high densities of mosses in Sierra Nevada springs have been correlated with habitat stability (Erman and Erman 1990).

The success and wide distribution of *R. verrula* may be attributed to its ability to exploit other food sources than bryophytes and liverworts, such as algae. This change in food requirements may have been advantageous to *R. verrula*. The isolation of several species of the verrula-group suggest that physiological needs restrict their distribution to cold, stenothermal streams and springs. The ability to exploit warmer thermal regimes has also allowed *R. verrula* to inhabit larger streams and rivers rather than being restricted to seeps and springs. While *R. verrula* is abundant in, and often restricted to spring streams and their sources (Erman and Erman 1990), this species may also be commonly collected in lower order stream sections (Gustafson 1990).

In contrast to the cocoon of *R. potteri* and *R. rickeri*, the cocoon of *R. verrula* is covered with a loose sheath of sand, stones, or plant material. As the pupal mandibles of *R. verrula* are much longer than those of *R. rickeri* and *R. potteri*, future data on the morphology of the pupae of these three species should shed light on the relationship of *R. leechi* and *R. haddocki* to the other species in the group.

Biogeography of the verrula-group

The current phylogeny and distribution of *Rhyacophila* species of the verrula-group may have largely been driven by isolation of disjunct populations following Pleistocene glaciation. At the peak of the Pleistocene glaciation, the Cordilleran ice sheet

largely covered Canada and part of the western United States, and the Laurentide ice sheet covered much of north-eastern North America (Pielou 1991). The land masses underneath the ice were devoid of insect life, and only after the ice fields retreated did animals recolonize the previously inaccessible habitats (Nimmo 1971). As the climate changed, heat intolerant species may have followed vertical or longitudinal thermal gradients (Britten et al. 1994). Following Pleistocene glaciation, species from glacial refugia near the edges of the ice could have followed the cold stream temperatures north and to higher elevations, eventually isolating populations in discontinuous habitats that were separated by low lying areas (Kavanaugh 1988). This isolation provided an opportunity for speciation as gene flow between isolated populations was severed (Freeman and Herron 2001).

Ancestors of the verrula-group likely spent the Pleistocene south and along the coastal margins of the ice sheets in western North America, with small populations isolated in glacial refugia. Nimmo (1971) hypothesized that the source for most post-Pleistocene recolonization of *Rhyacophila* species in Alberta was south of the ice sheets, with populations moving into Alberta as the ice melted. Pike (1980) also reported that most of the tundra-inhabiting species of butterflies recolonized Alberta from south of the glacial ice, from northern Washington, Idaho and Montana. During the Pleistocene, the area between the Cordilleran and Laurentide ice sheets was also open and provided a refugium for many species, and coastal refugia also existed along the Pacific Northwest as sea levels were lower during the Pleistocene (Pielou 1991). Kavanaugh (1988) reported that coastal refugia existed in the Aleutian Islands, Southeastern Alaskan

panhandle, Queen Charlotte Islands, the Olympic peninsula, Vancouver Island, Northern Cascades, Klamath Mountains, and the Sierra Nevada.

Several species of plants and animals are hypothesized to have originated from glacial refugia in Alberta. A refugium near Mountain Park, Alberta was first proposed by Packer and Vitt (1974) as a source for endemic alpine plants in the region, and was hypothesized as a refugium for tundra butterflies (Pike 1980). In a study of the North American fish fauna, Crossman and McAllister (1986) hypothesized the presence of a refugium near Waterton Lake, although the location of this refugium may correspond with that of the Mountain Park refugium.

Levanidova (1980) hypothesized that the verrula-group originated in Asia, then dispersed to the Nearctic when an ancestor of *R. singularis* migrated across Beringia, giving rise to Nearctic members of the verrula-group. My phylogenetic hypothesis (fig. 22) of the verrula-group is not congruent with her hypothesis of an eastern origin for the verrula-group, as my phylogenetic reconstruction shows *R. chandleri* and *R. rickeri* to both be basal to *R. singularis*. Therefore, the verrula-group likely originated in North America, with *R. singularis* likely being the result of a secondary dispersal of the group to Asia (fig. 19).

In North America, *Rhyacophila chandleri*, the basal species of the verrula-group, is a highly autapomorphic species which may have originated from an early member of the group that experienced isolation in northern California and southern Oregon (fig. 7).

Although *R. rickeri* occurs from Alaska to Oregon (fig. 16), it is restricted to very cold, alpine habitats. This species may have passed the Pleistocene in cold, proglacial

streams along the terminal southern and coastal refugia at the margins of the ice sheets. Populations could have followed the cold stream temperatures up in latitude and altitude as temperatures warmed, becoming isolated to glacial streams and alpine springs on mountain peaks of western North America.

Rhyacophila potteri may have evolved from an isolated population of the verrula-group along the Montana/Idaho border and southern British Columbia and Alberta (fig. 13). Perhaps because of ecological constraints such as temperature, or perhaps even host distribution, *R. potteri* could have been confined to its present distribution in cold, mossy springs and seeps after glaciation. *Rhyacophila singularis*, the sister species of *R. potteri*, evolved from a population of the verrula-group that was isolated to the far east Asia by rising sea levels following the melting of Pleistocene ice caps (fig. 19).

The verrula-subgroup, comprised of *R. haddocki*, *R. leechi* and *R. verrula,* radiated from a common ancestor of the rest of the verrula-group. After glaciation, *R. haddocki* may have evolved from an ancestor that was unable to tolerate warm stream temperatures and was therefore ecologically isolated to springs (fig. 9). The sister species *R. leechi* and *R. verrula* likely evolved as species that had wider ecological tolerances, with *R. leechi* being isolated to headwaters of the coastal ranges of Oregon and northern California (fig. 11). In contrast, *R. verrula* may have evolved as a species with a still wider ecological tolerance that enabled it to exploit warmer streams, resulting in a wider distribution (fig. 21).

I predict that further collecting in small alpine or spring-fed streams in the Pacific Northwest and far east Asia will yield the pupae of the yet unassociated species of the

verrula-group. According to Dr. Tatyana Arefina (personal communication), pupae of *R. singularis* have not been collected. This may be due to the fact that this is a rare species, or, in light of the new discovery of *R. rickeri* pupae in liverwort mats and *R. potteri* pupae in moss mats, it is probable that *R. singularis* has therefore not been collected because collectors have used standard benthic collection protocols that concentrate on sampling cobbles in riffles of larger streams.

CHAPTER 8

REVISION OF THE ALBERTA-GROUP

History of the concept of the group

Ross (1956) considered the male genitalia of the alberta-group to be plesiomorphic, having a simplified aedeagus with long parameres, large anal sclerites, simplified tenth tergite and unsclerotized tergal strap of *R. alberta* Banks and *R. tucula* Ross. Denning (1965) described *R. glaciera* Denning, but was unable to place the species in a phylogenetic context. Schmid (1970) included *R. kincaidi* Schmid and *R. glaciera* Denning in the group, but saw the placement of the alberta-group differently than Ross (1956). Schmid (1970) placed the alberta-group in the castanea-twig of the philopotamoides-branch. While he considered the castanea-twig to be the most plesiomorphic of the philopotamoides-branch, he believed that the carolina- and alberta-groups are the most apomorphic of the castanea-twig.

Schmid's (1970) hypothesis proposes that the castanea-twig originated in Asia, with two secondary dispersals to the Nearctic. Schmid (1970) also hypothesized that the carolina-group is derived from the castanea-group and the alberta-group arose from the annulicornis-group. He considered these two groups to be the philopotamoides-branch, due to the presence of the apico-dorsal lobe of IX and the sclerotized tergal strap of other groups within the castanea-twig. Therefore, while it is difficult to place the alberta-group in the philopotamoides-branch by itself, it is possible to do so in the context of the most closely related group, the annulicornis-group, which Schmid (1970) considered to be the

precursor of the alberta-group. Schmid's (1970) evidence for the alberta-group as arising from the annulicornis-group include the presence of modification and secondary reduction of several characters in the alberta-group. The phallic apparatus of the annulicornis- and alberta-groups are both simple, with thin parameres tipped by spines, flanking a thin, tube-like phallicata. However, the general structure of the phallic apparatus of these two groups differs in that the annulicornis-group has a ventral plate extending below the phallicata. This plate has been secondarily lost in the alberta-group. Schmid also interpreted the shape of segment X of the alberta-group to be a modification of that of the annulicornis-group. In the annulicornis-group, tergite X is composed of two long, thin parts, articulated one against the other: a long, thin horizontal part articulated against a vertical part. In both the annulicornis- and alberta-groups, segment X is articulated anterad with segment IX, and it can rock downwards and be invaginated entirely into the segment.

Diagnosis of the castanea-twig (translated from Schmid 1970):

Segment IX without apical dorsal lobe, strongly shortened latero-ventrally; segment X small, in vertical position, apical dorsal angles prominent. Anal sclerites present as small button-shaped sclerites; apical band small, with apparent median tongue, arms thin and median section small; tergal strap very long and narrow; very long phallic apparatus, strongly invaginated in abdomen and equipped with dorsal appendage; phallicata slim; ventral lobe of the aedeagus a broad well sclerotized plate, of complex form, largely distant from aedeagus, equipped with thin lateral arms.

New diagnosis of the alberta-group

Male: Segment V with scent gland opening on small tubercle. Segment IX dorsally sclerotized, elongate, domed at mid-portion, tapering to thin apex; ventral portion lightly sclerotized; lobes flanking anal sclerites. Anal sclerites large, paired, horizontal plates. Tergal strap membranous. Phallicata apically acuminate. Parameres simple, with apical spines. Female: Segment V with scent gland opening on small tubercle. Base of segment VIII sclerotized collar, apical portion invaginated within. Larva: Short, finger-like gills on mesothorax, metathorax, and segments I-VIII of abdomen. Pupa: Abdomen with anterior hook plates on segments VI and VIII. Posterior hook plates wider than anterior plates.

In lateral view, tergite X in the alberta-group is roughly triangular, dorsally domed, and tapering to an acute apex. The sclerite is composed of two sections, the dorsal section being well sclerotized and the latero-ventral portion being more lightly sclerotized and is in the form of a pair of vertical plates that flank the anal sclerites. *Rhyacophila alberta*, *R. tucula* and *Rhyacophila* n. sp. have the subdivided tergite X, which may be a remnant of the secondary division of the tergite exhibited by members of the annulicornis-group. This character is not present in either *R. kincaidi* or *R. glaciera.*

In contrast to the small anal sclerites of the annulicornis-group, those of the alberta-group are massive, vertical plates, that are fused basally, diverging apically. This paired structure of the anal sclerites is typical of the philopotamoides-branch. The shape of the root of the anal sclerites is complex, set deeply within segment X.

The tergal strap, present and well sclerotized in the annulicornis-group, is reduced and membranous in the alberta-group, in which the apical band has also been expanded into a pair of large, desclerotized lobes.

Species included in the alberta-group

R. alberta Banks: placed by Ross (1956)

R. glaciera Denning: placed by Schmid (1970)

R. kincaidi Schmid: placed by Schmid (1970)

R. tucula Ross: placed by Ross (1950)

Rhyacophila new species

Table 3. Species included in the *Rhyacophila* alberta-group, showing previously described and recently associated life stages.

Species	male	female	larva	pupa
R. alberta	■	■	▨	▨
R. glaciera	■	■	▨	▨
R. kincaidi	■	■	■	■
R. tucula	■	■	■	■
R. new species	▨	▨	▨	▨

■ previously described
▨ recent association

Biology summary

The alberta-group is considered to be predaceous based on the morphology of the larvae (Smith 1968). *Rhyacophila kincaidi* and *R. glaciera* are confined to cold alpine streams (Schmid 1970). The distribution of *R. tucula* is wide in the western United States, centered in the coastal states. The distribution of *R. tucula* overlaps with *R. alberta* in the

Rocky Mountains, although *R. alberta* occurs at higher elevations. *Rhyacophila* n. sp. is isolated to colder streams in the Sierra Nevada and Siskiyou mountains.

Key for the identification of males of the alberta-group

1. Harpago with deep incision (fig. 27B).....2

1' Harpago without deep incision, margin generally entire (fig. 29B).....3

2. Harpago with deep, triangular shaped incision; mesal face of dorsal lobe entirely covered with spicules, expanded anterad onto mesal face of coxopodite (fig. 27B).....

.....*R. kincaidi* Schmid

2' Harpago with deep, U-shaped incision; mesal face of dorsal lobe of harpago with two zones of spicules, not expanded reaching mesal face of coxopodite (fig. 25B).....

.....*R. glaciera* Denning

3. Dorsal lobe of harpago triangular; segment X with single apico-dorsal spine (fig. 23B)

.....*R. alberta* Banks

3' dorsal lobe of harpago elongate; segment X with pair of apico-dorsal spines (fig. 29B)

.....4

4. Ventral lobe of harpago triangular; parameres without subapical bulge (fig. 29B).....

.....*R. tucula* Ross

4' Ventral lobe of harpago rectangular basally, apically narrowed; apex of parameres with subapical bulge (fig. 31B).....*Rhyacophila* n. sp.

Key for the identification of females of the alberta-group

1. Sclerotized basal portion of segment VIII with postero-ventral edge concave in lateral view.....*R. kincaidi* Schmid

1' Sclerotized basal portion of segment VIII with ventral edge smoothly angled from anterior to posterior margin in lateral view.....2

2. Posterior margin of sclerotized venter of segment VIII evenly rounded.....3

2' Posterior margin of sclerotized venter of segment VIII acute.....4

3. Posterior process of vaginal apparatus short, truncate.....*R. glaciera* Denning

3' Posterior process of vaginal apparatus long, narrowing apically, with an apical rounded head.....*R. tucula* Ross

4. Posterior margin of sclerotized venter of segment VIII produced as a triangular projection.....*R. alberta* Banks

4' Posterior margin of sclerotized venter of segment VIII extended caudad as an elongate, nearly parallel-sided extension.....*Rhyacophila* n. sp.

Key for the identification of larvae of the alberta-group

1. Posterior margin of frontoclypeus with distinct muscle scars.....

.....*R. alberta* Banks, *R. tucula* Ross, *Rhyacophila* n. sp.

1' Posterior margin of frontoclypeus with dark coloring obscuring individual muscle scars.....*R. glaciera, R. kincaidi*

Rhyacophila alberta Banks

Figure 23.

Rhyacophila alberta Banks, 1918: 21. Banks, 1919: 3. Dodds and Hisaw, 1925: 386. Ulmer, 1932: 209. Betten, 1934: 135. Milne, 1936: 98. Ross, 1944: 291. Ross, 1950: 261. Ross, 1956: 76. Schmid, 1958: 13. Fischer, 1960: 70. Ross, 1965: 591. Schmid, 1970: 55. Nimmo, 1971: 19. Newell and Potter, 1973: 13. Allan, 1975: 1044. Ellis, 1978: 204. Newell and Minshall, 1979: 39. Schmid, 1981: 19. Vineyard, 1981: 98. Ward, 1981: 380. Roemhild, 1982: 10. Vineyard, 1982: 74. Ruiter and Lavigne, 1985: 84. Herrmann et al., 1986: 449. Gustafson, 1990: 99.

