

AN ABSTRACT OF THE THESIS OF

Philip A. Schapker for the degree of Master of Science in Environmental Science  
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Title: A Review of the Lepturinae (Coleoptera: Cerambycidae) of the Pacific Northwest,  
with Special Attention to the Elderberry Longhorn Beetle, *Desmocerus* Dejean.

Abstract approved: \_\_\_\_\_  
Christopher J. Marshall

Here presented is a photographic catalogue, a key, and literature review for the 35 genera and 90 species of lepturine longhorn beetles (Cerambycidae: Lepturinae) found in the Pacific Northwest. Several nomenclatural changes, recognized by the global taxonomic community, but previously unknown to North American authors, are adopted, and one new nomenclatural act is given. Within one genus, *Desmocerus* Dejean (Tribe Desmocerini), individuals were found that were inconsistent with the already described species. Additional specimens were obtained from throughout the known distribution of *Desmocerus* populations, and two genes, mitochondrial CO1 and nuclear 28S rDNA, were sequenced and analyzed to clarify species limits, and to construct a preliminary phylogenetic analysis for the genus. Based on the accumulated evidence, two new species from the Pacific Northwest are proposed, along with a revised taxonomy for *Desmocerus*. The review is intended to be legible to the non-professional public, like a field guide, but contains as much technical information as possible to facilitate further study by researchers, citizen scientists, and teachers who might incorporate the study of insects into their classroom.

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A Review of the Lepturinae (Coleoptera: Cerambycidae) of the Pacific Northwest:  
with Special Attention to the Elderberry Longhorn Beetle, *Desmocerus* Dejean.

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Philip A. Schapker

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APPROVED:

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Major Professor, representing Environmental Science

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Director of the Environmental Science Program

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Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Philip A. Schapker, Author



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## CHAPTER 1: Introduction

*“The answer is never the answer. What's really interesting is the mystery. If you seek the mystery instead of the answer, you'll always be seeking. I've never seen anybody really find the answer—they think they have, so they stop thinking. But the job is to seek mystery, evoke mystery, plant a garden in which strange plants grow and mysteries bloom. The need for mystery is greater than the need for an answer.”*

- Ken Kesey<sup>1</sup>

There is a bicycle path in Corvallis, Oregon, that runs along a seasonally flooded wetland area at the base of the Mary's River watershed, just southwest of 35<sup>th</sup> and Philomath Boulevard. In late May, the path is lined with the ample pink blossoms of wild Nootka rose, and bustles with cyclists and pet-walkers, out to enjoy the view in the new sunny weather of spring. On May 30<sup>st</sup> of this year, at around 3 in the afternoon, I walked about 20 yards into the flat, open woodland along the path, and in the shade below the large ash trees and spindly *Quercus garryana*, I found a large thicket of Nootka rose, and began peering into the flowers. After noticing a couple of flies, and some speck of an animal crawling around the base of a petal, I came across what appeared to be a pair of pale, bean-sized longhorn beetles, engaged in copulation. I watched the two for a while. The male, with his tarsal claws firmly fixed to the back of his mate, appeared to be rapidly tapping and licking the female's elytra with his labial palps. At the same time, he used a part of his genitalia (called the *paramere*) to grasp<sup>2</sup> at the abdomen of the female, each attempt being made in a sudden, powerful thrusting motion at a regular tempo, slightly less than once per second. This went on for some time, and I scooped them into a vial. Nearby, the male of a different couple had

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<sup>1</sup> "The Art of Fiction," interview by Robert Faggen, *The Paris Review* No. 130, (Spring 1994)

<sup>2</sup> The exact role of the paramere in cerambycid copulation is a subject for further investigation. See discussion in Hubweber and Schmidt (2010).

succeeded in extracting the female's ovipositor, and was locked in, still thrusting at the same tempo, while the female calmly fed at the pollen-covered stamens of the rose blossom. Elsewhere in the thicket, I noticed several unpaired individuals flying from flower to flower, briefly walking the perimeter of each bloom while waving their long antennae, presumably in search of a mate. A number of longhorn beetles find mates in this manner: apparently in some species, males can walk right past a female and miss her entirely if the antennae fail to make contact (Heintze, 1923; Linsley, 1959). On another flower, I saw an individual being approached cautiously by a spider. The beetle's antennae barely brushed the legs of the hopeful predator, and in an instant, releasing its hold of the flower and dropping to the ground, the beetle was gone.

At my home, using an old 40x microscope, I could observe on my specimens the pseudotetramerous tarsi (Fig. 1.1) common to the beetle superfamily Chrysomeloidea, the leaf and longhorn beetles. The relatively long antennae, situated atop small tubercles on the head, differentiated this species from the chrysomelid leaf beetles, and verified it as a member of the family Cerambycidae, the wood-boring longhorns. Finally, as I noted the forward-slanting face and slender, tapering body form, I nudged forward the pronotum of one specimen, to reveal a minutely-ribbed stridulatory plate bearing a small division in the middle — a lepturine — one of more than 1500 species in the subfamily worldwide.

**Fig. 1.1.** Pseudotetramerous tarsi of *Brachysomida californica*. The fourth tarsal segment is reduced and hidden within the lobed third tarsomere, giving the appearance that there are just four total tarsal segments instead of five.



The species was *Pidonia scripta* LeConte, encountered quite commonly in the spring on wild rose, and a few other flowers, from British Columbia to the San Francisco Bay. According to Linsley and Chemsak (1976), who conducted the last major taxonomic revision of the longhorn beetles of North America, the larvae of *P. scripta* had only been verified as developing in the bark of *Quercus agrifolia* in California. But that tree's range does not extend into the Pacific Northwest, leaving the host plant for our regional populations of *P. scripta* a mystery. Upon finding BugGuide.net, and various other internet sources, to be devoid of additional information on the habits of *P. scripta*, I pedaled towards the library of the Oregon State Arthropod Collection. After accessing the Zoological Records database through the library's subscription, and consulting a number of papers and tattered old manuscripts, I found just one more brief note on this species's natural history. These were Cope's (1984) observations of two more host records for *P. scripta*, from trees that are also absent in the Willamette Valley—the mystery remained. To my surprise, and delight, I found that practically all of my observations on the behavior *P. scripta* that day had yet to be documented in the scientific literature. In fact, more digging revealed that some of the sexual behaviors I observed in this very common species, appeared to be novel in the entire subfamily Lepturinae!<sup>3</sup>

This anecdote points to the great amount of work still to be done in recording even the most rudimentary biological facts for many species of insects, even in North America, and even in relatively charismatic groups like butterflies and longhorn beetles. Beetles especially, with over a 387 thousand species worldwide (and counting—see Zhang, 2011), are simply too numerous for scientists to study each species in detail. The totality of our knowledge on some Pacific Northwestern lepturine species can be

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<sup>3</sup> Other lepturines reported on have not had a prolonged period between the initiation of copulation and the connection of the male and female genitalia (see Michelsen, 1963; Hubweber and Schmidt, 2010). The intense movements of the male during copulation differed from my previous observations of the lepturine *Desmocerus aureipennis*, and seem to contradict Michelsen's statement (p.159), regarding the 12 lepturine species he studied, that "the period after the establishment of contact between the sexual organs is usually relatively calm."

summed up by either one or a small handful of pinned specimens sitting in a research museum. Small labels attached to the pins indicate the specimens' locality and date of collection—perhaps our only hope of ever finding them again. Fortunately, the abundance and accessibility of beetles in general offers a great opportunity for those outside of professional academia to become active, and important participants in a fertile area of ongoing basic research. Any high school student with a glass jar, a case of pins, and a foam-bottomed cigar box can walk outside and immediately begin constructing an insect collection: an act that for many becomes a life-long pursuit and art form. Not only is a specimen collection a personalized database of one's encounters with nature, but a scientific object to be probed and explored in all of its dimensions, from the intricately webbed wings and dimpled planes, to forests of sensillae and scales. Populations may be returned to each year, and seemingly trivial, but nevertheless factual notes (like the ones at the beginning of this chapter) may be taken, for some future generation that could make use of them.

The amateur insect collector will certainly find and collect lepturines—but they will not necessarily know what to do with them. Popular printed field guides normally do not contain comprehensive keys to species, nor the information needed for amateurs to realize what may or may not already be known about the specimens in their collections. This represents a major roadblock to participation in basic research for non-professional enthusiasts. More recently, the internet has begun to bridge the limitation of access to printed technical manuals and keys. A currently popular website, [www.BugGuide.net](http://www.BugGuide.net), allows anyone to upload an image of an insect specimen which is then identified by a volunteer specialist, who may be motivated to comb through the images for the opportunity to catch new distribution records, or sightings of rare species. For certain insect taxa, a number of impressive, content-rich online resources are also beginning to appear, such as Antweb and the Pacific Northwest Moths site, however, more often than not, there is a dearth of publically-available scientific content online.

My primary goal at the outset of this project was to produce a field guide for a charismatic, diverse, and relatively poorly-understood group of beetles, which would promote the further study of that group by professional scientists and amateurs alike. With more than 34,000 species worldwide, cerambycid longhorn beetles are among the most recognizable insects in the world, and include some of the most colorful, peculiar, and surprisingly large species in the entire beetle order. Due to the habit of cerambycids to bore into wood or other plant tissues during the larval stage, the family also includes a number of species that are invasive, economically-damaging pests. Both factors have historically driven taxonomic interest in the group, especially in the subfamilies Cerambycinae and Lamiinae, which contain a large number of nocturnal species that bore into living wood. However not all cerambycid groups have received equal attention by scientists. The Lepturinae, or “the flower-visiting longhorn beetles” as they are known, comprise a much smaller group of diurnal species that tend to use decaying, rather than living, plants as larval hosts, making them less of a threat economically. Although diverse and elegant in their own right, lepturines are generally smaller and less extravagantly colored than other cerambycid subfamilies, and this may also account for the relative dearth of information on lepturines in the scientific literature. This fact of the lepturines’ relative obscurity, combined with the observation that the (mostly) diurnal, flower-visiting lepturines should be particularly easy to observe and collect by amateurs, led me to believe that the group would make an ideal candidate for a field guide.

Perhaps the lepturines are the ugly ducklings among longhorn beetles, but they are not uninteresting — far from it. Lepturine species are often implicated as important pollinators and decomposers in forest ecosystems (Bond and Phillips, 1999; Abdel Moniem and Holland, 2013; Kevan, 1983), and some species in the subfamily have drawn attention from a surprising variety of scientific interests. Adults of the species *Rhagium inquisitor*, for example, which are able to overwinter under bark in temperatures lower than -20°C, possess a protein in their haemolymph that chemists

have identified as the most potent antifreeze protein known in the world (Zachariassen et al., 2008). The molecular structure and behavior of this protein has been of recent interest to physics (Kristiansen et al., 2011). Another example is a very rare lepturine species that occurs in the deserts of southeastern Oregon, *Typocerus serraticornis*, which appears to account for the only known instance of silk-production in the Cerambycidae (Robertson, 1988). Worth noting is that these are two of many examples in the Lepturinae of species that have diverged from the typical lepturine life history, and we suspect that more surprises await in the investigation of other atypical lepturines, particularly those that appear to have evolved obligate relationships with living host-plants. Such species occur in our Pacific Northwestern fauna, and are almost entirely unstudied.

