



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  
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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* 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.

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REVISION AND PHYLOGENETIC ANALYSIS OF THE VERRULA AND  
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Jonathan Joseph Giersch

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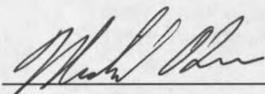
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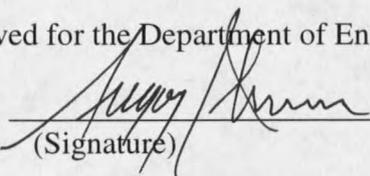
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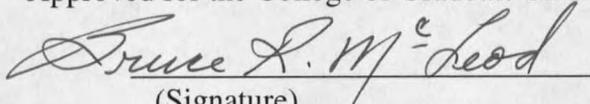
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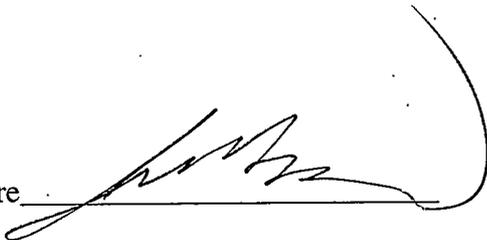
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A handwritten signature in black ink, appearing to be "J. M. ...", written over a horizontal line.

Date

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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* Botoșăneanu, 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, Huryñ 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 bryophytes, 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 (Botoșăneanu 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 bioassessment 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







































































































































































































































































































































































