Rhyacophila mirus Denning, 1948b: 21. Ross, 1950: 261 (synonymy).

Diagnosis. Male: segment X domed at center, apico-dorsal carina leading to single spine at apex; parameres thin, well sclerotized, distally with abrupt concave ventral lobe ventrally covered by stout spines; harpago with triangular, caudad directed ventral lobe covered with patch of spines and dorsal triangular lobe directed meso-anterad. Larva: muscle scars distinct on posterior margin of frontoclypeus, finger-like gills on mesothorax, metathorax, and segments I-VIII of abdomen.

Description. Male. Forewing length 9.5-12 mm; light brown with darker brown irrorate pattern. Head brown, setal warts lighter; frons brown, setal warts rounded, ventrally concave; large rounded triangular setal wart posterad of median ocellus, with postero-lateral lobes; small rounded setal warts postero-mediad of lateral ocelli; posterior setal wart horizontal, oblong. Thorax light brown dorsally, pleurites lighter, darker highlights. Antennae brown. Legs yellowish brown, tibiae lighter apically beyond subapical spur. Spur formula 3-4-4; spurs and spines light brown; apical protibial spurs shorter than on other legs. All tarsal claws identical in size and form. Abdominal tergites yellow, sternites darker. Segment V scent gland opening on small tubercle. Venter of abdominal segments VII and VIII with sharp spine. Segment IX rectangular in dorsal half, posterior margin of ventral half laterally thinned by rounded excavation to receive coxopodite. Segment X dorsal portion in lateral view thin proximally and apically, domed at center, small depressions dorsally; apico-dorsal carina leading to single spine at apex; ventral portion lightly sclerotized, bilobed, cleft dorso-ventrally, flanking anal sclerites. Anal sclerites large horizontal plates, fused at base, cleft apically. Phallic complex with phallicata medially bulbous, tapering to thin shaft; parameres thin, well sclerotized, distally with concave ventral lobe, ventrally covered by about six stout spines, single spine toward apex, most proximal spines curved caudad, following contour of paramere lobe. Coxopodite rectangular, mesally concave, more so at base. Harpago with triangular, caudally directed ventral lobe, covered with patch of spines; dorsal lobe triangular, directed meso-anterad onto mesal face of coxopodite, covered with patch of spicules.

Female. Wings, head, thorax, and base of abdomen as in male. Base of segment VIII a heavily sclerotized collar; venter projecting caudad as stout, triangular tooth; distal membranous portion invaginated within basal collar. Processus spermathecae of vaginal apparatus quadrate. Posterior process flexible at midlength, with lateral sclerotized rods that do not meet at truncate apex.

Larva. Mature larva approximately 12 mm. Head wedge shaped, narrowing in anterior half, light brown with darkened muscle scars dorsoposteriorly; frontoclypeus with distinct muscle scars concentrated on hind margin; maxillary palpus stout, second segment slightly longer than first. Left mandible with single apical tooth, one subapical tooth, mesal margin smooth. Right mandible with one apical tooth, one small mesal tooth. Pronotum brown with several darkened muscle scars posteriorly. Mesothorax with one pair of small single gills on dorsum. Metathorax with two pairs of single gills on dorsum. Abdomen with four pairs of single gills on segment I-VI, three pairs of single gills on segment VII, and small, single, vestigial gill pair of gills on segment VIII. Anal proleg with baso-ventral hook; no apico-lateral spur. Anal claw with two large, stout ventral teeth posterad of weakened break in claw.

Pupa. Length of male 9.5 mm; length of female 10 mm. Wing pads reach abdominal segment IV in male and female. Antennae reach abdominal segment X in male, segment VI in female; scape with 3-4 black setae. Head with eight long, black dorsal setae; one submedian seta on each side posterad of median ocellus, one posterad of each lateral ocellus, postero-lateral pair on each side. Frons with row of two submedian setae on either side; clypeus short and apically truncate, three dark antero-lateral setae on

each side. Labrum with five antero-lateral setae on each side; one seta on anterior margin of eye; one short genal seta posterad of ventral articulation of mandible. Each mandible with two dark basal setae; length of mandible apex to inner margin 1.7 times basal width of mandible; right mandible with three basal teeth, row of smaller denticles leading to apex; left mandible with two large basal teeth with three smaller teeth between, row of smaller denticles leading to apex. Pronotum with five dorsal setae on each side. Each side of mesonotum and metanotum with one anterior seta and one dorsal seta laterad of scutellum. Dorsal presegmental hook plates on segments III to VII, postsegmental hook plates on segments III to V; approximate plate spinule formula: III: 11+26; IV: 18+29; V: 31+41; VI: 22+0; VII: 21+0. Abdominal segments I-VIII with one dark dorsal seta at Sa1 and Sa2, three to four setae on pleurites I-VII, one seta at ventral Sa_1 and Sa_2 on segments I-VIII. Legs with five long black setae on anterior face of each coxa, one distally on each femur. Swimming setae on mesotarsal segments I-IV.

Distribution. Alberta, British Columbia, Alaska, Colorado, Idaho, Utah, and Wyoming (fig. 24).

Type material studied. None. Type repository: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Other material studied. ALBERTA: 1 ♂- Banff; 5-IX-1922; C.B.D. Garrett (CNCI)/1 ♂, 1 ♀- Banff, Consolidation Ck.; VIII-3-69 C.M. Yarmoloy (CASC)/1 ♂, 1 ♀ mtype pupa- Ck. n. of Pass,; S. of Mtn. Park.; 28 Sept. 1975; A.P. Nimmo (ROME)/2 ♂♂- Rapid Creek Gap; T. C. Hwy. 'Bridge'. 630 PM; A. Nimmo, 25/9/66 (UASM).

IDAHO: Idaho County: 2 ♂♂- IX-10-71 Big Creek; N. Savage Pass; Elk Summit Road; D.S. Potter, R. A. Haick (CASC)/7 ♂♂- E. side Grave Peak; outlet of 2nd lake; 46.3885°N, 114.7213°W, 2256 m; 16 VIII 2000; J. Giersch (JJGC).

MONTANA: Broadwater County: 1 l- Spring Creek; N. Fk. Deep Creek Rd.;46.3813°N, 111.2222°W, 1828 m; 12 VII 2000; J. Giersch (JJGC).

Flathead County: 1 ♂- Cattle Queen Cr. @ Mineral trail; 48.8201°N, 113.822°W; 27 IX 1996(FLBS)/ 1 ♂, 1 ♀- Gateway Cr. 11 AUG 80 (MTEC)/ 1 ♀- Logan Cr below road, above Oberlin Falls; 48.6995°N, 113.723°W; 10 IX 1997(FLBS)/ 1 ♀- ibid., 16 X 1997(FLBS)/ 1 ♀- ibid., 24 IX 1997(FLBS)/ 3 ♀♀- ibid., 24 IX 1997(FLBS)/ 1 ♂- ibid., 22 IX 1998; J. Giersch (JJGC)/ 8 ♀♀- Logan Cr. @ Logan Pass; 48.6969°N, 113.727°W; 1 VIII 1996(FLBS)/ 1 ♀- Logan Cr. @ sourcepond, above springhead; 48.6988°N, 113.732°W; 24 IX 1997(FLBS)/ 1 ♀- Logan Cr. @ Springhead; 48.6985°N, 113.732°W; 9 IX 1994(FLBS)/ 9 ♂♂, 9 ♀♀- Logan Cr. near water tank- Logan Pass; 48.697°N, 113.725°W; 22 IX 1998(FLBS)/ 1 ♂- McDonald Cr. @ Logan Cr.; 48.7249°N, 113.763°W; 16 X 1997(FLBS)/ 6 ♂♂, 1 ♀- ibid., 48.7249°N, 113.763°W; 6 IX 1997(FLBS)/ 1 ♂- McDonald Cr. above Lake @ Bridge; 48.6386°N, 113.856°W; 14 IX 1996(FLBS)/ 1 ♂- ibid., 24 VIII 1997(FLBS)/ 1 ♂- Mineral Creek @ suspension bridge; 48.7582°N, 113.82°W; 25 IX 1996(FLBS)/ 1 ♂- ibid., 27 IX 1996(FLBS)/ 1 ♀- ibid., 28 VIII 1996(FLBS).

Glacier County: 5 l- Bullhead Lake inlet strm; E. side Swiftcurrent Pass, GNP; 48.7803°N, 113.7422°W, 1656 m; 05 VIII 2000; J. Giersch (JJGC)/ 1 ♀- Kennedy Cr. @ Pioa Lake outlet; 48.8516°N, 113.604°W; 23 VIII 1997(FLBS)/ 8 ♂♂- Kootenai Creek

@ packers' camp below 50 mtn.; 48.8544°N, 113.899°W; 14 IX 1996(FLBS)/ 7 ♂♂- ibid., 30 IX 1997(FLBS)/ 1 ♀- Lower Reynolds Cr@ Gorge- Logan Pass; 48.6924°N, 113.713°W; 14 IX 1997(FLBS)/ 4 l- Lunch Cr. below H2O falls; Above Going to the Sun Rd.; 48.7007°N, 113.7023°W, 1991 m; 16 VIII 2001; J. Giersch (JJGC)/ 4 p- ibid., 16 VIII 2001; J. Giersch (JJGC)/ 1 l- Reynolds Cr.; Logan Pass, GNP; 48.6872°N, 113.7294°W, 2075 m; 17 VIII 2001; J. Giersch (JJGC).

Madison County: 1 ♀- Louise Lake Outlet; Deerlodge National Forest; 45.5971°N; 112.0463°W; 2677m; 16IX 2000; J. Giersch (JJGC)/1 l- Rossiter Cr. at Gravelly Range Rd.; 44.8733°N, 111.8419°W, 2675 m; 15 VIII 2001; J. Giersch (JJGC)/3 l- Spring Cr. E. facing base of Black Butte; Gravelly Range; 44.9023°N, 111.8441°W, 2896 m; 19 VII 2001; J. Giersch (JJGC)/3 ♂♂, 2 ♀♀ metamorphotype pupae- Beaverhead/Deerlodge F.R.237; 3 km NE of Black Butte, Standard Cr. hdwtrs; 44.9110°N, 111.8127°W, 2682 m; 30VIII2001; J. Giersch (JJGC).

Discussion. This species is closely related to *R. tucula* and *Rhyacophila* n. sp., but differs in the sharp dorso-apical spine on tergite X, shape of the harpago, and the very bulbous subapical area of the parameres. The parameres of *Rhyacophila* n. sp. also have a bulge, but it is not as distinct as in *R. alberta*. Dorsally, segment X bears a horizontal furrow near the base, which may be a remnant of the fusion of the division of this sclerite as seen in the annulicornis-group. *Rhyacophila alberta* is the most highly derived species of the *R. alberta/ R. tucula/ Rhyacophila* n. sp. complex. Ross (1950) reported that *R. alberta* is restricted to eastern montane region of the west, whereas the group is more well represented in the western ranges by *R. tucula*. The ranges overlap in the Rocky

Mountains. In Montana, Gustafson (1990) reported collecting *R. alberta* in higher elevations than *R. tucula.* Vineyard (1982) reported *R. alberta* to be the most abundant *Rhyacophila* species collected from Sashin Creek in SE Alaska, and was common in other third and fourth order, low gradient streams. As all of the records for the larval *R. tucula* specimens reported by Swegman and Ferrington (1980) are from streams above 2000 meters in elevation, it is likely that these specimens were actually *R. alberta.*

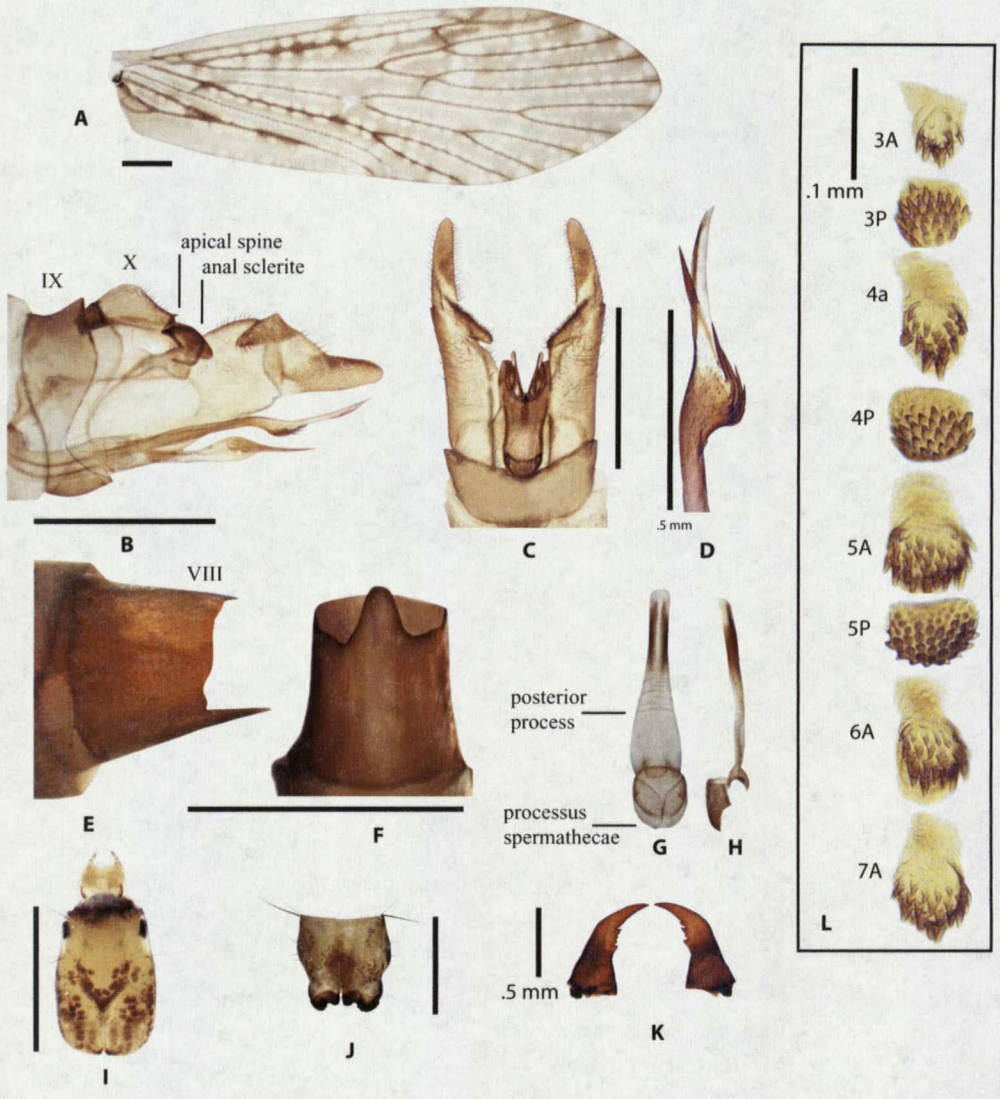

Figure 23: *Rhyacophila alberta* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male genitalia, lateral, (C) male genitalia, dorsal, (D) paramere apex, (E) female segment VIII lateral, (F) female segment VIII, ventral, (G) vaginal apparatus, ventral, (H) same, lateral, (I) larval head, dorsal, (J) larval pronotum, lateral, (K) pupal mandibles, (L) dorsal hook plates of pupa.