The last survey of lepturines occurring specifically in the Pacific Northwest was conducted by Melville Hatch (1971), as part of his major work, *The Beetles of the Pacific Northwest*. Dr. Hatch, professor of entomology at Washington University and curator of the Burke Museum, was famous for having one of the largest and most important collections of Pacific Northwest beetles at the time (now housed in part at Oregon State University). By describing the patterns of variation he could observe in his ample specimens, with reference to the special geography of the Pacific Northwest, Hatch was able to significantly augment what was then known about the diversity of lepturines in our region. However, within one year, Linsley and Chemsak (1972), published the first of two volumes of a major taxonomic revision to the North American Lepturinae that involved a significantly broader sampling of specimens from collections all around North America. Their study, which also provided sketches, distribution maps, and comprehensive biological data for each species, was a major turning point, and remains today as the most significant and authoritative reference used by biologists. Surprisingly, Linsley and Chemsak (1972) do not appear to have made extensive use of the Hatch collection—a significant piece of the available data—and we can observe series in a number of species that are in direct contradiction to statements made by

those authors. Aside from this, the technical format, and clinical descriptions that are only occasionally accompanied by a sketch, make it difficult to rely on Linsley and Chamsak (1972) for identifications, especially for non-experts and those without access to a comprehensive research collection with pre-determined material for comparison. After forty years of specimen acquisition and research on lepturines both in the Pacific Northwest and around the globe, an update is now due.

Chapter 2 is both a field guide and review of the 34 genera, and 90 species and subspecies of lepturines known to occur in the Pacific Northwest, an area in North America roughly extending from Southern Oregon to British Columbia and Idaho. It begins with a key to the genera, based on that of Linsley and Chamsak (1972; 1976), but revised and updated specifically for our region. Importantly, the key reflects the most up-to-date consensus by the global taxonomic community on the valid application of names in the Lepturinae, some of which have changed since Linsley and Chamsak's publications. To aid in identification, high-resolution, color photographs were included for as many genera and species as possible. For each genus, I have also included updated keys to species that occur in the Pacific Northwest, and a brief review of those species biology and distributions. Whenever possible, I have tried to indicate areas where further biological or ecological research in each genus would be useful.

Field guides are only the first step in really understanding diversity. Like a roadmap, they necessarily generalize but cannot replace the scenic view witnessed while traveling an actual road. The role of a systematist when conducting a revision of a group is to look at the actual specimens – as many as they can get – and from them distill the general patterns. The patterns that correspond to what we generally believe to be species or subspecies are given proper scientific names, and if done correctly, these concepts will encompass all (or most) of the existing specimens and observations. For each genus and species, I have made an attempt to examine the specimens in the Oregon State Arthropod Collection against the descriptive literature and any type

specimens or photos that were available. This was done both to make sure that our physical specimens were properly identified with valid names, but also to identify whether any of the species represented in the museum material included populations that deviate from the way those species are typically construed in the taxonomic literature. In a number of cases this process revealed the need for amendments to the species keys given by Linsley and Chemsak. In many genera I have also left comments on difficult, or intermediate populations that should be of interest to future investigators who may want to carry out a more thorough investigation using DNA or internal anatomy.

Readers who are familiar with the North American lepturines today will find a few, perhaps annoying, instances where names that have been in use since the earliest North American taxonomists have now been superseded by older names established by still earlier European taxonomists. At least one of these should be a cause for some excitement: one of our region's most bizarre-looking lepturines, which for all this time we have been calling *Pyrotrichus vitticollis* LeConte, 1862, actually turns out to have two equally peculiar sister species in Japan and the Middle East. Since the Mid-Eastern species was first described as the type of a new genus, *Enoploderes*, almost 30 years before John LeConte thought he had discovered and named a new genus, *Pyrotrichus*, the International Code of Zoological Nomenclature requires that LeConte's (1862) name be treated as a junior synonym of *Enoploderes* Faldermann, 1837. This fact was first recognized by Kasuma & Hayashi (1971), but apparently never communicated to North American taxonomists (see also Miroshnikov, 2000). At any rate, the revelation of two additional, but widely globally disjunct species related to *E. vitticollis*, adds a new intriguing dimension to the questions surrounding the history of that singular genus.

#### *Desmocerus – the elderberry longhorns*

As demonstrated by the case of *Enoploderes*, though the Pacific Northwestern fauna only makes up a small percentage of the total lepturine species worldwide (the



majority being found in Asia), it nevertheless contains an important set of taxa that will be critical to understanding the group as a whole. Another particularly anomalous genus, *Desmocerus*, has the bulk of its diversity in the Pacific Northwest, and the rest of its species are entirely restricted to the North American continent. All of the species in *Desmocerus* have a close, obligate relationship with a living elderberry host plant (*Sambucus*), and display a whole suite of additional life history characteristics that differ drastically from that of the “typical” lepturine. These include aposematism and metallicism, leaf eating, and the use of a female-produced, long-distance sexual pheromone (the pheromone was recently described and synthesized by Ray et al., (2012)). Whether, or to what extent any of these traits may have evolved in *Desmocerus* as adaptations specifically associated with its life in elderberry, or whether these traits were merely derived from some lepturine ancestor, is an open question. There are other lepturines, such as the genus *Pseudogaurotina*, that share at least some of the same life history, and morphological characteristics as *Desmocerus*, perhaps indicative of common ancestry. However, since a robust molecular phylogenetic study of the lepturines has yet to be performed, and since many aspects of *Desmocerus* structure are also atypical, the relationship among these genera is at present unknown (cf., Sýkorová, 2008, discussed in Chapter 3). While systematists have been able to designate groups of genera, called *tribes*, that appear to represent major sub-lineages within the Lepturinae, *Desmocerus* has for a long time stood as an outlier, occupying its own monotypic tribe, the Desmocerini. For these reasons, and others, *Desmocerus* stood out as worthy candidate for further study.

My original intention for Chapter 3 was to perform a more detailed survey of the scientific literature on *Desmocerus*, and to investigate, as thoroughly as I could, the distribution and diversity of forms of that genus in our region. At the time the study was initiated in 2012, only one species, *D. aureipennis* Chevrolat, was recognized in the Pacific Northwest, with four “subspecies” ranging from British Columbia to the Sierra Nevada mountain range of California and Nevada. Although the main populations of the

supposed subspecies were markedly divergent, and were even known to use different species of elderberry as host plants, both Hatch (1971) and Linsley and Chemsak (1972) decided that the existence of apparently intermediate forms between the allopatric populations precluded any of the populations from being true species. (A detailed account of Linsley's subspecies concept can be found in Mayr, Linsley and Usinger's *Methods and Principles of Systematic Zoology*, 1953: 30-33.)

The peculiar nature of this arrangement did not go unnoticed for long however. In 1990, two researchers by the names of Jeffrey Halstead and Jonathan Oldham produced a revision to *Desmocerus* that called into question the *D. aureipennis* subspecies concept, and even revealed previously unstudied museum specimens that proved several of the "subspecies" to exist in sympatry — thus violating Mayr et al.'s rule for subspecies as well-defined allopatric populations. Unfortunately, that obscure revision was published in the form of a special studies staff report for the Kings Valley Conservation District in California, and only available by special request to the office of the KVCD. This made for an awkward situation in *Desmocerus*, in which two competing hypotheses were in existence: one of them an older, and more cursive treatment, which had the advantage of being part of a well-respected and widely available manuscript, and another which, although based on more evidence and appearing to falsify the former, was disadvantaged by being almost entirely unknown and difficult to obtain. Adding to this, other authors (see Barr, 1990) had flatly rejected Halstead and Oldham's controversial synonymy of *D. californicus dimorphus*, a federally threatened subspecies in the Sacramento River Valley of California. This must have been the last nail in the coffin for the credibility of Halstead and Oldham's report, as none of their recommendations for the *D. aureipennis*-related species were ever accepted by the professional taxonomic community. My assumption was that a re-inspection of the specimens in the *D. aureipennis* complex would resolve the matter in favor of one hypothesis or the other.

In actuality, *Desmocerus* turns out to be quite a rabbit hole. As is not uncommon for a systematist who begins turning over long unturned stones, my own inspection of the *Desmocerus* specimens led me down a circuitous path, with a number of surprises. Almost immediately, I noticed a large series from the old M. Hatch collection of specimens identified as the nominative subspecies, *D. a. aureipennis*, from the peak of Mt. Ashland in southern Oregon. Although the males, at first glance, appeared superficially identical to those of the abundant populations of *D. a. aureipennis* that occur throughout the Sierra Nevadas, the elytral coloration of the females were markedly different, being fully clad in a brilliant semi-metallic blue or green, rather than the black keystone shape typical of the California females. Further investigation revealed that the hindwings and male genitalia also bear discrete differences, indicative of species-level segregation. This created yet another problem: which population was the true *D. aureipennis*, the population on which Louis Chevrolat based his original description of the species in 1855? How indeed did the Parisian entomologist come to acquire the first *D. aureipennis* specimen in the first place? The answer to this question involved an arcane manuscript held at the Royal Botanical Gardens of Edinburgh, Scotland, and the story of a young man who had snow-shoed across Canada from the Hudson's Bay and over the Rocky Mountains of British Columbia, to find, among other things, our beetle, and the pine tree that bears his name, *Pinus jeffreyi*. The full details and evidence surrounding the origins of *D. aureipennis* are discussed in Chapter 3. The unexpected result is that the California populations, which have been well-known and collected for over a century, still require an official description and name.

I also encountered the rest of the supposed "intermediate" populations of *Desmocerus*, taken from localities throughout Oregon, Washington, and British Columbia. I became acutely aware of the vexation that these specimens must have caused those earlier taxonomists, and it was resolved that additional comparative data from DNA, and internal anatomy might provide further evidence to help resolve species limits within *Desmocerus*. Since species are sets of individuals or populations that

regularly share the same gene pool, it could be expected that at least some minor anatomical traits arose and spread throughout the species, serving as unique identifying features. Likewise, DNA sequences obtained from individuals of the same species might provide support for distinct clades when examined in a phylogenetic analysis. Although care must be taken when using only a small set of genes and morphological characters, in many cases, even a relatively small data set can serve as a useful framework for evaluating evolutionary hypotheses, such as when certain traits may have developed, and why. Such questions are posed, and discussed at the end of Chapter 3.