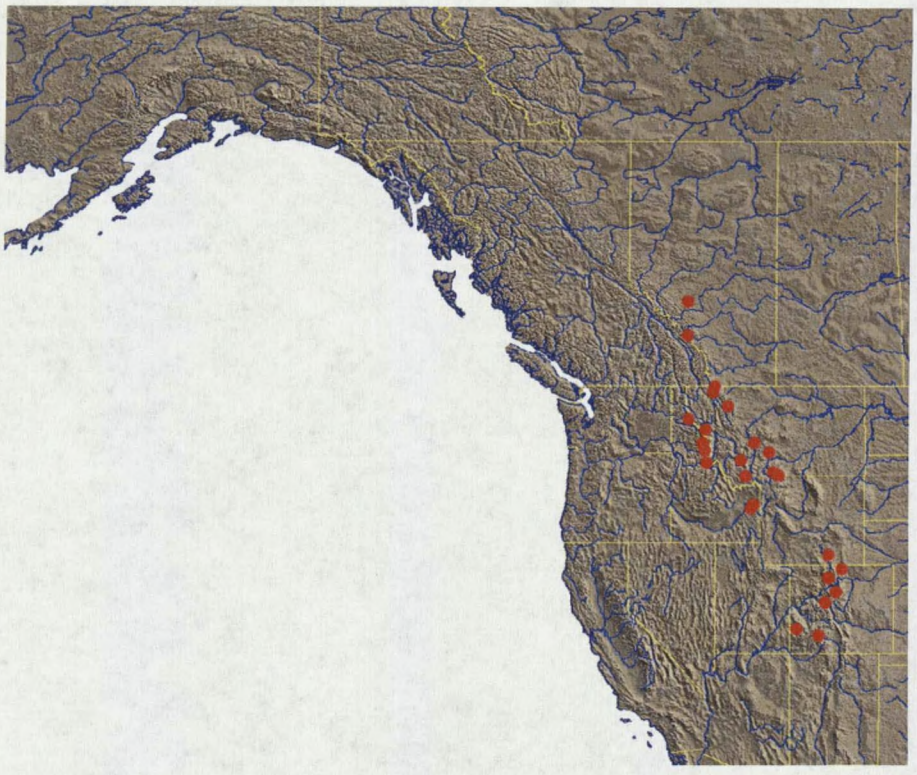

Figure 24: Distribution of *Rhyacophila alberta*.

Rhyacophila glaciera Denning

Figure 25.

Rhyacophila glaciera Denning, 1965: 263. Schmid, 1970: 55. Nimmo, 1971: 21. Newell and Potter, 1973: 13. Schmid, 1981: 20. Roemhild, 1982: 10.

Diagnosis. Male: segment X dorsally concave as a hump at midlength, apically narrowing, apically with pair of spines, ventral portion lightly sclerotized, with massive lobes enclosing anal sclerites; coxopodite short; harpago with deep U-shaped incision; parameres long, thin, clavate, with apical brush of setae. Female with segment VIII heavily sclerotized basally, ventrally with rounded posterior margin. Posterior portion of vaginal apparatus nearly parallel laterally, without folds, tapering to a blunt apex. Larva:

posterior margin of frontoclypeus with dark shading, making individual muscle scars indistinct; short, finger-like gills on mesothorax, metathorax, and segments I-VIII of abdomen.

Description. Male. Forewing 8.5- 9.5 mm, yellow with smoky bands on apical half. Head brown, setal warts lighter. Frons brown, setal warts rounded, ventrally concave. Large rounded triangular setal wart posterad of median ocellus, with postero-lateral lobes. Small rounded setal warts postero-mediad of lateral ocelli. Posterior setal wart horizontal, oblong. Thorax light brown dorsally, pleurites lighter, highlights brown. Antennae brown. Legs yellowish brown, tibiae lighter apically beyond subapical spur. Spur formula 3-4-4; spurs and spines light brown; apical protibial spurs shorter than on other legs. All tarsal claws identical in size and form. Abdomen with yellow tergites, sternites darker. Scent gland on segment V protrudes as small tubercle. Venter of abdominal segment VIII with sharp spine. Segment IX short, annular, strongly constricted to receive coxopodite. Segment X narrow in dorsal view, not secondarily subdivided by a furrow; in lateral view dorsally concave as hump at midlength, with few indentations dorsally, apically narrowing, pair of spines at apex; ventral portion lightly sclerotized, with massive lobes enclosing anal sclerites. Coxopodite shorter than extended segment X; with deep channel on mesal face; dorsal edge with setae. Harpago longer than coxopodite, with deep U-shaped incision dividing it into two lobes; dorsal lobe long, digiform, apically rounded, with basal and apical setal patches; ventral lobe thinner, apically acute, with apical patch of spicules. Endotheca basally with minute spines.

Phallicata broad basally, narrowing to thin, tube-like apex. Parameres long, thin, clavate, with apical brush of setae.

Female. Wings, thorax, and abdomen as in male. Segment VIII a heavily sclerotized collar, in lateral view dorsal half vertical, vertical half deflected caudad; ventrally with rounded posterior margin. Posterior portion of vaginal apparatus nearly parallel laterally, without folds, tapering to a blunt apex.

Larva. Mature larva approximately 10 mm. Posterior margin of frontoclypeus with dark pattern, obscuring distinct muscle scars. Head wedge shaped, narrowing in anterior half, light brown with darkened muscle scars dorsoposteriorly, darker areas laterally; posterior margin of frontoclypeus with dark shading, separate muscle scars indistinct; maxillary palpus stout, second segment slightly longer than first; left mandible with single apical tooth, one subapical tooth on dorsal edge, mesal tooth at apical edge of ventral cutting surface, mesal margin smooth; right mandible with three apical teeth, one small mesal tooth. Pronotum brown with several darkened muscle scars posteriorly; segment II of thorax with small dorsal gill posterad of Sa2 seta; segment III with a seta posterad of each Sa2 seta, another more laterad. Abdomen with four pairs of single gills on segment I-VI, one posterad of each Sa2 seta, and another dorsal, one gill posterad of Sa3 seta, and another at lateral edge of tergite; segment VII with three single gills, one posterad of one posterad of each Sa2 seta, one gill posterad of Sa3 seta, another at lateral edge of tergite; segment VIII with single vestigial gill posterad of small, thin sclerite in Sa2 position. Dorsal sclerite on segment IX roughly quadrate, yellow with darker areas at the base of setae along anterior margin. Anal proleg with baso-ventral hook; no apico-

lateral spur; anal claw with two large, stout ventral teeth posterad of weakened break in claw.

Pupa: Length of male 7.5 mm, length of female 8 mm. Wing pads reach abdominal segment V in male and female. Antennae reach beyond abdomen in male, to segment VIII in female; scape with 3-4 black setae. Head with eight long, black dorsal setae; one submedian seta on each side posterad of median ocellus, one posterad of each lateral ocellus, and postero-lateral pair on each side. Frons with row of two submedian setae on either side; clypeus short and apically truncate, with three dark antero-lateral setae on each side; labrum with five antero-lateral setae on each side; one seta on anterior margin of eye; one short genal seta posterad of ventral articulation of mandible. Each mandible with two dark basal setae; length of mandible apex to inner margin 1.8 times basal width of mandible; right mandible with one large basal tooth followed by three smaller teeth, then two larger teeth followed by row of denticles to apex; left mandible with large basal tooth, three smaller teeth, larger tooth followed by row of denticles to apex. Pronotum with five dorsal setae on each side. Each side of mesonotum and metanotum with anterior seta and dorsal seta laterad of scutellum. Dorsal presegmental hook plates on segments III to VII, postsegmental on segments III to VI; approximate hook plate spinule formula III: 17+43; IV: 26+52; V: 27+41; VI: 24+21; VII: 22+0. Abdominal segments I-VIII with one dark dorsal seta at Sa1 and Sa2, three to four setae on pleurites I-VII, one seta at ventral Sa1 and Sa2on segments I-VIII. Legs with five long black setae on anterior face of each coxa, and distally on each femur. Swimming setae on mesotarsal segments I-IV.

Distribution. High alpine snowmelt and spring fed streams along the Rocky Mountain Cordillera, in Glacier National Park of Montana, and Waterton, Banff and Jasper National Parks of Alberta (fig. 26).

Type material studied. ♂ HOLOTYPE, ♀ALLOTOYE- GLACIER NATIONAL PARK, MONTANA; 13 September 1964; Joe Schuh and W. C. Peters (CASC).

Other material studied. ALBERTA: 1 ♂- above Mt. Edith; Cavell Teahouse, J.N.P.; 330PM; 23/9/67, A. Nimmo (UASM)/1 ♂- Cameron Ck, .5 mi. below C. Lk., Wat. Pk; hab: fast creek, 930 PM; 14/8/65, A. Nimmo (UASM)/1 ♂- Cavell Creek, from Mount Edith Cavell Teahouse; to Cavell Lake, Jasper National Park; HAB snow & fast mtn. creek; 3/10/64 A. Nimmo (CNCI)/2 ♂♂- Hector Cr., B.D. Hwy, B.N.P.; 11/9/68, A. Nimmo (UASM)

MONTANA: Flathead County: 1 ♀- Logan Cr below road, above Oberlin Falls; 48.6995°N, 113.723°W; 10 IX 1997(FLBS)/11 m 3 ♀♀- Logan Cr. near water tank- Logan Pass; 48.697°N, 113.725°W; 24 IX 1997(FLBS)/2 ♂♂, 1 ♀ metamorphotype pupae- Mineral Creek, trail crossing, East fork; Glacier National Park (FLBS)/2 ♂♂, 2 ♀♀- Logan Cr below road, above Oberlin Falls; 48.6995°N, 113.723°W; 24 IX 1997(FLBS)/5 ♀♀- Logan Cr. @ Springhead; 48.6985°N, 113.732°W; 9 IX 1994(FLBS)/63 ♂♂, 35 ♀♀- Logan Cr. near water tank- Logan Pass; 48.697°N, 113.725°W; 22 IX 1998(FLBS)

Glacier County: 1 ♀ metamorphotype pupa- Reynolds Cr.; Logan Pass, GNP; 48.6871°N, 113.7268°W, 2073 m; 17 VIII 2001; J. Giersch (JJGC)/1 ♀- Reynolds Cr. above top snowfields, below ponds- Logan Pass; 48.6879°N, 113.735°W; 14 IX

1997(FLBS)/1 ♀- Reynolds High- Logan Pass; 48.6874°N, 113.732°W; 14 IX 1997(FLBS)/1 ♀- Reynolds Mid- Logan Pass; 48.6868°N, 113.728°W; 19 IX 1997(FLBS)/1 l- South Face of Reynolds Peak; Glacier National Park; GCC192C Gross; 4 VIII 1998. J. Giersch (FLBS)/1 l- E. side Swiftcurrent Pass; 300m from top, GNP; 48.7799°N, 113.7608°W, 2136 m; 05 VIII 2000; J. Giersch (FLBS)/1 l- Lunch Cr. below H2O falls; Above Going to the Sun Rd.; 48.7007°N, 113.7023°W, 1991 m; 16 VIII 2001; J. Giersch (JJGC)/1 l- Reynolds Cr.; .7 km SW of Logan Pass VC; 48.6892°N, 113.7210°W, 2041 m; 04 VIII 2000; J. Giersch (JJGC)/1 l- SW face Reynolds Peak; Glacier National Park; 4 VII 1998; J. Giersch (JJGC)/1 ♂- Reynolds High- Logan Pass; 48.6874°N, 113.732°W; 10 IX 1997(FLBS)/1 ♂ metamorphotype pupa- Reynolds Cr.; Logan Pass, GNP; 48.6871°N, 113.7268°W, 2073 m; 17 VIII 2001; J. Giersch (JJGC)/2 l- Reynolds Cr.; Logan Pass, GNP; 48.6872°N, 113.7294°W, 2075 m; 17 VIII 2001; J. Giersch (JJGC)/2 ♂♂- Reynolds High- Logan Pass; 48.6874°N, 113.732°W; 14 IX 1997(FLBS)/4 ♂♂- Kootenai Creek @ packers' camp below 50 mtn.; 48.8544°N, 113.899°W; 30 IX 1997(FLBS)/4 ♂♂, 13 ♀♀- Reynolds High- Logan Pass; 48.6874°N, 113.732°W; 10 IX 1997(FLBS)/4 ♂♂, 3 ♀♀ metamorphotype pupae- S. face Piegan Mt.; 153 m. below springhead, GNP; 48.7010°N, 113.6945°W, 2245 m; 24 VIII 2000; J. Giersch (JJGC)/5 l, 1 ♂, 1 ♀ metamorphotype pupae - Lunch Cr., West branch; Above Sun Rd, GNP; 48.7019°N, 113.7032°W, 2020 m; 22 VIII 2001; J. Giersch (JJGC).

Discussion. Denning (1965) stated that this species did not resemble any other in the genus. However, Schmid (1970) placed *R. glaciera* in the alberta-group, noting its similarity to *R. kincaidi* on the basis of the notched harpago. *Rhyacophila glaciera* is

isolated to the northern Rocky Mountains, where it lives in cold alpine streams that are fed by permanent snowmelt or icefields. Along with *R. ebria* Denning, this species occurs in the highest, coldest streams in Glacier National Park. I have also collected *R. glaciera* pupating and emerging simultaneously with *R. alberta* (J. Giersch, personal observation). Adults have been collected from mid-August through early October. Nimmo (1971) reported this species from small, turbulent creeks to tiny alpine trickles, with adults emerging from mid-August to early October. The intolerance of warm temperatures caused the isolation of this species. This distribution may be associated with a glacial refugium in the area. This is a species that resulted from the isolation of an ancestor with *R. kincaidi*. *Rhyacophila glaciera* shares characters with *R. kincaidi* including the deeply incised harpago, but it has several synapomorphies that separate it from the rest of the alberta-group. The short coxopodite, spines on the endotheca, and the shallow insertion of segment X into IX set this species apart from the rest of the alberta-group.

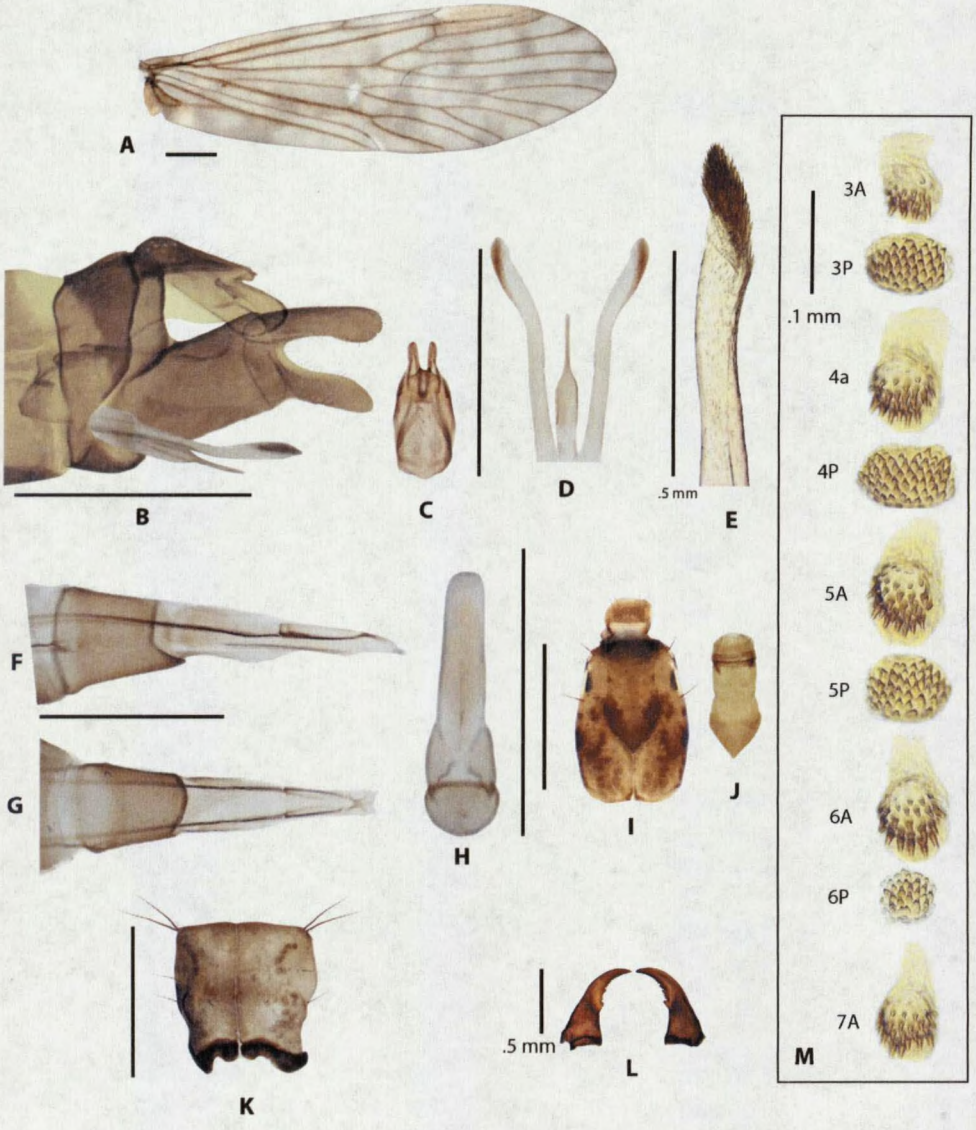

Figure 25: *Rhyacophila glaciera* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male genitalia, lateral, (C) segment X, dorsal, (D) parameres and phallicata, (E) paramere apex, (F) female terminalia, (G) female terminalia , ventral, (H) vaginal apparatus, ventral, (I) larval head, dorsal, (J) larval frontoclypeus, dorsal, (K) larval pronotum, lateral, (L) pupal mandibles, (M) dorsal hook plates of pupa.

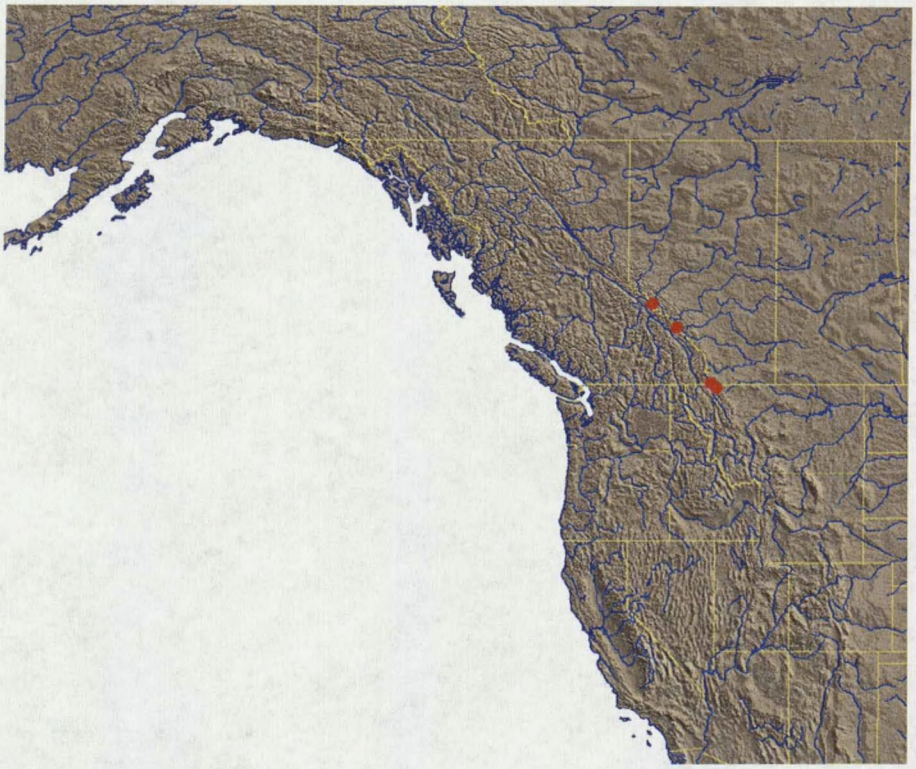

Figure 26: Distribution of *Rhyacophila glaciera*.

Rhyacophila kincaidi Schmid

Figure 27.

Rhyacophila kincaidi Schmid, 1970: 157. Anderson, 1976: 20. Schmid, 1981: 20. Vineyard, 1981: 99. Vineyard, 1982: 74

Diagnosis. Male: segment X roughly triangular, dorsally with hump at midlength, pair of spines at apex, ventral portion lightly sclerotized, with massive lobes enclosing large, apically pointed anal sclerites; inferior appendages longer than others in the alberta-group; harpago deeply incised with deep triangular notch; dorsal lobe long, rectangular, extending forward well onto mesal face of coxopodite; ventral lobe shorter, triangular; parameres with apical rows of spines on ventral and dorsal edge. Female:

segment VIII strongly narrowed ventrally at apex, posterior margin laterally with complex, shallow notches; vaginal apparatus with basally bulbous posterior process, tapering to wrinkled area at midlength, followed by pair of long, closely appressed sclerotized arms. Larva: posterior margin of frontoclypeus with dark shading, obscuring individual muscle scars, short, finger-like gills on mesothorax, metathorax, and segments I-VIII of abdomen.

Description. Male. Forewing 9-11 mm, brown with lighter irrorate pattern. Head brown, setal warts lighter. Frons brown, setal warts rounded, ventrally concave. Large rounded triangular setal wart posterad of median ocellus, with postero-lateral lobes. Small rounded setal warts postero-mediad of lateral ocelli. Posterior setal wart horizontal, oblong. Thorax light brown dorsally, pleurites lighter, highlights brown. Antennae brown. Legs yellowish brown, tibiae lighter apically beyond subapical spur. Spur formula 3-4-4; spurs and spines light brown; apical protibial spurs shorter than on other legs. All tarsal claws identical in size and form. Abdomen with yellow tergites, sternites darker. Scent gland on segment V protrudes as small tubercle. Venter of abdominal segment VIII with sharp spine. Segment IX short, annular, strongly constricted to receive coxopodite. Segment X narrow in dorsal view, in lateral view dorsally concave as a hump at the midlength, indentations dorsally, apically narrowing, with pair of spines at apex; subdivided by furrow near basal third; ventral portion lightly sclerotized, with massive lobes enclosing anal sclerites. Anal sclerites massive, rounded basally, apex narrowed. Inferior appendages longer than others in alberta-group; coxopodite with inner basal membranous area extending 2/3 length, mesal face slightly concave. Harpago deeply

incised with deep triangular notch forming long dorsal lobe extending forward well onto mesal face of coxopodite, covered with spicules, ventral lobe shorter, triangular with spicule patch covering dorsal edge of mesal face. Phallicata thin basally, evenly expanding to a wide mesal portion, apex narrowed to thin tube. Parameres evenly widening from base, apex thinner; apically with row of approximately twenty spines on ventral edge, eight spines on dorsal edge.

Female. Wings, head, thorax and base of abdomen as in male. Segment VIII a heavily sclerotized collar, tapering caudad, margin laterally incised, ventrally indented below edge of collar. Processus spermathecae of vaginal apparatus basally quadrate; posterior process basally bulbous, tapering to wrinkled area at midlength, with pair of closely appressed long sclerotized arms.

Larva. Mature larva approximately 9 mm. Head wedge shaped, narrowing in anterior half, light brown with darkened muscle scars dorsoposteriorly, darker areas laterally; posterior margin of frontoclypeus with dark coloration, obscuring individual muscle scars; maxillary palpus stout, second segment slightly longer than first; left mandible with single apical tooth, one subapical tooth on dorsal edge, mesal tooth at apical edge of ventral cutting surface, mesal margin smooth; right mandible with three apical teeth, one small mesal tooth. Pronotum brown with several darkened muscle scars posteriorly; segment II of thorax with a small dorsal gill posterad of Sa_2 seta; segment III with one gill posterad of each Sa_2 seta, and another more laterad. Abdomen with four pairs of single gills on segment I-VI, one posterad of each Sa_2 seta, another dorsal, one gill posterad of Sa_3 seta, another at lateral edge of tergite; segment VII with three single

gills, one posterad of each Sa_2 seta, one gill posterad of Sa_3 seta, one at lateral edge of tergite; segment VIII with single vestigial gill posterad of small, thin sclerite in Sa_2 position. Dorsal sclerite on segment IX roughly quadrate, yellow with darker areas at base of setae along anterior margin. Anal proleg with baso-ventral hook; no apico-lateral spur; anal claw with two large, stout ventral teeth posterad of weakened break in claw.

Pupa: Length of male 8.5 mm, female 9 mm. Wing pads reach abdominal segment V in male and female. Antennae extend to segment VIII in male, to segment VIII in female; scape with 3-4 black setae. Head with nine long, black dorsal setae; one submedian seta on each side posterad of median ocellus, one posterad of each lateral ocellus, and one group of three postero-laterally on each side. Frons with row of two submedian setae on either side; clypeus short, apically truncate, three dark antero-lateral setae on each side; labrum with five antero-lateral setae on each side; one seta at anterior margin of eye; one short genal seta posterad of ventral articulation of mandible. Each mandible with two basal setae, dorsal seta darker than ventral seta; length of mandible apex to inner margin 1.5 times basal width of mandible; right mandible with one large basal tooth followed by three smaller teeth, two larger teeth followed by row of denticles to apex; left mandible with large basal tooth, three smaller teeth, one larger tooth followed by row of denticles to apex. Pronotum with five dorsal setae on each side. Each side of mesonotum and metanotum with one anterior seta, one dorsal seta laterad of scutellum. Presegmental dorsal hook plates on segments III to VII, postsegmental plates on segments III to VI; approximate plate spinule formula III: 13+64; IV: 21+53; V: 22+51; VI: 16+5; VII: 24+0. Abdominal segments I-VIII with one dark dorsal seta at Sa_1

and Sa_2, three to four setae on pleurites I-VII, one seta at ventral Sa_1 and Sa_2 on segments I-VIII. Legs with five long black setae on anterior face of each coxa, one distally on each femur. Swimming setae on mesotarsal segments I-IV.

Distribution. Oregon, Washington, British Columbia, and Alaska (fig. 28).

Type material studied. 1 ♂ HOLOTYPE, 1 ♀ ALLOTYPE- Canada, B.C.; Skagit Camp; 3-VII-1965; F. Schmid (CNCI).

Other material studied. BRITISH COLUMBIA: 1 ♂, 1 ♀- Canada; Skagit Camp; 3-VII-1965; F. Schmid (CNCI).

ALASKA: 2 ♀♀ metamorphotype pupae- Kenai Penn.; trib. on Lower Russian; Lk. at base of falls; Aug. 4, 1969, #70, E. Charnov (RWW)/ 3 ♂♂- Kenai Penn.; trib to Lower Russian; Lk., 8-4-69 #71; E. Charnov coll. (RWW)/ 1 ♂- ibid., 7-15-69 #43; E. charnov, coll. (RWW)/ PP- Aniakchak Natl Mon; Alas Peninsula 56'56' N; 158' 6' W 300-400 m elev; Surprise Lk and tribs; VIII-28-88 (RWW)/ 1 ♂ metamorphotype pupa- Aniakchak Natl Mon; Alas Peninsula 56'56' N; 158' 6' W 300-400 m elev; Surprise Lk and tribs; VIII-28-88 (RWW)/ 2 ♀♀ metamorphotype pupae- Kenai Penn.; Mt. trib. to Lower Russian Lk.,#80; Aug 14, 1969; E. Charnov, coll. (RWW)/ 2 ♀♀ metamorphotype pupae- Kenai Penn.; trib. on Lower Russian; Lk. at base of falls; Aug. 4, 1969 #70 E. Charnov (RWW)/ 2 ♂♂ metamorphotype pupae- ibid., Aug 14, 1969; E. Charnov, coll. (RWW).OREGON: Deschutes County: 1 ♂- So. Sisters; Fall Cr. Green Lks. Trail; Sept. 18, 1982 B. Wissemann (RWW).

WASHINGTON: Skamania County: 1 ♀- Mt. St. Helens; Upper Clearwater R. 2450'; VIII-2-85 M.T.J. Bigelow (RWW)/ 1 ♂- Mt. St. Helens; Upper Clearwater 2450'; VII-26-85 J. Bigleow BLT (RWW).