This thesis, which ultimately resulted from a very simple question: “*how many lepturine species are there in the Pacific Northwest?*” is an example of what happens in the study of biodiversity (or anything else for that matter) when one begins digging into the details, and I believe it only scratches the surface. In the vast world of insects, wherever we look, we continue to find new forms and ways of being, new modes of communication, new chemicals, new microscopic landscapes—whole universes of mystery that are likely to keep curious minds occupied for millennia to come. *Desmocerus*, and the rest of the lepturines of the Pacific Northwest are a fairground for the scientific mind, with ample space left to be explored. My hope is that this work will help broaden the entranceway.

## REFERENCES – Chapter 1

- AntWeb. Available from <http://www.antweb.org>. Accessed 8 October 2014
- Abdel Moniem, H. A. M., & J. D. Holland. 2013. Habitat connectivity for pollinator beetles using surface metrics. *Landscape Ecology*, 28, 1251-1267.
- Bond, W.B. and T.K. Philips. 1999. Diversity, phenology, and flower hosts of anthophilous long-horned beetles (Coleoptera: Cerambycidae) in a southeastern Ohio forest. *Entomological News*. 110: 267-278.
- Heintze, A. 1925. Lepturinernas blombesök och sekundära könskaraktärer. *Ent. Tidskr.*, 46:21-34.
- Hubweber, L. and M. Schmitt. 2010. Differences in genitalia structure and function between subfamilies of longhorn beetles (Coleoptera: Cerambycidae). *Genetica*. 2010 Jan; 138(1):37-43. doi: 10.1007/s10709-009-9403-x.
- Kasuma, K. and M. Hayashi. 1971. Generic names and type species applied to Japanese Cerambycidae (Coleoptera). *Reports Facul. Sci.Shizuoka Univ.* 6: 95-126.
- Kevan, P.G. and H.G. Baker, 1983. Insects as Flower Visitors and Pollinators. *Ann. Rev. Entomol.* 28: 407-453.
- Kristiansen E., Ramløv, H., Højrup P., Pedersen S. A., Hagen L., and K. E. Zachariassen. 2011. Structural characteristics of a novel antifreeze protein from the longhorn beetle *Rhagium inquisitor*. *Insect Biochem Mol Biol.* 2011 Feb;41(2):109-17. doi: 10.1016/j.ibmb.2010.11.002. Epub 2010 Nov 13.
- Linsley, E. G. 1959. Ecology of Cerambycidae. *Annual Review of Entomology* 4: 99-138. [<PDF>](#)
- Linsley, E. G., and J. A. Chemsak. 1972. Cerambycidae of North America. Part VI. No. 1. Taxonomy and Classification of the Subfamily Lepturinae. University of California Publications in Entomology 69, xiii+138 pp, 2 pl.
- Linsley, E.G. and J.A. Chemsak. 1976. Cerambycidae of North America. Part VI, No.2. Taxonomy and Classification of the Subfamily Lepturinae. University of California Publications in Entomology 80, 186 pp.

- Mayr, E., Linsley, E. G., and R. L. Usinger. Methods and Principles of Systematic Zoology. New York-London: McGraw-Hill, 1953. 328 pp. Illus.
- Michelsen, A. 1963. Observations on the sexual behavior of some longicorn beetles, subfamily Lepturinae. Behavior 22(1/2): 152-166.  
<http://www.jstor.org/stable/4533068> .
- Miroshnikov A.I., 2000. On taxonomy of the genus *Enoploderes* Faldermann and distribution of its congener *Enoploderes sanguineum* Faldermann (Coleoptera Cerambycidae). Entomologia Kubanica, 1: 55-59.
- Pacific Northwest Moths. Available from: <http://pnwmoths.biol.wvu.edu/> Accessed 8 October, 2014
- Ray, A.M., Swift, I.P., McElfresh, J.S., Alten, R.L., and Millar, J.G. 2012. (R)-desmolactone, A female-produced sex pheromone component of the cerambycid beetle *Desmocerus californicus californicus* (subfamily Lepturinae). J. Chem. Ecol. 38:157-167.
- Robertson, J. A. 1988. Descriptions of the immatures of *Typocerus serraticornis* (Coleoptera: Cerambycidae), and new observations on biology, including “Varnish” production and usage by larva. The Pan-Pacific Entomologist. 64(3), 228-242.
- Sýkorová, M. 2008. Molecular phylogeny of the subfamilies Spondylidinae and Lepturinae (Coleoptera: Cerambycidae) based on mitochondrial 16S rDNA. Bachelor’s thesis, Faculty of Natural Sciences, South Bohemian University, Ceske Budejovice. <http://www.entu.cas.cz/popevol/lide/sykorova.pdf>
- Zachariassen, K. E., Li, N. G., Laugsand, A. E., Kristiansen, E., and S. A. Pedersen. 2008. Is the strategy for cold hardiness in insects determined by their water balance? A study on two closely related families of beetles: Cerambycidae and Chrysomelidae. J. Comp. Physiol. B 178, 977–984
- Zhang, Zhi-Qiang. 2011. “Phylum Arthropoda von Siebold, 1848 In: Zhang, Z.-Q. (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa 4138: 99-103.  
<http://www.mapress.com/zootaxa/2011/f/zt03148p103.pdf>

## CHAPTER 2: A Review of the Lepturine Longhorn Beetles (Cerambycidae: Lepturinae) of the Pacific Northwest, with a Key to Genera and Species

By Philip A. Schapker

### INTRODUCTION

#### *The Lepturines*

The Lepturinae is a subfamily of cerambycid longhorn beetles, often referred to as “the flower-visiting longhorn beetles,” or simply “the lepturines.” It is one of the mid-sized subfamilies, comprising about 1500 species in approximately 350 genera worldwide. Unlike the majority of longhorn beetles that are nocturnal, most lepturine species occur on flowers during daylight, making them easy to observe and collect (Fig. 2.1). Ecologists recognize lepturine species for their role as forest ecosystem pollinators (Gosling, 1986; Kakutani et al., 1990), and as decomposers, due to the tendency for lepturine larvae to develop in already dead, or decaying wood. For this reason lepturines are not commonly implicated as significant economic pests (Linsley, 1958b; 1959). In a four-year survey of a single, 800 meter forest edge in Ohio, Bond and Philips (1999) found 18 lepturine species in 14 genera on a wide variety of plants, with an average of 9.38 flower species visited, and a maximum of 16. The authors found a positive correlation between the number of different flowers used, and the abundance of individuals, suggesting that the most common lepturines are generalist flower feeders.

Although typically smaller and less colorful than species in the large subfamilies Lamiinae (>30,000 spp), Cerambycinae (~5,000 spp), and Prioninae (~2000 spp.), the lepturines are still a diverse and charismatic group. In the largest tribe, the Lepturini (a group of about 130 genera, and more than 1000 species thought to be closely related to the genus *Leptura* Linnaeus), there are commonalities in the basic body structure

(slender, with tapering bodies, and smooth-sided pronota) but a whole range of different colors, shapes and sizes – reflections of an equally diverse array of strategies for adapting to life on a flower. Bee mimicry, with bold black-and-yellow stripes, occurs in several genera like *Xestoleptura*, *Judolia*, and *Typocerus*. Other species, such as *Neobellamira delicata*, have taken on the slender form of a wasp. In the second largest tribe, Rhagiini (related to *Rhagium* – around 45 genera), the pronota are often sharply spined, the body forms are more variable, and a whole range of unique color patterns exist, but the tendency towards bee-mimicry appears to be absent. *Rhagium* itself is covered in thick black, grey and brown hairs, giving it a mottled appearance—a cryptic coloration suggesting something other than life on a flower. A number of smaller, more obscure tribes diverge even further from the appearance of the common lepturine, as exemplified in our fauna by the parallel, elongate forms found in the Encyclopiini, Xylosteini, and Rhamnusiini. Several atypical genera are difficult to place within the



**Figure 2.1.** Habitat of *Lepturobosca chrysocoma* and *Trachysida aspera aspera* at Colchuck Lake, Washington. Schapker is picking several specimens of both species from a single flower of Cow Parsnip, *Heracleum maximum*, in June of 2012.



Lepturinae, and occupy monotypic tribes. *Desmocerus*, for example, the sole genus in the tribe Desmocerini, exhibits a mix of characters shared by genera in several of the tribes, and its uniquely broad mandibles lack the internal pubescent fringe common to the rest of the subfamily.

### *Global distribution*

The bulk of lepturine species are distributed across the Northern Hemisphere, with many North American genera and species having close counterparts in Europe and Asia (Gressitt, 1953; Linsley and Chemsak, 1972, 1976; Bily & Mehl, 1989; Sama, 2002; Danilevsky, 2014a). The highest diversity of species are in the Asian continent (Aldlbauer et al., 2010; Danilevsky, 2014b; Cherepanov, 1990; Hayashi & Kimoto, 1984; Gressitt, 1951; Gressitt and Rondon, 1970; Hayashi and Villiers, 1985, 1987, 1989, 1995; Lobanov et al., 1981, 1982; Ohbayashi & Kojima, 1992). Although the mainland African continent appears to be almost entirely devoid of lepturines, [Madagascar](#) hosts a highly distinctive endemic lepturine fauna with 141 species in 43 genera – more than all the species that occur in [South America](#) (122 ssp.) and the Caribbean (4 spp.) combined (Ribardo & Cope, 2000; Bezark, 2012; Bezark & Monné, 2013; Di Iorio, 1998). At the extreme of its range in the eastern hemisphere, 44 species are currently known from Borneo, several of which are undescribed (Heffern, 2005). A similar, though less speciose fauna is also present in the Philippines. However, to the east of the "Wallace line" lepturines are suddenly absent, with just a single species known from New Guinea and none from Australia (Linsley, 1958b:103; Heffern, 2005). Greenland and the Hawaiian islands also lack lepturines (Böcher, 1988; Heffern, 2006).

### *The Pacific Northwestern lepturine fauna – history and present state of knowledge*

The Pacific Northwest region of North America is roughly defined as the area from British Columbia, south to the Siskiyou Mountain range of southern Oregon, and east to

the Rocky Mountains of Idaho and Southwest Alberta. The region as a whole is incredibly varied, with a suite of local biomes, from temperate rainforest along the coast range, to huge deserts east of the Cascades in Washington and Oregon. Nevertheless, a wide survey across plant and animal taxa tends to reveal endemic and closely-related sets of fauna in the region, indicative of a long history of shared geographical and a climactic events that have influenced and united the region as a whole (Linsley, 1958a; Galbreath et al., 2010). This makes the Pacific Northwest a sensible boundary within which to conduct a faunistic study.<sup>4</sup>

The earliest important contributions to the study of Pacific Northwest lepturine fauna were made by John L. LeConte, who described 38 of the species, and 6 genera now recognized to occur in our region. LeConte (1850; 1851) and LeConte and Horn (1883) also published the most important early revisions of the Cerambycidae to include Pacific Northwest taxa. Nearly a third of the modern generic concepts were described by Casey (1913, 1924), who, like LeConte, also described a large number of species. Unfortunately, many of Casey's names were based on only a few atypical specimens of previously-described species, and are now regarded as junior synonyms (see Appendix A: Checklist to Pacific Northwestern Lepturine). Swaine and Hopping (1928) and Hopping (1937), conducted the first revision of the Lepturinae of North America, and provided host and flower records, and photographs of hindwing venation for many of the species in our fauna. These authors placed many of Casey's generic names into synonymy, and arranged most of the species in the tribe Lepturini into a single large

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<sup>4</sup> **Note:** Hatch's *Century of Entomology in the Pacific Northwest* (1949:16) discusses Van Dyke's recognition of the unique fauna of PNW insects, which he termed the "Vancouverian fauna. Hatch: "I, on the other hand, am equally impressed by the forms which, although they ran all the way from the Atlantic Coast to the eastern foot of the Cascade Mountains, are unable to make that last climb to the Pacific." A footnote gives a long list of species as examples.

genus, *Anoplodera*. The key and review of Pacific Northwestern species by Hatch (1971) was based on that work.