Discussion. As in *R. glaciera* the harpago of *R. kincaidi* is deeply indented and the posterior hook plate on abdominal segment VI of the pupa is absent. Although this species shares similar habitats and morphology of the male genitalia with *R. glaciera*, the distributions do not overlap. *Rhyacophila kincaidi* is distributed north to south along the coastal ranges from Alaska to Oregon, including Oregon, Washington, British Columbia, and Alaska. The speciation was caused by the separation of the two populations. This species has been collected in Oregon, Washington, British Columbia, and Alaska. Wold (1974) collected pupae during June, July, and August, and adults in July and August. In Oregon, *R. kincaidi* was collected from cold, rapid streams on Mt. Hood. Wold hypothesized that the cold streams at this location allow for the extreme southern distribution of this species, and that it may have been more common in streams at lower elevations in colder times. *Rhyacophila kincaidi* has since been restricted to mountain islands in response to a warmer climate. Vineyard (1982) collected this species from first and second order high gradient, clear streams in Alaska.

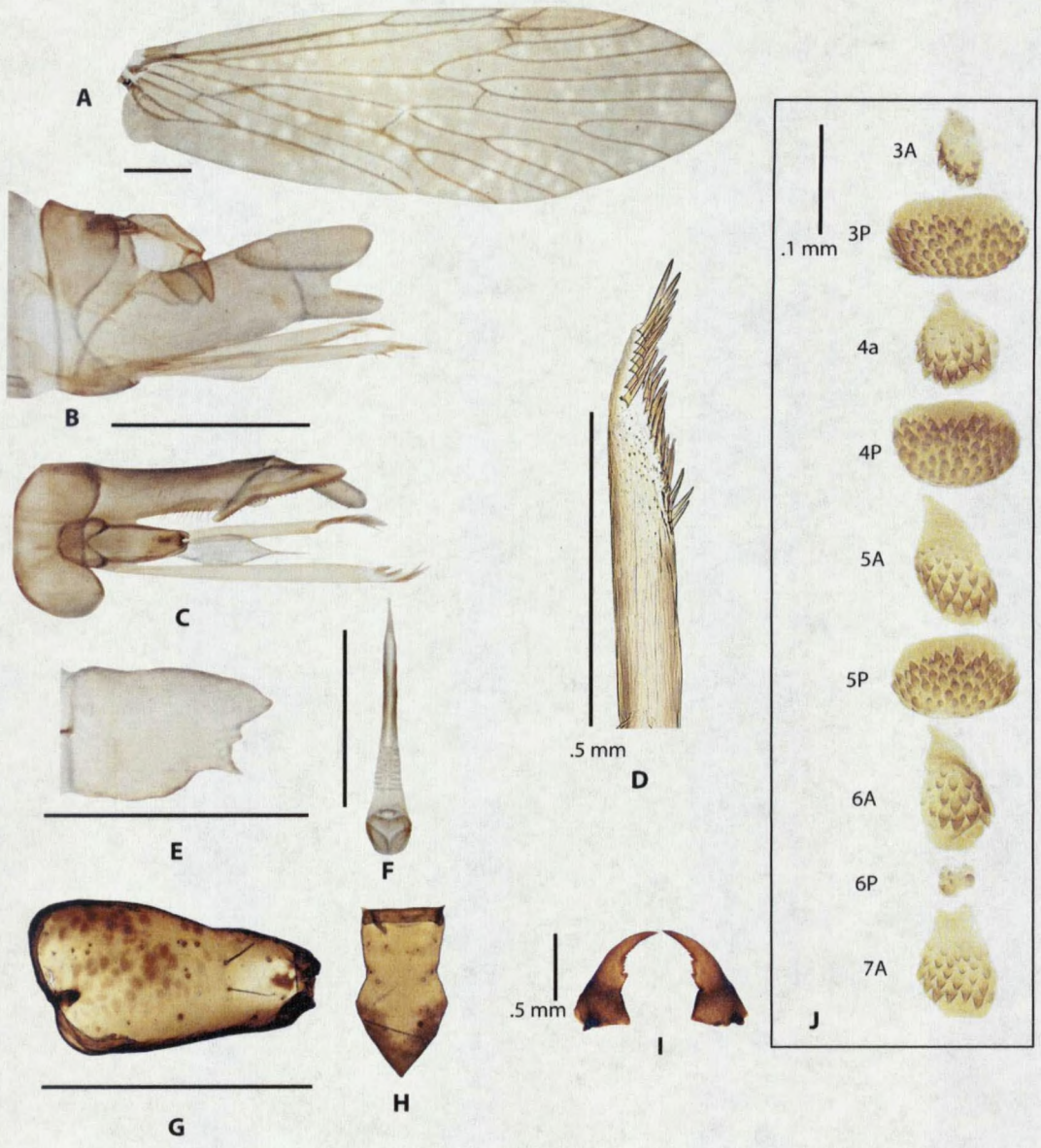

Figure 27: *Rhyacophila kincaidi* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male genitalia, lateral, (C) male genitalia, dorsal, (D) paramere apex, (E) female segment VIII lateral, (F) vaginal apparatus, ventral, (G) larval head, lateral, (H) larval frontoclypeus, dorsal, (I) pupal mandibles, (J) dorsal hook plates of pupa.

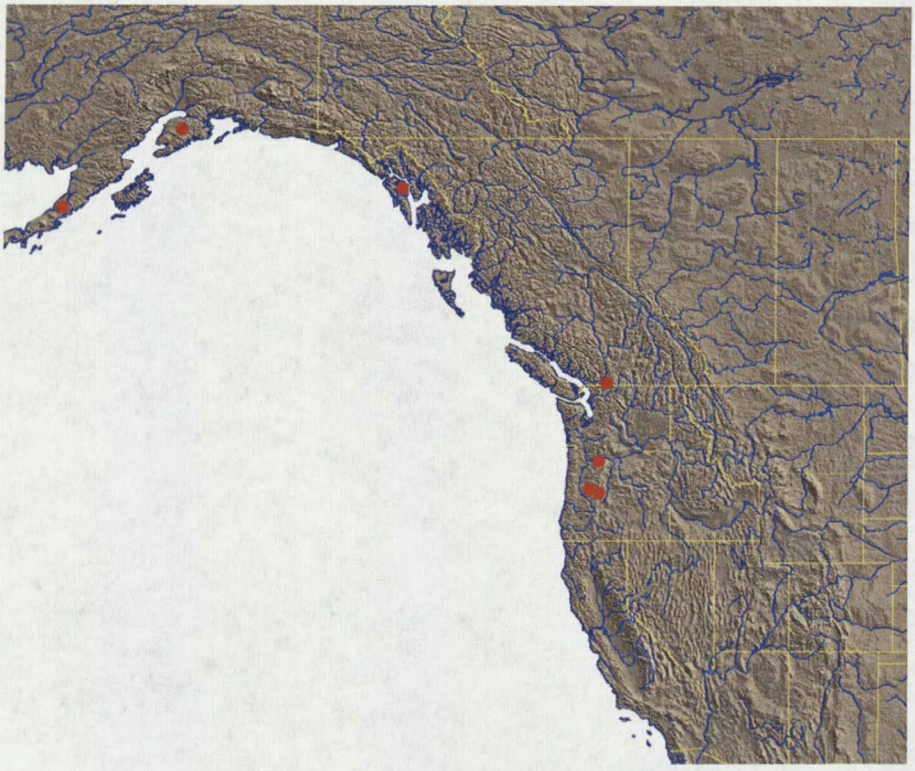

Figure 28: Distribution of *Rhyacophila kincaidi*.

Rhyacophila tucula Ross

Figure 29.

Rhyacophila tucula Ross, 1950: 261. Ross, 1956: 116. Ross, 1965: 591. Anderson, 1967: 508. Smith, 1968: 658. Schmid, 1970: 55. Nimmo, 1971: 20. Newell and Potter, 1973: 13. Anderson, 1976: 20. Short and Ward, 1980: 26. Schmid, 1981: 21. Vineyard, 1981: 99. Vineyard, 1982: 74. Anderson et al., 1984: 14. Roemhild, 1982: 10. Ruiter and Lavigne, 1985: 87. Ward, 1986: 191. Gustafson, 1990: 99.

Diagnosis. Male: segment X roughly triangular, dorsal portion heavily sclerotized and domed at midlength, tapering to pair of minute apical spines; ventrally more lightly sclerotized and flanking large anal sclerites; harpago with triangular ventral lobe,

rectangular dorsal lobe; parameres smoothly expanded to near apex, then thinning to acuminate apex, with dense row of spines. Female: segment VIII ventrally expanded as slightly projecting, evenly rounded lobe. Vaginal apparatus with folds along midlength of posterior portion, closely appressed sclerotized arms joining circular head at apex. Larva: frontoclypeus with distinct, darkened muscle posteriorly; short, finger-like gills on mesothorax, metathorax, and segments I-VIII of abdomen.

Description. Male. Length of forewing 9-12 mm, light brown with darker brown irrorate pattern. Head brown, setal warts lighter; frons brown, setal warts rounded, ventrally concave; large rounded, triangular setal wart posterad of median ocellus, with postero-lateral lobes; small, rounded setal warts postero-mediad of lateral ocelli; posterior setal wart horizontal, oblong. Thorax light brown dorsally, pleurites lighter, highlights brown. Antennae brown, lighter basally and apically. Legs yellowish brown, tibiae lighter apically beyond subapical spur. Spur formula 3-4-4; spurs and spines light brown; apical protibial spurs shorter than on other legs. All tarsal claws identical in size and form. Abdominal tergites yellow, sternites darker. Scent glands open on segment V on small tubercles. Venter of abdominal segments VII and VIII with sharp spine. Segment IX short, annular, strongly constricted to receive coxopodite. Segment X narrow in dorsal view, secondarily subdivided by furrow; in lateral view dorsally concave as hump at midlength, with indentations dorsally, apically narrowing, with pair of spines at apex; with lighter sclerotization and bifid ventral lobes cleft and flanking anal sclerites. Anal sclerites paired, horizontal plates, basally fused at root with long, dark, ventral projection leading ventro-caudad. Coxopodite mesal face concave, forming channel along entire

length. Harpago with triangular ventral lobe covered with spicules; dorsal lobe rectangular, transverse, covered with spicules. Phallicata long, slender, widening to midlength, apically thinning to slender tube. Parameres long, slender, smoothly expanded to near apex, thinning to acuminate apex; with dense row of approximately 15 spines along mesal edge from widened portion of paramere to apex.

Female. Head, thorax and basal segments of abdomen as in male. Segment VIII sclerotized collar basally, laterally excised, ventrally expanded, projecting slightly, evenly rounded lobe; posterior section membranous, invaginated into sclerotized collar. Processus spermathecae of vaginal apparatus with lateral edges dividing; posterior portion with folds along midlength, apically with closely appressed sclerotized arms joining circular head at apex.

Larva. Head wedge shaped, narrowing in anterior half, light brown with darkened muscle scars dorsoposteriorly; frontoclypeus with distinct muscle scars concentrated on hind margin; maxillary palpus stout, second segment slightly longer than first; left mandible with single apical tooth, one subapical tooth, smooth mesal margin; right mandible with one apical tooth, one small mesal tooth. Pronotum brown with several darkened muscle scars posteriorly. Mesothorax with one pair of small single gills on dorsum. Metathorax with two pairs of single gills on dorsum. Abdomen with four pairs of single gills on segment I-VI, three pairs of single gills on segment VII, small, single, vestigial gill on segment VIII. Anal proleg with baso-ventral hook; no apico-lateral spur. Anal claw with two large, stout ventral teeth posterad of weakened break in claw.

Pupa: Length of male 9.5 mm; length of female 10 mm. Wing pads reach abdominal segment IV in male and female. Antennae reach abdominal segment X in male, segment VI in female; scape with 3-4 black setae. Head with eight long, black dorsal setae; one submedian seta on each side posterad of median ocellus, one posterad of each lateral ocellus, postero-lateral pair on each side. Frons with row of two submedian setae on either side; clypeus short, apically truncate, with three dark antero-lateral setae on each side; labrum with five antero-lateral setae on each side; one seta on anterior margin of eye; one short genal seta posterad of ventral articulation of mandible. Each mandible with two dark basal setae; length of mandible apex to inner margin 1.7 times basal width of mandible; right mandible with three teeth, a row of smaller denticles leading to apex; left mandible with two large teeth, three smaller teeth between, row of smaller denticles leading to apex. Pronotum with five dorsal setae on each side. Each side of mesonotum and metanotum with one anterior seta, one dorsal seta laterad of scutellum. Dorsal presegmental hook plates on segments III to VII, postsegmental hook plates on segments III to V; approximate plate spinule formula: III: 11+26; IV: 18+29; V: 31+41; VI: 22+0; VII: 21+0. Abdominal segments I-VIII with one dark dorsal seta at Sa_1 and Sa_2, three to four setae on pleurites I-VII, one seta at ventral Sa_1 and Sa_2 on segments I-VIII. Legs with five long black setae on anterior face of each coxa, one distally on each femur. Mesotarsi with swimming setae on segments I-IV.

Distribution. Alaska, British Colombia, Alberta, Oregon, Washington, Wyoming, Idaho, and Utah (fig. 30).

Type material studied. None. Type Repository: Illinois Natural History Survey Insect Collection, Champaign, Illinois.

Other material studied. ALBERTA: 2 ♂♂- Sundance Ck., w/ of ?Idion?, Hwy 6, Culvert, 4PM; 24/9/66, A. Nimmo (UASM).

BRITISH COLUMBIA: 1 ♂- Lillooet: Meagher Creek, Hotsprings;08 OCT 1989; leg. Hutchins, Gordon E.; CN: ENT991-064745 (RBCM)/ 1 ♂- Qualicum R.; S. Vancouver Is.; 12-IX-1952; Richard Guppy (CNCI)/ 1 ♂- Wellington; 22 June, 1949; Richard Guppy (CNCI).

ALASKA: 1 ♂- Pt. Barrie, Kupreanof Isl.; 9.IX.1951; B. Malkin (CASC)/ 2 ♀♀- Falls Crek, Wrangell Narrows; Mitkof Island; Sept 1, 1951, B. Malkin (CASC)/ 2 ♂♂- Falls, N. Fk Staney Cr; Prince of Wales Is.; 17 Aug 78 (MTEC)/ 4 ♂♂, 1 ♀- Ohmers Slough; Lindenberg Penn.; Kupreanof Isl; 29.VIII.1951; B. Malkin (CASC).