The most recent modern revisions of North American Lepturinae were conducted by Linsley and Chemsak (1972; 1976), who removed from synonymy many of Casey's generic names, and defined several new ones. They also provided descriptions and keys to the genera and species, and a comprehensive review of flower records, host plants, other biological information, and distribution maps, based on a study of museum specimens. Since that work, subsequent publications have augmented our knowledge of many Pacific Northwestern species' distributions and life history (Penrose and Westcott, 1974a, 1974b; Hovore and Giesbert, 1976; Hovore and Penrose, 1982; Cope, 1984; Robertson, 1988; Westcott et al., 2006; MacRae and Rice, 2007; Swift, 2008; Hart et al., 2013), but these have not been reviewed comprehensively. Further refinements to the nomenclature or taxonomic composition of the Pacific Northwestern lepturines, particularly for Holarctic genera studied by European and Asian authors, have been tracked in the annual editions of the *Checklist to the Cerambycidae of the Western Hemisphere*, the most recent being Bezark and Monné (2013).

Ninety species, in 35 genera, representing seven lepturine tribes, are now thought to occur in the Pacific Northwest. Many of these species also extend into Alaska and California, or have close relatives elsewhere on the west coast. A number of these, such as *Pseudoxylosteus ornatus*, have their primary distribution in California, but extend into southern Oregon by way of the Siskiyou mountain range. Others, like *Typocerus serraticornis*, are probably more properly referred to as Great Basin species, which happen to have found themselves in the very southeastern tip of Oregon, in the area around the Steens Mountains. Because those areas are also occupied by species that have their primary distribution in the Pacific Northwest, or that occur throughout the entire west coast, we cannot rule out the possibility that *P. ornatus* and *T. serraticornis*

(both of them quite rare) have simply yet to be found more broadly in the Pacific Northwest. I have included these, and other similar species in the review.

The checklist to Pacific Northwest lepturine species in Appendix A at the end of this chapter is adapted, with additions and corrections from Bezark and Monné (2013). A full review of the literature related to our fauna revealed several important nomenclatural changes that have been recognized for some time by European and Asian workers, but apparently unknown to North American taxonomists. Following Miroshnikov (1998) and Miroshnikov (2000), the genera *Cosmosalia* Casey and *Pyrotrichus* LeConte are now listed as junior synonyms of *Lepturobosca* Linnaeus and *Enoploderes* Faldermann, respectively. The tribal system is arranged to reflect modern usage by the global taxonomic community. Other deviations from Bezark and Monné are also noted in Appendix A.

#### *The organization of genera in the review*

A few different strategies could have been employed for arranging the genera in the review, the simplest being to list them alphabetically. Another common method is to arrange the genera within each tribe according to their apparent phylogenetic relatedness (i.e., the arrangement in Linsley & Chemsak, 1972, 1976), and this is to some degree followed here. However, since the review is also intended to function as a field guide, in several instances I have placed genera closer together that might be easily confused, for example, the several genera that have striped elytral patterns that are actually quite distinct morphologically.

#### *A note on tribes*

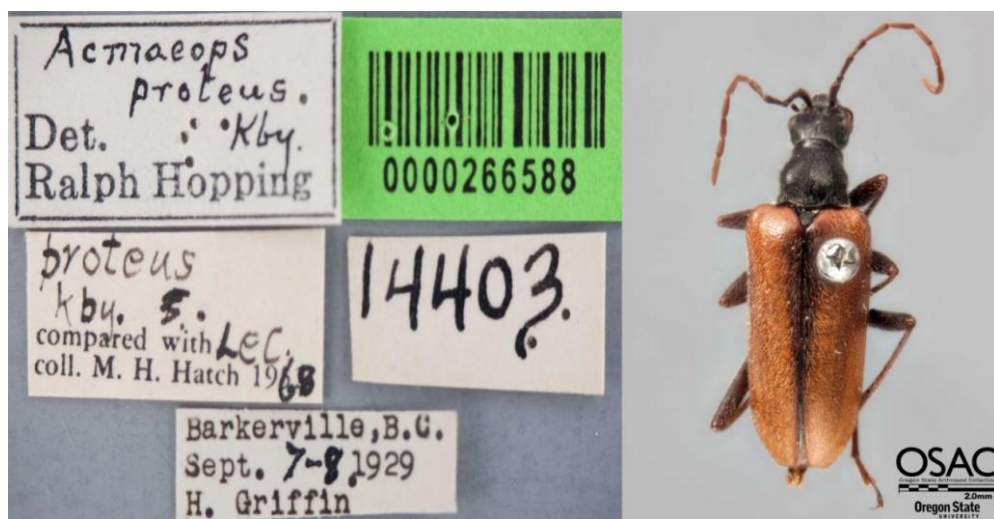
Nine tribal names within Lepturinae were recognized as available and valid by Bosquet et al. (2009) and Bouchard et al. (2011). However, many of these have never had a universally accepted definition, and the proper arrangement of the tribes continues to be a subject of debate, or simply confusion, among cerambycid

systematists (see: Gressitt and Rondon, 1970; Linsley and Chemsak, 1972; Sama, 1993). More recently, larval characters (Švácha & Danilevsky, 1989) and DNA sequence data (Sýkorová, 2008) have been used to assess the tribal hypotheses that were historically based on adult external morphology alone and led various authors to adopt widely different classification schemes (reviewed in Sýkorová, 2008). Vives (2000), for example, rejected a large, inclusive Rhagiini, restricting it to only *Rhagium* and *Rhamnusium* (see also Cebeci & Özdikmen, 2010). A phylogenetic study by Sýkorová (2008) supported the Lepturini (including *Desmocerus*), and Oxymirini (see Özdikmen, 2010) as natural, monophyletic lineages. In attempting to arrange the PNW tribes according to a system that will be broadly acceptable to the global taxonomic community, I have made some subjective judgements where competing hypotheses for our taxa exist, which I note in the review. It was outside the scope of this study to perform a detailed phylogenetic analysis of the tribes, and so my classification should be regarded as more or less preliminary at this time.

#### *The use of specimens in conducting the review*

In addition to reviewing the taxonomic literature, I was able to obtain specimens from all but three of the 90 species and subspecies in the Pacific Northwest. The Oregon State Arthropod Collection had 84 species and subspecies in its holdings, a large number of which bore determination labels from previous experts, in particular Melville Hatch, Ralph Hopping, E. G. Linsley and John Chemsak. Figure 2.2 shows a single specimen that was determined as *Acmaeops proteus* by Ralph Hopping, and then again in 1968 by Melville Hatch, who indicates that he compared it with the collection of the eminent John LeConte. Comparing the determined material to photographs of type specimens available online, along with their original descriptions, assisted me in my own species determinations. I also sorted and identified more than 1000 lepturine specimens that had arrived at the OSAC over the last few decades. To a more limited extent, I also viewed and accessed specimens from other museums, namely, the Collection of the

California Academy of Sciences, in San Francisco, the Essig Museum at the University of California, Berkely, and the Snow Museum at the University of Kansas. Given limited time and resources, I was not able visit some important Pacific Northwestern collections, like the Canadian National Collection or the Bill Barr collection at the University of Idaho. I am certain that a wealth of valuable information remains to be discovered in those, and other collections.



**Figure 2.2.** *Acmaeops pratensis* (Kirby in Richardson, 1837), with determination labels by Ralph Hopping and Melville H. Hatch

## DIAGNOSIS OF THE SUBFAMILY LEPTURINAE

The Lepturinae may be distinguished from other cerambycoids by the characters below (based on Linsley and Chemsak, 1972 and 1976). Following Lawrence and Newton (1995), Necydalinae is here treated as a separate subfamily from Lepturinae, not as a tribe Necydalini.

**Tarsi** padded beneath and *pseudotetramerous* (the fourth of fifth tarsomeres highly reduced and hidden within an expanded, bi-lobed third tarsomere.

(In Parandrinae and Spondylinae the tarsi are lacking ventral pads and distinctly *pentamerous*, or five-segmented.)

**Head** directed forward and rarely sub-vertical.

(The head in Lamiinae is often vertical or retracted with the genal margins always directed posteriorly.)

**Antennae** capable of laying backwards over the body and usually extending past the posterior margin ("base") of the pronotum (shorter in Parandrinae and Spondylinae).

The second segment as broad, or broader than long (longer than broad in Aseminae).

**Mandibles** often with a molar tooth, and (except tribe Desmocerini) densely fringed with pubescence on the inner margin. (Subfamily Aseminae lacks molar tooth.)

**Pronotum** either smooth or with pronounced tubercles laterally, but never with an elevated lateral margin (as in Prioninae).

**Stridulatory plate** on mesonotum divided longitudinally by a thin vitta, or line (except the tribe Xylosteini). (Mesonotum is also divided in Aseminae but undivided in Cerambycinae and Necydalinae.)

**Elytra** extending the length of abdomen (abbreviated in Necydalinae).

**Wings** with or without a closed cell in the anal sector (never present in Cerambycinae);

Vein 1A connected with  $2A_{1+2}$ . ( $2A_2$  is absent in Prioninae, and in Cerambycinae either  $2A_1$ , or  $2A_1$  and  $2A_2$  is absent.)

# KEY TO THE GENERA OF LEPTURINAE IN THE PACIFIC NORTHWEST<sup>5</sup>

1. Mandibles short, broad, without an internal pubescent fringe..... **Desmocerus**  
Mandibles slender, acute, with a pubescent frindge along inner margin..... 2
2. Pronotum with acute lateral spines or distinct tubercles and/or eyes entire..... 3  
Pronotum with sides sinuate, rounded or at most angulate, without spines  
or tubercles; eyes notched or emarginate..... 18
- 3(2). Eyes coarsely faceted (nocturnal species)..... 4  
Eyes finely faceted (diurnal species) ..... 5
- 4(3). Body brown or pale-colored; head with tempora absent; eyes deeply notched  
or emarginated..... **Centrodera**  
Body black with white or red markings on elytra, elongate and narrow;  
head with tempora inflated behind eyes; eyes shallowly emarginated.....  
**Pseudoxylosteus**
- 5(3). Tibial spurs subterminal, inserted into an emargination near tibial apex ..... 6  
Tibial spurs terminal, insterted at tibial apices ..... 7
- 6(5). Antennal segments short, stout, segments 3-11 subequal in length, not  
extending beyond middle of elytra; tempora subparallel; eyes entire.....**Piodes**  
Antennae with segments slender, elongate, extending well beyond middle  
of elytra; tempora convergent; eyes notched or emarginated.....**Stenocorus**
- 7(5). Eyes deeply emarginated or notched ..... 8  
Eyes entire, not deeply emarginated or notched, at most very shallowly  
concave along inside margin ..... 12
- 8(7). Front of head verticle, front and vertex meeting at an angle of nearly 90  
degrees; front short, distance from tips of mandibles to forward edge of eyes  
shorter than width between outside edges of genae .....9

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<sup>5</sup> Modified from Linsley and Chemsak (1972; 1976)



- Front of head oblique, meeting vertex at an angle of more than 90 degrees;  
front long, distance from tips of mandibles to forward edges of eyes greater  
than width across genae ..... 10
- 9(8). First segment of antennae shorter than third; hind tarsi with second segment  
much longer than third; intercoxal process of prosternum narrow, straight.....
- Encyclops***
- First segment of antennae longer than third; hind tarsi with second segment  
subequal to third; intercoxal process of prosternum broad, arcuate
- Enoploderes***
- 10(8). Hind tarsi with third segment cleft to base; basal margins of elytra not elevated  
around scutellum ..... 11
- Hind tarsi with third segment cleft about to middle; basal margins of elytra  
elevated around scutellum ..... ***Pachyta***
- 11(10). Pronotum transverse, sides strongly tuberculate or spined; eyes deeply  
emarginated ..... ***Neanthophylax***
- Pronotum longer than broad, sides very feebly tuberculate; eyes shallowly  
notched dorsally ..... ***Evodinus***
- 12(7). Prosternum with intercoxal process narrow, extending between coxae;  
antennae extending well beyond humeri; pronotal spines, if present, small,  
obtuse..... 13
- Prosternum with intercoxal process broad, extending over coxae, abruptly  
declivous behind; antennae very short; pronotal spines large, acute.... ***Rhagium***
- 13(12). Pronotum with disk convex, not flattened behind nor elevated on each  
side into a broad, obtuse tubercle..... 14
- Pronotum with disk flattened behind and elevated on each side into a  
broad, obtuse tubercle ..... ***Acmaeops (part)***

- 14(13). Head with tempora inflated, parallel, abruptly constricted at neck ..... 15  
 Head with tempora not inflated, convergent, not abruptly constricted  
 at neck ..... 16
- 15(14). Pronotum with lateral tubercles; prosternum with intercoxal process  
 extending behind coxae ..... **Leptalia**  
 Pronotum with sides rounded to angulate, not tuberculate; prosternum  
 with intercoxal process not extending beyond coxae ..... **Cortodera**
- 16(14). Elytra with basal margin not elevated around scutellum..... 17  
 Elytra with basal margin strongly elevated around scutellum; integument  
 bright metallic green or bluish ..... **Pseudogaurotina**
- 17(16). Head with front longer than broad; antennae with outer segments slender,  
 without poriferous areas ..... **Acmaeops (part)**  
 Head with front short; antennae with outer segments thickened, usually  
 with small poriferous areas ..... **Brachysomida**
- 18(2). Pronotum with hind angles acute and/or expanded over humeri..... 19  
 Pronotum with hind angles rounded, not acute nor produced over humeri..... 28
- 19(18). Elytra elongate, narrow, strongly attenuated posteriorly and strongly  
 constricted behind middle; ..... **Neobellamira**  
 Elytra not as above ..... 20
- 20(19). Elytra broadly to narrowly rounded or transversely truncate at apices..... 21  
 Elytra obliquely emarginated to acuminate at apices, outer angles usually  
 produced..... 24
- 21(20). Pronotum with sides sinuate, disk inflated or plane, base usually impressed  
 across middle, hind angles not toothed-appearing..... 22  
 Pronotum campanuliform (bell-shaped), hind angles tooth-like and produced  
 over elytral humeri, dorsal surface lacking an impressed area. Small species,  
 less than 1 cm in length..... **Grammoptera**

- 22(21). Head with front short, quadrate, tempora prominent, parallel; antennae stout, usually thickened ..... 23
- Head with front moderately long, tempora not prominently produced, usually convergent; antennae slender; body form short, stout ..... **Judolia**
- 23(22). Antennae elongate, longer than body in males, extending to a little behind humeri in females; Elytra about twice as long as broad, form robust, short....
- Dorcasina**
- Antennae short, subserrate, shorter than body in males, extending to a little behind humeri in females; form more elongate, elytra more than twice as long as broad ..... **Pygoleptura**
- 24(20). Antennae with distinct, elongate poriferous areas on outer segments..... 25
- Antennae lacking poriferous areas or these reduced to small round pits near apices of outer segments ..... 26
- 25(24). Pronotum deeply, transversely impressed at apex; antennae prominently expanded apically; form robust, tapering ..... **Typocerus**
- Pronotum not impressed at apex; antennae slender, segments not expanded apically; form elongate, subparallel ..... **Neostalerna**
- 26(24). Tempora not inflated, usually short and convergent; antennae slender, not subserrate, third and fourth segments together much longer than fifth segment in males ..... 27
- Tempora inflated, parallel; antennae subserrate, third and fourth segments together as long as fifth segment in males ..... **Pygoleptura**
- 27(26). Elytra about 2 ½ times as long as broad, color variable; antennae usually lacking poriferous areas ..... **Leptura**
- Elytra less than 2 ½ times as long as broad, always with transverse yellow and black bands; antennae with small poriferous areas ..... **Stenostrophia**

- 28(18). Intercoxal process of prosternum very narrow, not expanded at apex,  
coxal cavities wide open behind..... 29
- Intercoxal process of prosternum expanded at apex, coxal cavities closed  
or nearly closed behind..... 30
- 29(28). Pronotum barely impressed at apex and base, disk almost plane; palpi with  
apical segments dilated ..... ***Trachysida***
- Pronotum deeply impressed at base and apex, disk convex; palpi with apical  
segments dilated ..... ***Pidonia***
- 30(28). Eyes finely faceted; form small to moderate sized, not elongate and  
subparallel. Diurnal species. .... 31
- Eyes coarsely faceted; Body elongate and subparallel, color testaceous  
or pale yellow and brown; Body either large (2-3 cm long), with elytra  
prominently spined at inner angles at apex, or small (1-2 cm) with elytral  
apices rounded and unarmed. Nocturnal species..... ***Ortholeptura***
- 31(30). Elytra rounded, truncate, or shallowly emarginated at apices, angles not  
strongly produced; antennae never 12-segmented ..... 32
- Elytra strongly emarginated at apices, angles strongly produced;  
antennae 12-segmented or eleventh segment very strongly appendiculate,  
outer segments subserrate..... ***Stictoleptura***
- 32(31). Pronotum with disk strongly convex, basal and apical transverse impressions  
deep ..... 33
- Pronotum with disk very feebly convex, almost plane, apical and basal  
impressions very shallow. .... ***Anastrangalia***
- 33(32). Pronotum with basal margin sinuate to straight, disk often deeply impressed  
longitudinally; elytra not bilobed around scutellum; if bilobed, pronotum  
deeply impressed longitudinally..... 34

- Pronotum with basal margin broadly lobed at middle, disk not or barely impressed longitudinally; elytra bilobed around scutellum; body usually rather slender, subparallel ..... ***Xestoleptura***
- 34(33). Pronotum not or very shallowly impressed longitudinally, impression if present not extending length of disk..... 35  
 Pronotum deeply impressed longitudinally, impression extending length of disk..... ***Lepturopsis***
- 35(34). Elytra not strongly dehiscent at apex, sides not strongly sinuate behind middle; hind tibiae of males normal..... 36  
 Elytra rather strongly dehiscent at apex, sides strongly sinuate behind middle; hind tibiae of males often modified..... ***Brachyleptura***
- 36(35). Elytra with apices obliquely truncate, outer angles produced, surface always yellow and black banded ..... ***Strophiona***  
 Elytra with outer apical angles not produced, surface never yellow and black banded ..... ***Lepturobosca***

## REVIEW OF GENERA

*Tribe Lepturini Latreille, 1802*



**Figure 2.3a.** *Xestoleptura crassicornis* (LeConte, 1873), on leaf of blue elderberry, *Sambucus nigra cerulea*. Specimen: OSAC\_0000556476

***Xestoleptura* Casey, 1913**

Type species: *Xestoleptura corusca* Casey (by original designation).

*Xestoleptura* is one of several genera in the tribe Lepturini recognizable for its species' yellow and black-striped elytra. The genus is represented by 9 species worldwide, 6 of which occur in North America. The four Pacific Northwestern species are also found in California. The species *X. octonotata* is broadly distributed in Eastern North America, and *X. cockerelli* occurs on the Colorado Plateau. The species *X. rufiventris* (Gebler), *X. baechmanni* (Plavilstshikov), and *X. nigroflava* (Fuss), recently transferred from the genus *Anoplodera*, occur in Europe and Asia (Miroshnikov, 1998; Kadlec and Hájek, 2005).

Four species of *Xestoleptura* occur in the Pacific Northwest, three of which are very likely to be encountered, even by the casual collector. In the Oregon State Arthropod Collection, a huge number of specimens are present for *X. crassipes*, and to a somewhat lesser degree, *X. tibialis*. As might be expected (see Bond and Philips, 1999), these common species are both found on a wide variety of flowers. The two species *X. behrensi* and *X. crassicornis* are more scarce in the collection, however, and relatively little is known about their basic life history and biology.

*Xestoleptura crassicornis*, the species that is depicted at beginning of this section (Fig. 2.3) is intriguing. The species occurs throughout the west, from Washington and Idaho to southern California, but most of what we know about it is derived from two host plant, and three flower records. In August of 2013, Schapker found several populations of *X. crassicornis* scurrying around on the leaves of blue elderberry (*Sambucus nigra cerulea*) at high elevation in the Warner Mountains of Northern California. No individuals were observed on the elderberry flowers, but three specimens were observed clustered and apparently drinking from an open wound on the base of a

1 cm green stem. The only other lepturines known to feed on the leaves of *Sambucus* are those in the genus *Desmocerus*, for which *Sambucus* is an obligate host. *Sambucus* is known to contain cyanogenic glucocides, and it has been speculated that the brightly-colored species of *Desmocerus* sequester these as defensive chemicals. It is possible that *X. crassicornis* are following a similar strategy in the Warner Mountains. In addition to that observation, Jim Labonte of the Oregon Department of Agriculture informs me that since 1997, the ODA has turned up quite a number of *X. crassicornis* through its invasive species trapping and monitoring efforts across Oregon, indicating (1) that the species is attracted to plant volatiles, and (2), that it is probably more common than indicated by the number of museum specimens present.