MONTANA: Flathead County: 4 ♂♂, 2♀♀- Avalanche Creek @ road; 48.6801°N, 113.814°W; 24 X 1996(FLBS)/ 1 ♂- ibid., 6 IX 1997(FLBS)/ 2 ♂♂, 3 ♀♀- ibid., 48.6801°N, 113.814°W; 24 IX 1997(FLBS)/ 2 ♂♂, 3 ♀♀- Fish Creek @ Amphitheater; 48.549°N, 113.983°W; 6 IX 1997(FLBS)/ 4 ♂♂- McDonald Cr. above Lake @ Bridge; 48.6386°N, 113.856°W; 22 X 1994(FLBS)/ 1 ♂- ibid., 12 X 1995(FLBS)/ 4 ♂♂, 4 ♀♀- ibid., 10 IX 1997(FLBS)/ 10 ♂♂, 6 ♀♀- ibid., 14 IX 1997(FLBS)/ 1 ♀- ibid., 23 IX 1997(FLBS)/ 4 ♂♂, 14 ♀♀- ibid., 24 IX 1997(FLBS)/ 7 ♂♂, 6 ♀♀- ibid., 26 IX 1997(FLBS)/ 1 ♂- ibid., 27 VIII 1997(FLBS)/ 2 ♀♀- ibid., 28 IX 1996(FLBS)/ 8 ♂♂- ibid., 28 IX 1996(FLBS)/ 1 ♂- ibid., 29 IX 1996(FLBS)/ 1 ♀- ibid., 29 IX 1997(FLBS)/ 1 ♂- Mineral Creek @ suspension bridge; 48.7582°N, 113.82°W; 21 X 1997(FLBS)/ 1 ♂-

ibid., 27 IX 1996(FLBS)/ 2 ♂♂- Upper McDonald Creek above Mineral cr.; 48.7589°N, 113.838°W; 9 X 1996(FLBS).

Missoula County: 6 ♀♀- Rattlesnake Cr.; 12 M. N. Missoula; Oct 3, 1965; D. Lehmkuhl (RWW).

Ravalli County: 1 ♀- Skalkaho Cr. at Black Bear Campground; 46.1660°N, 113.9245°W, 1403 m; 08 IX 2001; J. Giersch (JJGC).

OREGON: Clackamas County: 4 ♂♂-Mt. Hood, Still Cr.; Still Cr. Forest Camp; Sept. 28-29, 1966, u-v light; Wiggins, Yamamoto, Odum (ROME)/ 1 ♂-Clear; Creek, 10 road km.; SW Estacada; 24-VI-1974; Paul H. Arnaud, Jr.; Calif. Acad. Sci.. Coll. (CASC).

Hood River County: 4 ♂♂, 4 ♀♀-Cold Springs Cr.; 9-9-84 BW EPA site (RWW).

Jefferson County: 2 ♀♀-Metolius R.; bridge at rt. 99. 9-23-65; NHA (RWW).

Lake County: 1 ♂-Bridge Cr.; 26506 EPA 8-84 BW (RWW).

Lane County: 1 ♂-HJA headwat. L.O. Cr.; at 4019' & 1506 xing; 8-17-78 Frost (RWW).

Linn County: 1 ♂-N. Fk. Santiam River; nr. Marion Forks Aug. 16,; 1964 S.G. Jewett (ROME).

Marion County: 7 ♀♀-Niagara, Sept. 21, 1968; Elwin Evans coll. (RWW).

Wallowa County: 1 ♂, 1 ♀-Wallowa Lake; Sept 12, 1949, Vince Roth (CASC)/ 5 ♂♂, 1 ♀-stream nr. Rt. 204, e.; Spout Springs, Blue Mts.; Sept 18, 1966; Wiggins, Yamamoto, Odum (ROME).

Wasco County: 1 ♂, 1 ♀-Barlow Cr. at; confl. W. White R.; 9-25-84. Scacia (RWW).

Discussion. *Rhyacophila tucula* has a broad distribution in western North America, but is most common in the coastal chains. Adult records from mid-June to mid-

October. In Alberta and British Columbia, Nimmo (1971) reports this species from fast, rocky streams below 4,000 feet elevation, emerging from late August to early October. The wider distribution and occurrence of *R. tucula* at lower elevations than other species in the alberta-group suggests higher temperature requirements for this species. Gustafson (1990) reports that *R. tucula* is common in lower reaches of larger streams, rare in warmer, more productive mountain streams, and sporadic in the coldest high mountain streams. Vineyard (1982) reported this species emerging from August through September. In Oregon, Wold (1974) reported fourth instars of *R. tucula* in late June to late July, fifth instars in late July to mid-August, and prepupae in mid-late July. Adults were collected in early fall through October. Swegman and Ferrington's (1980) *R. tucula* records are likely *R. alberta*.

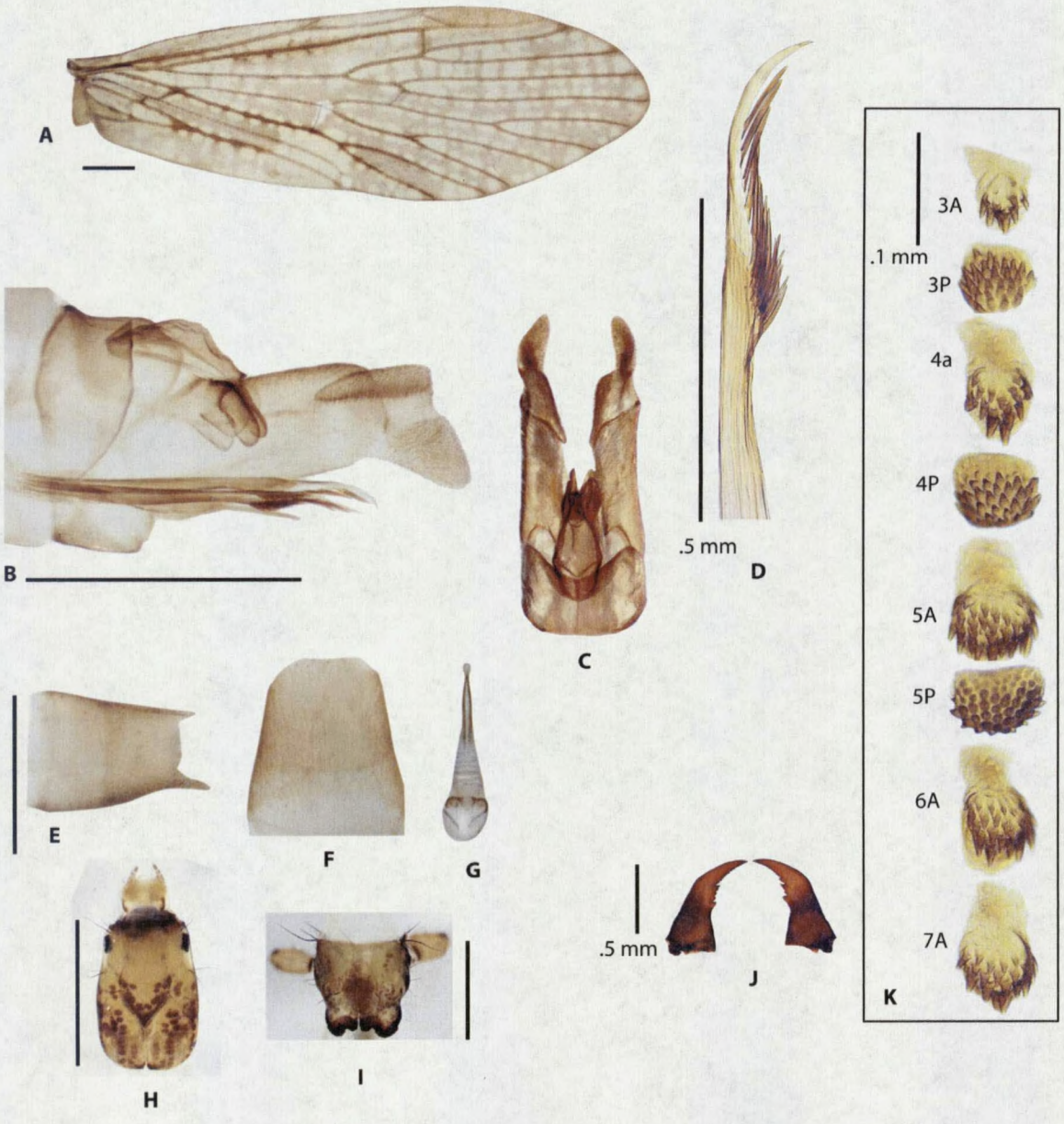

Figure 29: *Rhyacophila tucula* morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male genitalia, lateral, (C) male genitalia, dorsal, (D) paramere apex, (E) female segment VIII lateral, (F) female segment VIII, ventral, (G) vaginal apparatus, ventral, (H) larval head, dorsal, (I) larval pronotum, (J) pupal mandibles, (K) dorsal hook plates of pupa.

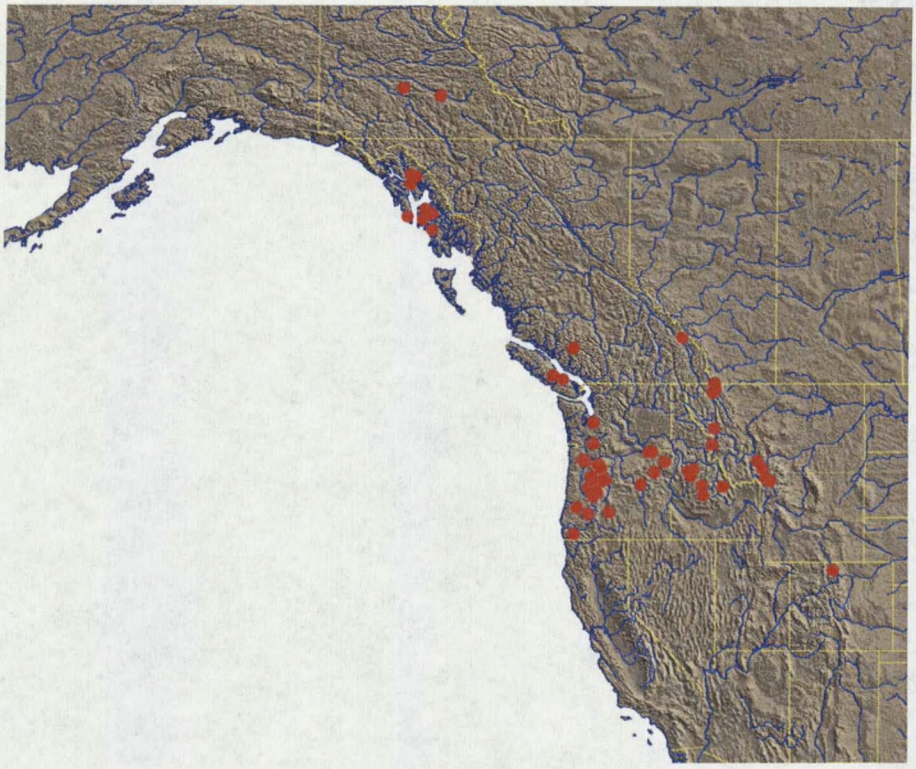

Figure 30: Distribution of *Rhyacophila tucula*.

<u>*Rhyacophila* new species</u>

Figure 31.

Diagnosis. Male: segment X roughly triangular, dorsal portion heavily sclerotized and domed at midlength, tapering to pair of minute apical spines; ventrally lightly sclerotized, flanking large anal sclerites; harpago with ventral lobe directed caudad as elongate lobe. Parameres with lobe near apex, thinning to acuminate apex, with row of apical spines. Female: segment VIII ventrally expanded as elongate, apically pointed extension; vaginal apparatus nearly identical to that of *R. tucula*; processus spermathecae with lateral edges dividing; posterior portion with folds along midlength; circular head at apex. Larva: frontoclypeus with distinct darkened muscle scars dorsoposteriorly; finger-

like gills on mesothorax, metathorax, and segments I-VIII of abdomen longer than other species of the alberta-group.

Description. Male. Length of forewing 9-11 mm, light brown with lighter irrorate pattern. Head brown, setal warts lighter; frons brown, setal warts rounded, ventrally concave; large, rounded, triangular setal wart posterad of median ocellus, with postero-lateral lobes; small, rounded setal warts postero-mediad of lateral ocelli; posterior setal wart horizontal, oblong. Thorax light brown dorsally, pleurites lighter, highlights brown. Antennae brown, lighter basally and apically. Legs yellowish brown, tibiae lighter apically beyond subapical spur. Spur formula 3-4-4; spurs and spines light brown; apical protibial spurs shorter than on other legs. All tarsal claws identical in size and form. Abdomen with yellow tergites, sternites darker. Segment V scent glands open on small tubercles. Venter of abdominal segments VII and VIII with sharp spine. Segment IX short, annular, strongly constricted to receive coxopodite. Segment X narrow in dorsal view, secondarily subdivided by furrow; in lateral view dorsally concave as hump at midlength, with few indentations dorsally, apically narrowing, with pair of spines at apex; ventrally lightly sclerotized, bifid ventral lobes cleft, flanking anal sclerites. Anal sclerites paired horizontal plates, basally fused at root, with long, dark, ventral projection leading ventro-caudad. Coxopodite mesal face concave, forming channel along entire length. Harpago not deeply incised; ventral lobe with patch of spicules, directed caudad as rectangular, apically rounded lobe; Phallicata long, slender, widening to midlength, apically thinning to slender tube. Parameres long, slender, with bulge near apex, then

thinning to acuminate apex, with row of six or seven stout spines along mesal edge running from the widened portion of paramere to apex.

Female. Wings, head, thorax, and base of abdomen as in male. Segment VIII basally as a sclerotized collar, laterally excised, ventrally expanded as nearly parallel sided, apically pointed extension; posterior section membranous, invaginated into sclerotized collar. Vaginal apparatus nearly identical to that of *R. tucula*; processus spermathecae with lateral edges dividing; posterior portion with folds along midlength, apically with closely appressed sclerotized arms joining circular head at apex.

Larva. Head wedge shaped, narrowing in anterior half, light brown with darkened muscle scars dorsoposteriorly; frontoclypeus with distinct muscle scars concentrated on hind margin; maxillary palpus stout, second segment slightly longer than first; left mandible with single apical tooth, one subapical tooth, smooth mesal margin; right mandible with one apical tooth, one small mesal tooth. Pronotum brown with several darkened muscle scars posteriorly. Mesothorax, metathorax, and abdomen with longer gills than other species in alberta-group; mesothorax with one pair of small single gills on dorsum. Metathorax with two pairs of single gills on dorsum. Abdomen with four pairs of single gills on segment I-VI, three pairs of single gills on segment VII, one small, single, vestigial gill on segment VIII. Anal proleg with baso-ventral hook; no apico-lateral spur; anal claw with two large, stout ventral teeth posterad of weakened break in claw.