Who knows if we will ever figure out *X. behrensi* — the species is incredibly rare, and may not visit flowers at all (no records exist). The most specific label data for this specimen at OSAC was collected in the Cascades of Oregon, at the H. J. Andrews Experimental Forest. It reads “ex *Tsuga martensiana*,” which may indicate a previously unrecorded host plant for the species. The locality is “ORE: Lane-Linn Co., HJ Andrews ExpFor, ½ mi N FisselPt, T15S R6E Sec 29 SE1/2, Elev. 4850’. VIII-20-[19]80.” Someone there should go find it again.



### Diagnosis of *Xestoleptura* in the Pacific Northwest.

*Xestoleptura* can be distinguished from other lepturine genera with similar elytral patterns (*Brachyleptura*, *Dorcasina*, *Judolia*, *Leptura*, *Stenostrophia*, *Strophiona*, and *Typocerus*) by its distinctive pronotum, which is convex and subequal to the width of the head, deeply constricted dorsally at both the anterior and posterior margins, and with the posterior margin strongly sinuate and rounded at the lateral angles. The elytra in *Xestoleptura* are strongly bilobed at the base (anterior), especially in *crassipes* and *crassicornis*. On the global scale, Miroshnikov (1998, figs. 26-39) has made a convincing case for the generic concept of *Xestoleptura* based on the structure of the male genitalia, which have the parameres distinctively notched on the inner angles.

### <sup>6</sup>Key to Pacific Northwest species of *Xestoleptura*

1. Femurs either pale or dark; if dark, then elytra only moderately densely punctate at base and suture entirely black (*berhensii* males) or bordered along its entire length by thick black line (*berhensii* females)..... **2**
- 1'. Femurs black. Elytra densely, closely punctate at base (anterior), the inner elytral margin never bordered along its entire length by a thick black line; elytra sub-parallel, not strongly tapering posteriorly. Pronotum with disc weakly convex or flattened, sometimes strongly bi-lobed posteriorly due to a longitudinal posterior impression. Antennal segments not strongly expanded at apices. Inner hind tibial spurs of males never modified into a plate-like structure. Length, 10-16mm. British Columbia to California, Rocky Mts. and Labrador..... ***X. tibialis***

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<sup>6</sup> Modified substantially from the key in Linsley and Chemsak (1976). I have attempted to include additional characters where the descriptions of elytral punctuation and the shape of the antennae might lead to confusion in individual specimens.

- 2(1). Antennae stout, segments usually thickened and expanded at apices. Elytra usually with humeral angles pale, and lacking a thick black stripe that runs the entire length of the interior elytral margin..... **3**
- 2'. Antennae slender, segments not distinctly thickened nor expanded at apices. Elytra usually with humeral angles darkened or black; elytral suture black, in females bordered along entire length with thick black line; elytra with punctures course, irregular, often confluent or sub-confluent latitudinally, punctures at base irregularly, sparsely punctate, becoming denser near interior margin. Abdomen and tibiae either orange, pale or dark. Pronotum with disc flattened or weakly convex, never strongly bilobed posteriorly. Males strongly tapering posteriorly, never with hind tibial spur modified into a plate. Length, 10-16mm. Western North America from British Columbia to California..... ***X. behrensii***
- 3(2). Elytra distinctly, irregularly, sometimes sub-confluently punctate, densely pubescent; elytra with anterior black band absent or reduced to two lateral spots in males, in females obliquely angled, sometimes meeting at the inner elytral margin, but often often fading medially to a pale brownish spot. Pronotum densely pubescent. Antennae black, yellowish or striped, not strongly expanded apically in males. Hind tibiae of males with the inside spur often modified into a plate. Length, 8-15mm. British Columbia to Colorado and California..... ***X. crassipes***
- 3'. Elytra very sparsely punctate and pubescent; pronotum moderately pubescent; elytra with anterior black band transverse, meeting horizontally at the inner elytral margin. Antennae always reddish, those of male strongly expanded at apices. Hind tibiae of males with normal spurs. Length, 10-17 mm. Western North America to southern California ..... ***X. crassicornis***



**Figure. 2.3b.** *Xestoleptura berthensii* (LeConte, 1873). Female (*left*, Ketchikan, Alaska) and male (*right*, HJ Andrews Experimental Forest, Oregon). (OSAC\_0000598975, \_0000143421)



**Figure. 2.3c.** *Xestoleptura crassicornis* (LeConte, 1873). 2 females (*far left*, Sequoia N.F., Cal., and *left*, Lassen N.F., Cal) and 2 males (*right*, both taken at Milk Creek Rd., 12 mi. SE Union Co., Oregon). (OSAC\_0000324233, \_0000324227, \_0000617561, \_0000617564).



**Figure 2.3d.** *Xestoleptura crassipes* (LeConte, 1857). 1 male (*left*, Mt. Rainier, Longmire, Washington) and 4 females (*middle three*, Mt. Rainier, Wash.; *right*, Bremerton, Wash.). (OSAC\_0000600330, OSAC\_0000600336, OSAC\_0000600361, OSAC\_0000600332).



**Figure. 2.3e.** *Xestoleptura tibialis* (Leconte, 1850). 1 male (*left*, 4000 ft. at Kelsay Camp in Umpqua N.F., Oregon) and 3 females (*middle-left*, Woods, Oregon; *middle-right*, 4200 ft., ½ mi. E. Frog Camp, Hwy. 242, Lane Co., Oregon; and *right*, Seaside, Oregon). OSAC\_0000583019, \_0000583016, \_0000582969, \_0000583018).

***Judolia*** Mulsant, 1863

Type species: *Leptura 6-maculata* Linnaeus (Casey designation, 1913)

*Judolia* is a diverse genus consisting of 17 species distributed throughout the Northern Hemisphere (see Ödikmen, 2011). Five of these species occur in the Pacific Northwest, including the commonly-encountered *J. instabilis*, one of the most variable lepturines in North America.

Many species in *Judolia* can be collected during the daytime in the spring and summer, often in natural areas where wildflowers are abundant. Based on records from museum specimens, most species in *Judolia* appear to be generalists in their use of flowers. In California and Oregon, *J. instabilis* is most frequently observed on lupines, which has led to some speculation that lupine might be a host plant. *Pinus* is known to be the host for *J. instabilis* in the southern extent of its range in Arizona and Mexico, as well as in British Columbia. A photo (#320303) recently posted to BugGuide.net by Mark Brown appears to be the first record of *J. gaurotoides gaurotoides* visiting a lupine, at Yellowstone National Park.

Like many lepturines that share a similar life history, species in *Judolia* usually bear a striking black-and-yellow patterning on their elytral shell, probably as an adaptation against predation. The patterning of some species, like *J. montivigans montivigans*, is fairly distinctive, and can be used reliably to identify the species on sight. On the other hand, the species *J. instabilis*, *J. gaurotoides*, and *J. montivigans* each possess three transverse black lines on their elytra which fluctuate in their extent, and each species can achieve almost exactly the same patterns, ranging from all black, to mostly yellow with just a few black spots. It is not surprising, then, that a careful re-examination of the specimens at OSAC identified by Melville Hatch as *J. instabilis* revealed several misidentified *gaurotoides*. Proper identification of these species requires the use of a microscope to examine subtle features in the shape and punctuation of the elytra and pronotum (see key, below).

Additional notes: The fossil species *Leptura antecurrens* Wickham, 1913: 295, described from the Miocene shales of Florissant, Colorado, is thought to belong to the genus *Judolia* (see Ödikmen, 2011). The chromosome number of *Judolia erraticus* was determined to be  $2n = 18$ . (Okutaner et al., 2012).



**Figure 2.4a.** *Judolia gaurotoides*  
*gaurotoides* (Casey, 1893). Yellowstone  
N. Park, 7-5-[19]27, Hopk[ins], US; H.E.  
Burke, Collector. OSAC\_0000026660



**Figure 2.4b.** *Judolia instabilis* (Haldeman, 1847).  
OSAC\_0000331475





**Figure 2.4c.** *Judolia montivigans montivigans* (Couper, 1864).  
OSAC\_0000331626

#### **Diagnosis of *Judolia* in the Pacific Northwest**

According to Linsley and Chemsak (1976, p. 47) the genus *Judolia* can be distinguished from other North American lepturines "by the convex disk and acute hind angles of the pronotum, and usually short, stout body form, and by the proportions of the basal antennal segments" (Linsley and Chemsak, 1976, p. 47). In *Judolia*, the scape (1st antennal segment) is "usually longer than, or subequal to the third segment, fourth shorter than the third, and the outer segments subopaque."

Several other PNW lepturine genera contain species which closely resemble *Judolia* in their overall form and coloration. These include the black and yellow species, *Stenostrophia tribalteata*, *Strophiona laeta*, *Xestoleptura tibialis*, and *Dorcasina matthewsii*, as well as the all- or mostly-black lepturines *Brachysomida atra*, *Cortodera nitidipennis*, *Lepturopsis dolorosa*, and *Brachyleptura vexatrix*.

### Key to Species of *Judolia* in the Pacific Northwest<sup>7</sup>

1. Pronotum with anterior edge bearing a distinct margin and narrow transverse depression. Elytra either all black, or black and yellow—never brown or red..... 2  
 Pronotum lacking anterior margin and transverse depression. Elytra either black with red stripes, or brown with two lateral spots ..... 4
- 2(1). Pronotum densely, confluent punctate. Scutellum deeply recessed below base of elytra. Elytral apices truncate to sub-truncate ..... ***J. montivigans***  
 Pronotum either separately or densely, but rarely confluent punctate.  
 Scutellum more-or-less even with the base of the elytra. Elytral apices either broadly rounded or narrowly, obliquely rounded, or pointed..... 3
- 3(2). Pronotum with a depression extending across the entire basal (posterior) edge.  
 Pubescence on pronotum either long and erect or short and depressed.  
 Elytra narrowly rounded or pointed at apex. Elytral pattern varies from all black to mostly yellow with a few transverse black lines or spots. Occasionally anterior, median, and basal spots connected by narrow longitudinal lines.....  

***J. instabilis***

 Pronotum with basal depression at sides only, pubescence usually long and erect in both sexes. Elytra broadly rounded at apex. Elytra yellow, with anterior, median and basal black lines or spots which vary in shape and extent, but are never connected by longitudinal lines..... ***J. gaurotoides***
- 4(1). Elytra frequently all black except for reddish basal band extending back from humeri (shoulders), apices always black. Males with tooth-like projections on metasternum near median suture and before hind coxal cavities. Southern Oregon to north central Arizona..... ***J. scapularis***  
 Elytra pale brown, usually with two large lateral dark spots at the middle.  
 Males lacking tooth-like projections on metasternum. Oregon to central California..... ***J. impura***

<sup>7</sup> The couplet for *J. scapularis* and *J. impura* is taken directly from the key provided by Linsley and Chemsak (1976: 49). I have not had the opportunity to view specimens of these species.



***Typocerus*** LeConte, 1850

Type species: *Leptura zebra* Fabricius (Thomson designation, 1860).



**Figure 2.5.** *Typocerus serraticornis* Linsley & Chemsak, 1976. Female taken from Little Cottonwood Creek, near Fields, Oregon.  
OSAC\_0000613179

The only representative of *Typocerus* in western North America, the charismatic *T. serraticornis* Linsley and Chemsak, is found along the shorelines of dry lakes in the Great Basin region, extending into southern Idaho and southeastern Oregon (Penrose, 1979). Larvae of *T. serraticornis* develop in the living stems of Indian ricegrass (*Oryzopsis hymenoides*), and employ the varnish, or silk-like substance in constructing their pupal chambers. This is apparently the only known case of silk production in the Cermabycidae (see Robertson, 1988). *Typocerus serraticornis* and the eastern North American *T. octonotatus* are among a very small handful of cerambycids known to use grass as a host plant. The host plants for the majority of *Typocerus* species remain unknown at present, while the rest utilize either decaying *Pinus* (for *T. zebra*, *T. sparsus*, *T. lunulatus lunulatus*, and *T. lugubris*) or a hardwood (in the case of *T. velutinus velutinus*) for their larval hosts (Linsley and Chemsak, 1976).

Aside from *T. serraticornis*, there are 14 additional *Typocerus* species, all of which are restricted to eastern North America. There is a related genus *Pseudotypocerus* Linsley and Chemsak, 1971 with 8 species in South America.

### **Diagnosis of *Typocerus* in the Pacific Northwest**

*Typocerus* is set apart from other lepturine genera primarily by the characters of the pronotum and antennae. In *Typocerus* the base of the pronotum is broad and unconstricted, and the outer antennal segments bare sizeable depressions, called “poriferous areas.” The antennal segments are usually expanded apically, which is most pronounced in the Pacific Northwestern *T. serraticornis*. The antennal poriferous areas may be used to distinguish *Typocerus* from *Leptura*, which has a similarly broad-based pronotum. Other genera that superficially resemble *Typocerus*, such as *Xestoleptura*, *Strophiona* and *Stenostrophia*, have a constriction at the base of the pronotum near the elytra, making the pronotum appear almost spherical from above.

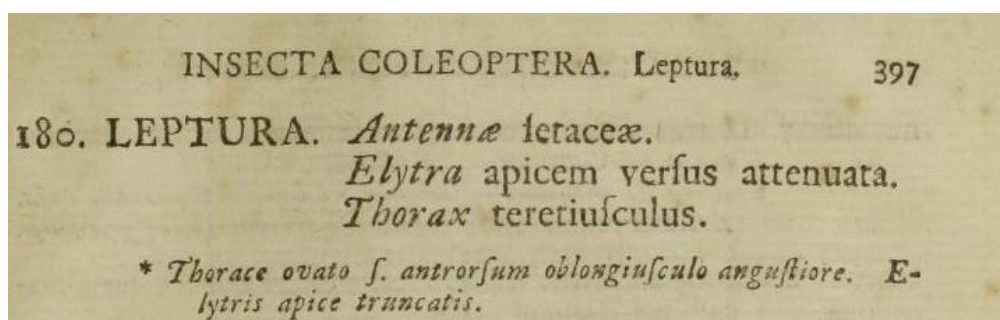
***Leptura (Leptura)* Linnaeus, 1758**

(*Stenura* Haldeman, 1847:62 (part); *Strangalia*; LeConte, 1850:327 (part);  
*Nakane & Ohbayashi*, 1963:9)

Type species: *Leptura 4-fasciata* Linnaeus (Westwood designation, 1840).

*Leptura* Linnaeus is the type genus for the tribe Lepturini, and the subfamily Lepturinae. Five species occur in the Pacific Northwest, all of them diurnal flower-feeders. They are usually medium- to large in size, and recognizable for the unique shape of their pronota, with the hind angles acute and extended over the humeral angles of the elytra, as well as other features appearing in the key to genera. The genus was historically comprised of a huge number of diverse species, but over time, systematists carved out little sections from that group to name new genera. (See Linsley and Chemsak (1976:91-92) for a detailed review of the complicated nomenclatural history of *Leptura*.)

*Leptura propinqua* and *Leptura oblitterata oblitterata* are both very common throughout the Pacific Northwest. Each species has been recorded from a wide variety of flowers, and their larvae reared from the decaying wood of numerous species of Pinaceae, and other coniferous hosts (see Linsley & Chemsak, 1976 for a complete review of habits). These are “typical” lepturines, however, other species in *Leptura* are known to utilize living plants as hosts. Cope (1984) observed larvae of the Pacific Northwestern species *L. anthracina* in healthy, living white fir (*Abies concolor*), occurring in the decaying tissue of scars high off the ground. The Californian species *L. pacifica* is apparently obligated to use living scrub oak *Quercus john-tuckeri*, as a host (see Swift, 2008).



**Figure 2.6a.** Original description of the genus *Leptura* Linnaeus, 1758.

#### Key to *Leptura* in the Pacific Northwest

1. Hairs on pronotum subdepressed and pointed backwards ..... 2  
     Hairs on pronotum sparse and erect ..... 3
2. Elytra black, or black with anterior (basal) portion reddish.....***L. anthracina***
- 2'. Elytra yellowish with black stripes and blotches, sometimes reduced to two  
     medio-lateral dots and an apical band (*common species*)..... ***L. obliterated***
3. Abdomen with golden hairs not obscuring surface. Elytra yellow-reddish or red  
     with a large discal black spot..... 4
- 3'. Abdomen densely clothed with golden pubescence. Elytra yellow always with  
     two medio-lateral spots and an apical band ..... ***L. propinqua***
4. Elytra red with large discal black spot extending over most of area. Pronotum  
     with short, erect bristles..... ***L. plagifera***
- 4'. Elytra with only very faint splotches on a mostly reddish-yellow or yellow-brown  
     base. Pronotum with hairs long and wavy (*rare species*)..... ***L. kerniana***



**Figure 2.6b.** *Leptura propinqua* Bland, 1865.  
OSAC\_0000583337



**Figure 2.6c.** *Leptura anthracina* LeConte, 1875.  
OSAC\_0000261812



**Figure 2.6d.** *Leptura kerniana* Fall, 1907.  
OSAC\_0000300419



**Figure 2.6e.** *Leptura plagifera* LeConte, 1873.  
OSAC\_0000583264



**Figure 2.6f.** *Leptura obliterated obliterated* (Haldeman, 1847) - two common elytral patterns. Left, OSAC\_0000497351. Right, OSAC\_0000338641.

*Leptura o. obliterated* (Fig. 2.6c) occurs from British Columbia and Washington, to Montana and Idaho, and south to the coastal ranges of California. The subspecies *L. o. soror* is restricted to the Sierra Nevada mountain range of California, and the eastern subspecies, *L. obliterated deleta* (LeConte, 1850) is apparently extremely rare in collections and its host plant is unknown. *Leptura obliterated obliterated* is quite variable in size, and obtains two extreme forms in its elytral coloration which often occur within the same locality. The form with the black markings reduced to just the apical and medial band closely resembles *L. propinqua* (Fig. 2.6d) as well as the Sierra Nevadan subspecies *L. obliterated soror*. However, the subdepressed pubescence of the pronotum should separate *L. obliterated* from *L. propinqua*, which has the pronotal hairs sparse and erect. The subspecies *L. o. soror* is indistinguishable from *L. o. obliterated* in its physical structure except the medial band is continuous across the central elytral margins.

***Dorcasina* Casey, 1913**

Type species: *Leptura matthewsii* LeConte (by original designation)

*Dorcasina* is represented by only two species worldwide, both of which are endemic to North America. One species, *Dorcasina matthewsii* (LeConte) inhabits the Pacific Northwest, ranging from British Columbia to California. Its congener, *D. grossa* (LeConte) is restricted to the Sierra Nevada mountain range of California. *Dorcasina* specimens are relatively sparse in the Arthropod collection at Oregon State.

**Diagnosis of *Dorcasina* in the Pacific Northwest**

Males of *Dorcasina matthewsi* are easily identified among our northwestern lepturines by their antennae, which are longer than the length of the body. According to Linsley and Chemsak (1976, p. 63), *Dorcasina* is recognized among the North American Lepturinae "by the elongate, opaque male antennae with segments three to five thickened. Also characteristic are the parallel tempora, the short front of the head, and the acute hind angles of the pronotum. Females have much shorter opaque antennae and the body form is very robust and parallel."

**Note on Pacific Northwest species**

*Dorcasina matthewsii* ranges from British Columbia to coastal central California, and reportedly uses a number of host plants, including *Sequoia sempervirens*, *Thuja plicata*, and *Libocedrus*. Garnett (1918, p. 250) reported rearing *D. matthewsii* from the sapwood of the redwood tree, and noted that *D. matthewsii* is "never found on flowers, but resting on leaves," including *Vaccinium ovatum* (Linsley and Chemsak, 1976). See also: Hardy (1926:30) and Hardy and Preece (1927:198).





**Figure 2.7.** *Dorcasina matthewsii* (LeConte, 1869).

OSAC\_0000496365



***Lepturobosca*** Reitter, 1913

(*Cosmosalia*, Casey, 1913:267)

Type species: *Leptura virens* Linnaeus, 1758 (monobasic)



**Figure 2.8.** *Lepturobosca chrysocoma* (Kirby in Richardson, 1837:179).

OSAC\_0000556501

One of the most commonly-encountered lepturines in the Pacific Northwest is *Lepturobosca chrysocoma*, which is immediately recognizable for the dense golden hairs that cover its entire body. The species is a generalist flower-feeder, and uses a wide variety of larval host plants across its broad range in North America (see <sup>8</sup>Gardiner, 1970, and range map in Linsley & Chemsak, 1972, fig. 49). The species is most active when flowers are blooming in June and July, and many of the ample museum specimens are caked in pollen. The other North American species, *L. nigrolineata* occurs primarily in the southwestern United States, in New Mexico and Colorado. Hatch (1971:135) included *L. nigrolineata* in his review of Pacific Northwest Coleoptera, indicating that the species also occurs in southwest Idaho and southeastern Oregon, but I have not been able to verify this based on the Hatch specimens in OSAC.