Pupa. Length of male 8.5 mm, female 9 mm. Wing pads reach abdominal segment V in male and female. Antennae reach beyond abdomen in male, to segment VIII in female; scape with 3-4 black setae. Head with nine long, black dorsal setae; one

submedian seta on each side posterad of median ocellus, one posterad of each lateral ocellus, group of three setae postero-laterally on each side. Frons with row of two submedian setae on either side; clypeus short and apically truncate, with three dark antero-lateral setae on each side; labrum with five antero-lateral setae on each side; one seta on the anterior margin of eye; one short genal seta posterad of ventral articulation of mandible. Mandibles 1.7 times length of mandible apex to inner margin; right mandible with three teeth, row of smaller denticles leading to apex; left mandible with two large teeth with three smaller teeth between, row of smaller denticles leading to apex. Pronotum with five dorsal setae on each side. Each side of mesonotum and metanotum with one anterior seta and one dorsal seta laterad of scutellum. Presegmental dorsal hook plates on segments III to VII, postsegmental plates on segments III to V; approximate plate spinule formula: III: 8+34; IV: 13+42; V: 20+43; VI: 17+0; VII: 10+0. Abdominal segments I-VIII with one dark dorsal seta at Sa_1 and Sa_2, three to four setae on pleurites I-VII, one seta at ventral Sa_1, one Sa_2 seta on segments I-VIII. Legs with five long black setae on anterior face of each coxa, one distally on each femur. Swimming setae on mesotarsal segments I-IV.

Distribution. California, restricted to the Sierra Nevada and Siskiyou mountains (fig. 32).

Material studied. CALIFORNIA: El Dorado County: 5 l, 4 ♂♂ metamorphotype pupae- Rt. 89 sm. strm.; top Luther Pass VIII-5-85 BW; 7500' (RWW).

Fresno County: 1 ♂- Sierra Summit; 21-28 Aug 84; J.A. Halstead (CASC)/ 1 ♂- Billy Cr. at; Huntington Lk.; 14-22 Aug, 84' coll. J. Halstead (CASC)/ 1 ♂- Round Meadow; at Kaiser Cr.; Aug 16-17, 1984; coll. John Macdonald, Malaise Trap (CASC)/ 1 ♂- Sierra

Summit; Nr. China Peak; 17-18 Sept 84; coll. D.J. Burdick (CASC)/ 1 ♂- Billy Cr. at; Huntington Lk.; 14-23 Aug 84; Coll. J. Halstead (CASC)/ 1 ♂- Billy Cr. at; Huntington Lk.; 11-18 Sept. 1984; Coll. Jeff Halstead. (CASC)/ 5 ♂♂- Sample Meadow; 9000' 29 Aug 85; coll. Bert Tribbey (CASC)/ 1 ♂- Billy Cr. at; Huntington Lk.; 6-13 Sept. 1984; Coll Jeff Halstead (CASC).

Madera County: 1 ♂- T65 R236:25; Lewis Cr.; 28 Oct-8 Nov 83 (CASC).

Modoc County: 1 ♂- X-9-76A S. Warner Mts.; North Fork Shields Ck.; (RWW).

Mono County: 3 ♀♀- 1 mi. W. Tom's; Place; VIII-13-57 (EMEC).

Nevada County: 1 ♂- Sagehen Basin; UC Res. Sta. 25.IX.99 BL C. Barr (EMEC)/ 1 ♂- springs nr. source; Sagehen Cr., 7900 ft.; 8mi. N. Truckee, Nevada; Co., Oct. 7, 1966; Wiggins, Yamamoto, Odum (ROME).

Plumas County: 1 ♂- 1 mi. S Meadow; Valley 14 Sept, 1983; G. Ulrich (CASC).

Siskiyou County: 11 ♂♂- Mt. Shasta, stream; at Panther Meadows, ca.; 7500 ft; Oct. 2, 1966; Wiggins, Yamamoto, Odum (ROME).

Tulare County: 1 ♂- Quaking Aspen; 29 Aug-3 Sept 84; coll. J. Shelton (CASC)/ 1 ♂- Quaking Aspen;14-21 Aug. 84t 84; coll. D.J. Burdick (CASC)/ 1 ♂- Quaking Aspen; 11-18 Sept 84; coll. D.J. Burdick (CASC)/ 1 ♂- Quaking Aspen; 3-11 Sept 84; coll. D.J. Burdick (CASC)/ 1 ♂ metamorphotype pupa- Quaking Aspen; 6 Aug. 1984; coll: R.F. Gill (CASC)/ 3 ♂♂- Quaking Aspen; 29 Aug-3 Sept 84; coll. D.J. Burdick (CASC).

Tuolumne County: 1 l, 1 ♂ metamorphotype pupa- Rt. 108 E. side; Sonora Pass 7500-8000' 3rd ord.; st. by rd. VIII-6-85 BW (RWW)/ 1 ♂ metamorphotype pupa- rt. 108 E. Side; Sonora Pass~7000'. 1st order.; cliff-roadcut-pool VIII-6-85 (RWW).

Discussion. Specimens of this species have been previously identified as either *R. alberta* or *R. tucula*. The subapical bulge of the parameres resemble those of *R. alberta*, whereas the double apical spines on segment X resemble that of *R. tucula*. The most striking characteristic of this species is the females. The female genitalia of *Rhyacophila* n. sp. is distinctive, as the venter of segment VIII is expanded as a long, nearly parallel sided extension that is apically pointed. This is in contrast to segment VIII of *R. tucula*, which is bluntly rounded, and *R. alberta* which is a short, triangular point. The vaginal apparatus of *Rhyacophila* n. sp. is nearly identical to that of *R. tucula*, having a rounded head at the apex of the posterior process.

This species has been collected from the Sierra Nevada and Siskiyou mountains of California.

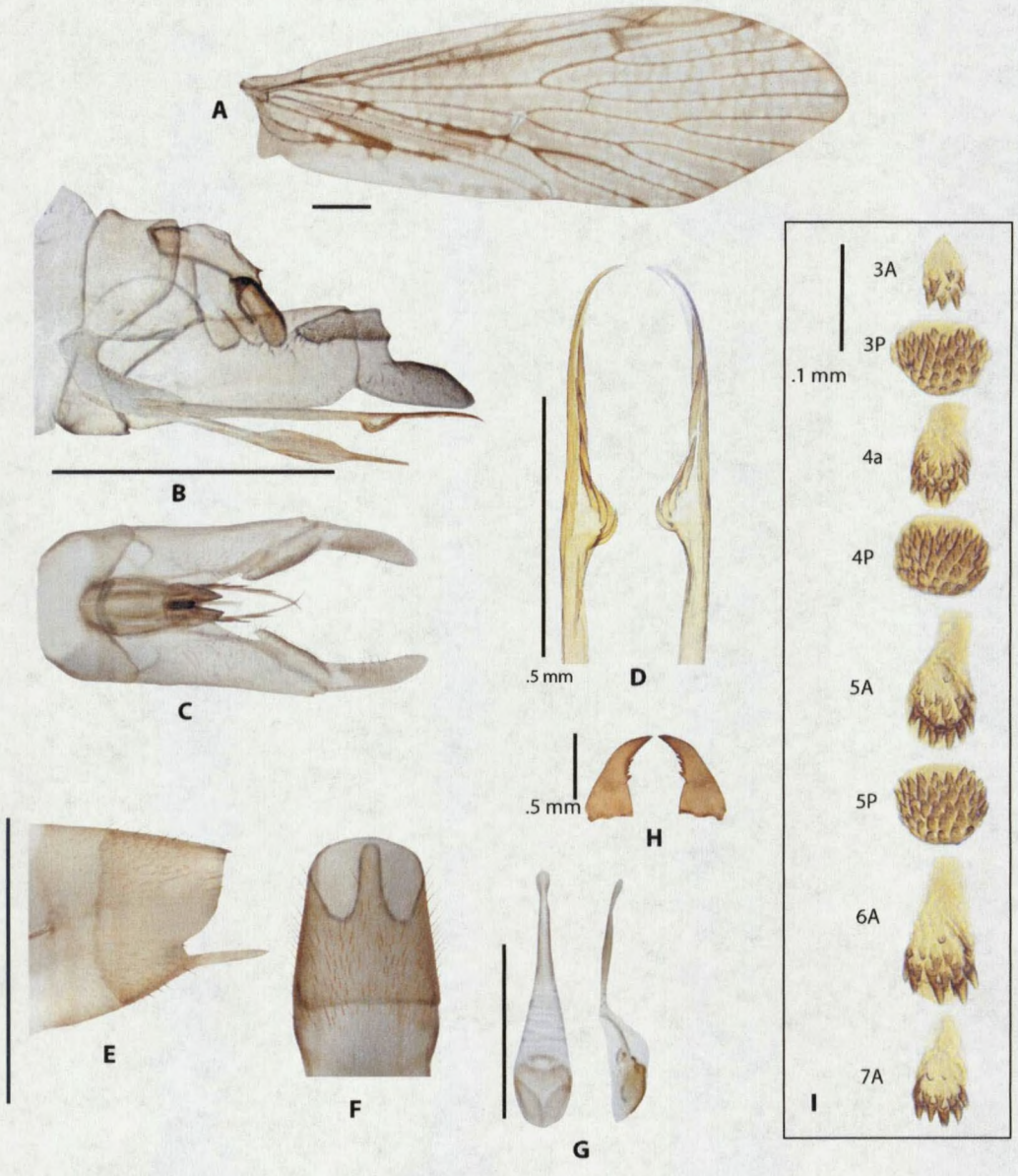

Figure 31: *Rhyacophila* new species morphology. All scale bars 1 mm unless otherwise noted. (A) Male forewing, (B) male genitalia, lateral, (C) male genitalia, dorsal, (D) paramere apices, (E) female segment VIII lateral, (F) female segment VIII, ventral, (G) vaginal apparatus, ventral and lateral, (H) pupal mandibles, (I) dorsal hook plates of pupa.

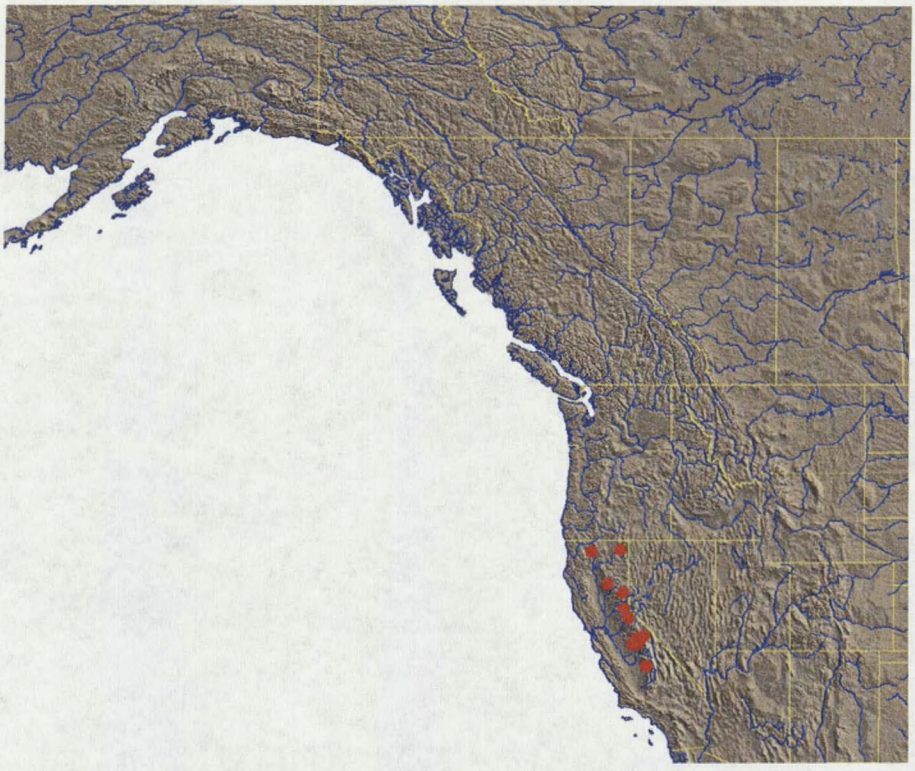

Figure 32: Distribution of *Rhyacophila* new species.

CHAPTER 9

PHYLOGENETIC ANALYSIS OF THE ALBERTA-GROUP

To determine a hypothesis of the relationship between the species of the alberta-group, a cladistic analysis was done using *R. arnaudi* and *R. tshiringpa* as outgroup taxa. *Rhyacophila tshiringpa* was used as it is a representative of the annulicornis-group, and as is the alberta-group, belongs to the castanea-twig (Schmid 1970). Twenty nine characters representing 61 character states were used in the analysis and construction of cladograms.

Characters, states, and definitions are as follows:

Male Characters:

Character 1. - IX apico-dorsal lobe: this character refers to the presence or absence of an apico-dorsal lobe on segment IX of the abdomen of the male.

(0) absent;

(1) present (fig. 23B).

Character 2. - X shape: refers to whether segment X has the characteristic shape of the alberta-group, where the segment has a convex bulge at its midlength (state 1) or otherwise (state 0):

(0) not domed;

(1) domed (fig. 23B).

Character 3. - X deeply recessed into IX: the base of segment X may articulate with the edge of segment IX (state 0), or may be recessed into the segment (state 1):

(0) articulating with margin of IX (fig. 25B);

(1) deeply recessed (fig. 23B).

Character 4. - X subdivided: Segment X may be entire, without a furrow or secondary subdivision (state 0). In *R. annulicornis*, segment X is entirely divided into two parts, the remnant of which is retained in some species of the alberta-group as a shallow furrow in the basal third of the segment (state 1):

(0) not subdivided (fig. 25C);

(1) subdivided (fig. 27C).

Character 5. - apical points on X: the apex of segment X may be blunt (state 0), have a carina leading to a single point (state 1), or a pair of carinae leading to two minute points (state 2):

(0) 0;

(1) 1 (fig. 23C);

(2) 2 (fig. 25C).

Character 6. - root of anal sclerite long ventral piece: basally, the anal sclerites have a sclerotized ventral extension at that is perpendicular to the base of the sclerite (state 1), whereas in some species, this character is absent (state 0):

(0) present (fig. 25B);

(1) absent (fig. 29B).

Character 7. – phallic apparatus ventral plate: the phallic apparatus is simple in species of the alberta-group (state 0), but an extension in the form of a plate in present in the *R. annulicornis* Group (state 1):

(0) without (fig. 23B);

(1) with.

Character 8. - tergal strap: a sclerotized tergal strap is the plesiomorphic condition for the *Rhyacophila philopotamoides* Branch (state 0), whereas this character is unsclerotized in the alberta-group (state 1).

(0) sclerotized;

(1) unsclerotized (fig. 23B).

Character 9. - dorsal lobe of harpago extending onto median face of coxopodite:

(0) no (fig. 25B);

(1) yes (fig. 27B).

Character 10. - distal lobe on coxopodite: the presence of an apical lobe on the mesal face of the coxopodite is autapomorphic for *R. glaciera:*

(0) absent (fig. 27B):

(1) present (fig. 25B).

Character 11. - harpago shape: this character addresses whether or not the harpago slopes directly dorso-anterad (state 0), or there is an indentation to some degree (state 1):

(0) not indented (fig. 23B);

(1) indented (fig. 31B).

Character 12. - harpago indent depth: when the harpago is indented, it may be slight (state 0), or pronounced (state 1), as in *R. glaciera* and *R. kincaidi*:

(0) shallow (fig. 31B);

(1) deep (fig. 27B).

Character 13. - spicule zones on dorsal lobe of harpago

(0) 1 (fig. 27B);

(1) 2 (fig. 25B).

Character 14. - endotheca spicules: the presence of minute spicules, visible only under high magnification with a compound microscope (state 1) is autapomorphic for *R. glaciera:*

(0) without;

(1) with.

Character 15. - parameres subapical bulge:

(0) absent (fig. 27D);

(1) present (fig. 31D).

Character 16. - ventral spine on VII: while this character is present on both segments VI and VIII, it is very sharp and prominent on segment VII of some species (state 1)

(0) not prominent;

(1) prominent.

Female characters:

Character 17. - posterior process VA: the posterior process of the vaginal apparatus may be somewhat parallel sided (state 0) or gradually narrowed to a long apex (state 1):

(0) parallel sided (fig. 25H);

(1) narrowed apically (fig. 27F).

Character 18. - apex of posterior process of vaginal apparatus:

(0) truncate (fig. 25H);

(1) narrow (fig. 27F).

Character 19. - posterior process flexible: The base of the posterior process of the vaginal apparatus may have a series of perpendicular ribs or folds, allowing for a certain degree of flexibility of the sclerite:

(0) not flexible (fig. 25H);

(1) flexible (fig. 31G).

Character 20. - VA posterior process rounded head: this character refers to the apex of the posterior process of the vaginal apparatus, which may be blunt (state 0) or have a rounded apex (state 1):

(0) without (fig. 27F);

(1) with (fig. 31G).

Character 21. - Processus spermathecae shape: the processus spermathecae is truncate in *R. arnaudi* (state 0) and rounded (state 1) in the alberta-group.

(0) not rounded;

(1) rounded (fig. 31F).

Character 22. - VIII venter: this character addresses whether segment VIII of the female is expanded ventrally:

(0) not expanded;

(1) expanded (fig. 23F).

Character 23. - VIII venter expanded margin shape: if the venter of segment VIII is expanded, it may be evenly rounded (state 0), or pointed (state 1):

(0) rounded (fig. 25G);

(1) pointed (fig. 31F).

Larval Characters:

Character 24. - larval gills: single, finger-like gills may be present on the thorax and abdomen:

(0) absent;

(1) present.

Character 25. – apico-lateral spur may arise from the anal proleg:

(0) absent;

(1) present.

Character 26. - anal claw teeth: teeth on the ventral surface of the claw of the anal proleg:

(0) absent;

(1) present.

Character 27. - 3A pupal plate: the anterior hook plate on abdominal segment III of *R. kincaidi* is absent. As the presence of this plate is plesiomorphic in *Rhyacophila*, its absence is autapomorphic for this species and is ordered:

(0) present (fig. 25M);

(1) absent (fig. 27J).

Character 28. - 3P pupal plate: the posterior hook plate on abdominal segment III is absent in some species of *Rhyacophila* (state 1). As this is a reduction in the plesiomorphic state of a set of complete plates, this character is ordered.

(0) present (fig. 31I);

(1) absent.

Character 29. - 6P pupal plate: the posterior hook plate on abdominal segment VI of *R. kincaidi* and *R. glaciera* is present (state 0). As the absence of this plate is a reduction in the plesiomorphic state of a set of complete plates, this character is ordered.

(0) present (fig. 27J);

(1) absent (fig. 31I);

The character matrix is shown in Table 4.

Table 4. Character matrix used in the phylogenetic analysis of the *Rhyacophila* alberta-group.

Taxon/ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
R. alberta	0	1	1	1	1	1	0	1	1	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1	0	1	0	0	1
R. glaciera	0	1	0	0	2	0	0	1	0	1	1	1	1	1	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0
R. kincaidi	0	1	1	1	2	0	0	1	1	0	1	1	0	0	0	0	1	1	1	1	1	1	0	1	0	1	1	0	0
R. tucula	0	1	1	1	2	1	0	1	1	0	1	0	0	0	0	1	1	1	1	1	1	1	0	1	0	1	0	0	1
R. n. sp.	0	1	1	1	2	1	0	1	1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1
R. arnaudi	1	0	1	0	0	0	0	0	0	0	0	-	0	0	0	?	1	1	1	0	0	0	-	0	1	0	0	1	1
R. tshiringpa	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Results: Two trees were found using the exhaustive option of PAUP*, with the shortest tree requiring 34 steps, a Consistency Index (CI) of .85, a Retention Index of (RI) .69, and a Rescaled Consistency Index (RC) of .59. The tree was rooted and characters were traced in MacClade© 4.0.

Discussion of the alberta-group. The hypothetical phylogeny of the alberta-group can be seen in figure 33.

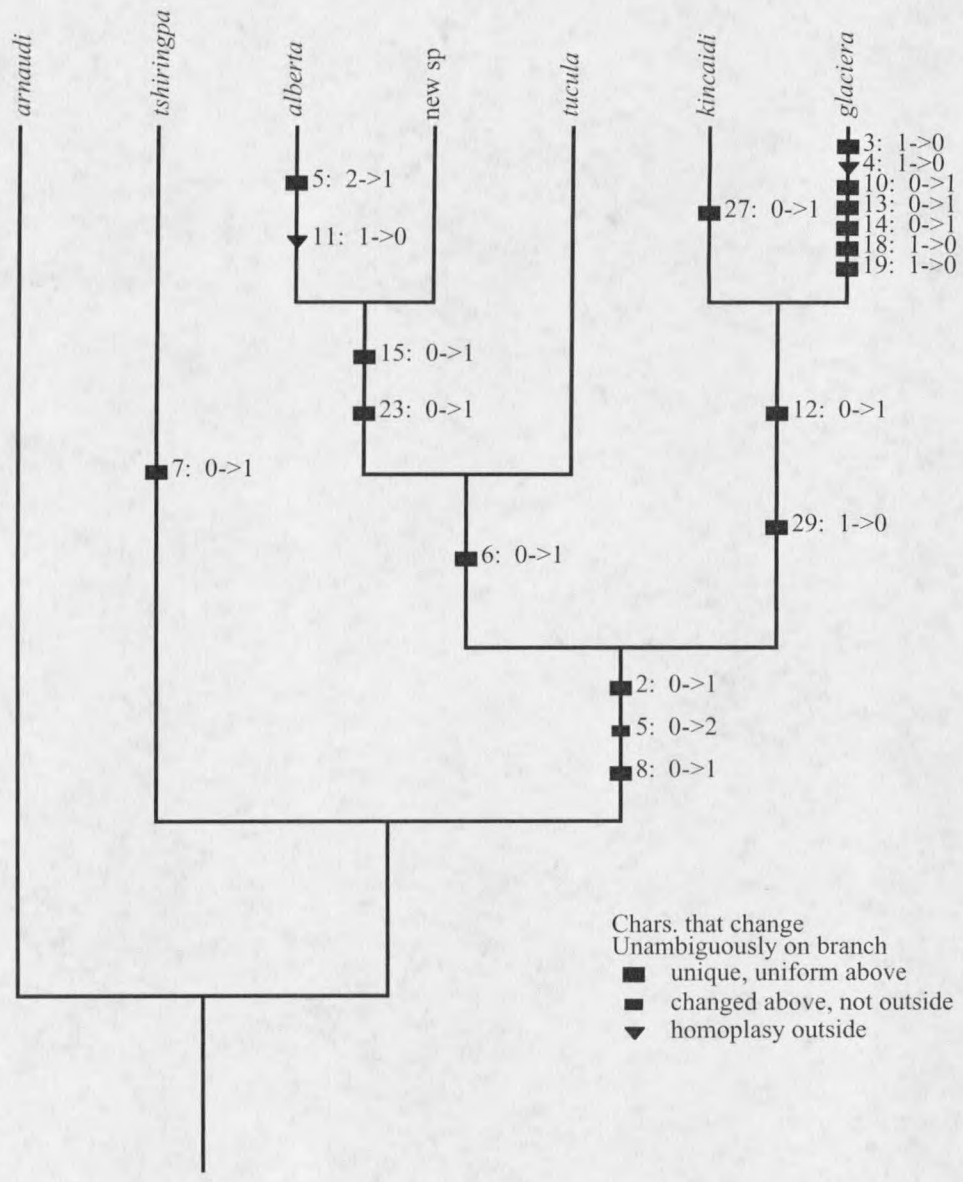

Figure 33: Cladogram showing the relationship hypothesis and monophyly of the alberta-group (only unambiguous changes shown).

The alberta-group is monophyletic based on the distinctive shape of segment X (fig. 33), as it is divided into a dorsal, domed portion and a ventral, lightly sclerotized portion (character 2, state 1) and the unsclerotized tergal strap (character 8, state 1).

Rhyacophila alberta, *R. tucula*, and *Rhyacophila* n. sp. form the alberta-subgroup (fig. 33), based on the synapomorphy of the ventral extension at the base of the anal sclerites (character 6, state 1).

Rhyacophila alberta and *Rhyacophila* n. sp. are sister species (fig 33), united by a subapical bulge of the parameres (character 15, state 1) and the expanded ventral margin of VIII of the female (character 23, state 1).

While *R. tucula* and *Rhyacophila* n. sp. superficially bear many similarities to each other, the harpago of *Rhyacophila* n. sp. (fig. 31B) is distinctive in that the ventral lobe is longer and parallel sided as opposed to being triangular as in *R. tucula* (fig. 29B). Whereas the harpago of *R. tucula* and *Rhyacophila* n. sp. have a shallow indentation separating the lower from the upper zone of spicules, and the dorsal edge of the apex of the harpago is parallel, the dorsal edge of the apex of the harpago of *R. alberta* (fig. 23B) is offset at an obtuse angle. The apices of the parameres in *Rhyacophila* n. sp. are expanded as in *R. alberta*, but the two species can be distinguished by the single apical point on segment X of *R. alberta*, as opposed to the double apical points on this segment in other species of the alberta-group.

My phylogenetic reconstruction shows that *R. kincaidi* and *R. glaciera* are sister species (fig. 33) allied by the deep incision of the harpago (character 12, state 1) and the presence of the posterior plate on segment VI of the pupa (character 29, state 0). This is congruent with Schmid's (1970) phylogeny of the group.

Several synapomorphies set *R. glaciera* apart from the rest of the alberta-group. These include a distal lobe on the mesal face of the coxopodite (character 10, state 1),

two zones of spicules on the mesal face of the dorsal lobe of the harpago (character 13, state 1), spines on the endotheca (character 14, state 1), truncate apex of the posterior process of the vaginal apparatus (character 18, state 0), and the inflexible base of the posterior process (character 19, state 0).

Problems still exist with the separation of larvae of the alberta-group, which are all remarkably similar. Wold (1974) was unable to confidently separate the larvae of *Rhyacophila kincaidi* from *R. tucula*, but reported that the gills of *R. tucula* tend to be shorter than those of *R. kincaidi*. *Rhyacophila kincaidi* always has a gill on the eighth abdominal segment, and Smith (1968) reported an absence of this gill in *R. tucula*. However, I have seen this gill in specimens of both species. This character is variable in specimens identified by Wold as *R. tucula*, though she thought that some of these specimens might have actually been *R. alberta* or *R. glaciera*. She expected the larvae of *R. glaciera* and *R. alberta* to be virtually identical to *R. tucula*. I have not been able to comfortably distinguish between larvae of the five species using morphological characters. The only character that may prove useful in separating the species may be the muscle scars on the head capsule. In *R. glaciera* and *R. kincaidi*, the muscle scars at the posterior portion of the frontoclypeus are close enough to form dark shading. In contrast, these scars are separated into distinct points in *R. alberta*, *R. tucula*, and *Rhyacophila* n. sp. This character is problematic, as it relies on late instar material.

Biogeography of the alberta-group

The current distributions of the alberta-group follow many of the same patterns as seen in the verrula-group, with speciation likely occurring as a result of populations isolated to glacial refugia during the Pleistocene or in mountain ranges following glaciation.

Rhyacophila tucula, *R. alberta,* and *Rhyacophila* n. sp. form a complex of species, with *R. alberta* and *R.* n. sp. being sister species. Although the distributions of *R. alberta* (fig. 24) and *R. tucula* (fig. 30) overlap in the Rocky Mountains, they are separated by elevation, with *R. alberta* occurring at higher elevations. During the Pleistocene, the ancestors of *R. alberta* may have become isolated to the Rocky Mountains, and those of *R.* n. sp. to the Sierra Nevada and Siskiyou mountains of California (fig. 32).

The sister species *R. kincaidi* and *R. glaciera* are morphologically united by the bifid harpago (character 12, state 1). Both of these species have an affinity for cold, alpine habitats. These species were probably separated during the Pleistocene (or perhaps even earlier glacial events), with *R. kincaidi* isolated to the coastal refugia from Alaska to Oregon (Kavanaugh 1988), becoming isolated to alpine streams following glaciation (fig. 28). The autapomorphies of *R. glaciera* suggest isolation of this species from the rest of the alberta-group. This species was likely isolated to the central Rocky Mountains of Montana, Alberta and British Columbia (fig. 26) by the Cordilleran ice sheet, likely passing the Pleistocene at the edges of the ice sheets in the ice-free corridor between the Cordilleran and Laurentide ice sheets (Nimmo 1971) or in the Mountain Park (Packer and Vitt 1974) or Waterton refugium (Crossman and McAllister 1986).

CHAPTER 10

CONCLUSIONS AND REMAINING PROBLEMS

Undoubtedly the discovery and association of more life stages or inclusion of molecular data of species of the verrula and alberta-groups will lead to a greater understanding of the phylogenetic history of these two groups. Because the verrula- and alberta-groups are represented by several species that inhabit difficult to find, reach or seldom sampled habitats, and because spring brooks and alpine streams create isolated habitats in which taxa may become disjunct and speciate, there is a strong likelihood that more species will be discovered through a greater collecting effort in northwestern North America as well as Asia.

Future studies of the biogeography of *Rhyacophila*, particularly the discovery of isolated species, will serve to further fortify or refute climate history models of the past and those developed in the future.

The verrula-group should be included in future investigations of the higher phylogeny of Trichoptera. Although treated as a synapomorphy in this thesis, the presence of the closed m-cell in the forewing of the verrula-group may be plesiomorphic, as its absence in other species groups of *Rhyacophila* may be a reduction. The presence of this character in the genus *Fansipangana* from Vietnam is a potentially informative character to be used in a higher-level phylogeny of the Rhyacophilidae.

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