#### **A new genus for the Old “*Cosmosalia*” *chrysocoma*:**

Readers who are already familiar with the Pacific Northwest beetle fauna may have a hard time adapting to a new genus name for *L. chrysocoma*, which until recently had been the type species of the genus *Cosmosalia*. North Americans since Casey (1913) had thought that no species directly related to *Cosmosalia* existed outside the continent. However, a heretofore unrecognized publication by the Russian taxonomist A. Miroshnikov (1998) points out the uncanny resemblance of those species to the Palearctic [Lepturobosca virens](#) Linnaeus. He also provided illustrations of the male genitalia of all three species as additional evidence for the group’s relatedness, and grouped them into one genus, *Lepturobosca*, with *Cosmosalia* as a subgenus. (The original description of *Lepturobosca* Reitter, 1913, was published slightly earlier in the year, and has priority over *Cosmosalia* Casey, 1913; see Miroshnikov, 1998.)

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<sup>8</sup> “this species is very common during June and July in Ontario, Quebec and western Alberta, on flowers of many plants including *Cornus*, *Viburnum*, *Sorbus*, *Heracleum*, *Rosa*, *Ledum*, *Chrysanthemum*, *Achillea* and *Epilobium*. Near Laniel, Quebec, it was found breeding in decaying *Achillea* and *Epilobium*. Near Laniel, Quebec, it was found breeding in decaying stems of fallen black spruce, *Picea mariana* (Mill.) BSP. The larvae mined extensively in the decaying heartwood, packing the gallery with granular and fibrous frass. Pupation occurred at the end of the gallery and the adult bored its way to the outside. Near Sault Ste. Marie, Ontario, larvae were found working in the base of a dead *Populus*. In black spruce, this species was parasitized by the ichneumonid *Coleocentrus quebecensis* Provancher.” Gardiner (1970)

***Strophiona* Casey, 1913**

Type species: *Leptura laeta* LeConte (by original designation)

*Strophiona* is thought to consist of three species, all in North America. One species, *S. nitens* is found throughout eastern North America, and the two western species, *S. laeta* and *S. tigrina*, occur, occasionally in sympatry, from Washington to California. *Strophiona laeta* also extends into New Mexico (Linsley and Chemsak, 1976). The two western species are morphologically almost identical, but may be separated based on the subbasal elytral black band and the punctuation of the pronotum.

According to Linsley & Chemsak (p. 175), *Strophiona* “is characterized by the quadrate head, the shape of the pronotum with a convex, unimpressed disk, and the obliquely truncate, dentate elytral apices.” *Strophiona* is easily confused with the genus *Typocerus*, many species of which have similar elytral patterning. *Typocerus* however is separated by having the base of the pronotum broad and unconstricted, and antennal segments expanded apically, and bearing extensive poriferous areas on the outer antennal segments. *Strophiona* is also closely allied to *Lepturobosca* (*Cosmosalia*) in overall body form and, like *Lepturobosca*, exhibits long golden pubescence in similar area on the head, abdomen and pronotum. All three genera have truncate posterior elytral apices. In *Lepturobosca* the apices are somewhat rounded, while in *Strophiona* and *Typocerus* the lateral angles of the apices are produced outward and pointed.

***Stenostrophia* Casey, 1913**

Type species: *Leptura tribalteata* LeConte (by original designation)

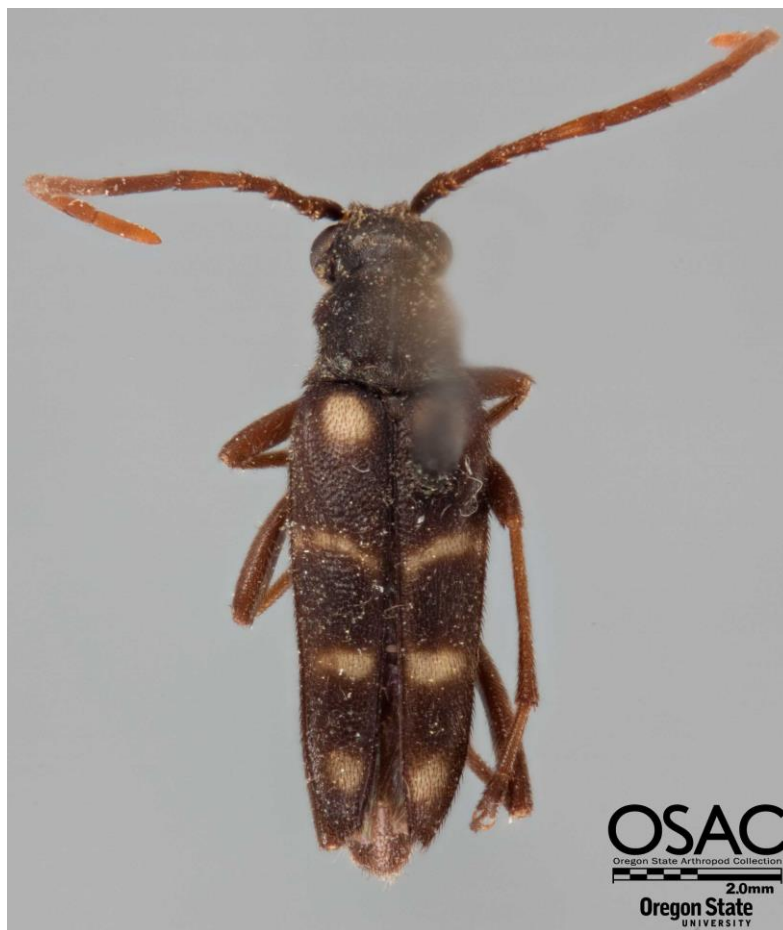
*Stenostrophia* is represented by three species worldwide, all in western North America. Two species occur in the Pacific Northwest, *S. amabilis* and *S. tribalteata*. The two subspecies of *S. tribalteata* can usually be separated by the color of their antennae, and the median transverse black band on the elytra. In *S. t. serpentina*, the median band is narrow and oblique at the center, while in *S. t. sierrae*, the band is broader, with the posterior edge meeting at the center of the elytra at a roughly 180° angle (See Fig. 2.9a).



**Figure 2.9a.** *Stenostrophia tribalteata serpentina* (Casey, 1891) (left, OSAC\_0000598388), and *Stenostrophia tribalteata sierrae* Linsley & Chemsak, 1976 (right, OSAC\_0000583780).

**Key to *Stenostrophia* species in the Pacific Northwest**

1. Pronotum with dense bands of golden pubescence at least on apical and basal margins; pubescence of elytra golden on yellow areas. Length, 7-12 mm.  
British Columbia to southern California to Wyoming.....***S. tribalteata***
- Pronotum lacking golden pubescent bands; pubescence of elytra all dark Length, 7-11 mm. British Columbia to southern Sierra Nevada..... ***S. amabilis***



**Figure 2.9b.** *Stenostrophia amabilis* (LeConte, 1857). Merion Forks, N. Santiam Hwy, Oregon. OSAC\_0000271206

***Grammoptera*** Audinet-Serville, 1835

(*Parallelina* Casey, 1913:247)

Type species: *Leptura praeusta* Fabricius (Westwood designation, 1840).

## Introduction

*Grammoptera* is a fairly large genus, with 34 species and subspecies presently recognized worldwide (see Adlbauer et al., 2010). Six species occur in North America. Two of the Pacific Northwestern species are generalist flower feeders, while *G. rhodopus* apparently lives in close association with a living host plant Coffeeberry, *Rhamnus californica* (see Cope, 1984; Gardiner, 1970). *Grammoptera* is one of several lepturines known from the Oligocene-era fossil beds in Florissant, Colorado. (see Linsley, 1958a, p. 302, table III.)

The author has observed *G. subargentata* foraging on thistle in early July in Corvallis, Oregon, near Avery Park. This is a new flower record for that species.

Only a handful of specimens of *G. rhodopus* are present at OSAC, from the following localities: Corvallis, Oregon (June 3, 1950, V. Roth), Dayton, Oregon (June 3, 1942, K.M. Fender), Cornucopia, Oregon (Aug. 7, 1937, Bolinger/Jewett) and Carkeek Park in Seattle, Washington (May 3, 1959, T.J. Growes).

## Diagnosis

*Grammoptera* has no close look-alike genera in the Pacific Northwest. The following characters of the pronotum make it easily identifiable: Pronotum campanuliform, hind angles tooth-like and produced over elytral humeri; sides sinuate, lacking tubercles; dorsal surface convex, lacking an impressed area. Smaller species, less than 1 cm in length.

**Key to *Grammoptera* species in the Pacific Northwest**

1. Head with tempora not inflated, convergent to neck ..... 2  
 Head with tempora inflated, usually subparallel, distinctly constricted  
 at neck. Length, 5-8 mm. Boreal North America.....***G. subargentata***
- 2(1). Elytra and integument metallic bluish or greenish; pronotum with disk not  
 inflated, rather finely, shallowly, subconfluently punctate; elytral humeral  
 area densely punctate. Length, 4-7 mm. British Columbia to Idaho and  
 southern California..... ***G. molybdica***
- Elytra and integument black; pronotum with disk inflated, moderately  
 coarsely, separately punctate; elytra coarsely punctate. Length, 6-10 mm.  
 Oregon to southern California. ....***G. rhodopus***



**Figure 2.10.** *Grammoptera subargentata* (Kirby in Richardson, 1837:184).  
OSAC\_0000555785



***Neobellamira* Swaine & Hopping, 1928**

Type species: *Strangalia delicata* LeConte (By original designation)

The genus consists of one species, *Neobellamira delicata* (LeConte, 1874), that is easily recognizable among Pacific Northwestern lepturine fauna for its modified elytra, which are strongly constricted at the middle, giving the species a wasp-like appearance. The nominative subspecies, *N. d. delicata* is found from western Oregon to the Sierra Nevada mountains of California. The species occurs on a variety of flowers, and its larvae have been taken from walnut wood (*Juglans*) (see Linsley and Chemsak, 1976:5). The latter authors note that “adults are readily attracted to codling moth baits and a long series was taken in a light trap during April at Linden, San Joaquin County, California.” The subspecies *N. delicata australis* Linsley and Chemsak, 1972, is restricted to southern California.

**Diagnosis among Pacific Northwestern Genera**

The strongly constricted elytra and bell-shaped pronotum, shallowly impressed at the base, will distinguish *Neobellamira* from other Pacific Northwestern genera. Three related genera found elsewhere in North America, *Bellamira* LeConte, *Strangalia* Audinet-Serville, and *Analeptura* Linsley and Chemsak, 1972, have antennae with distinct sensory poriferous areas on the outer segments (not present in *Neobellamira*) and characteristic pronota which differ from that of *Neobellamira*.



**Figure 2.11.** *Neobellamira delicata delicata* (LeConte, 1874).

OSAC\_0000588970

***Trachysida*** Casey, 1913

Type species: *Leptura mutabilis* Newman (by original designation)

*Trachysida* is represented by one species in the Pacific Northwest. *Trachysida aspera aspera* ranges from Alaska to Oregon and New Mexico, which is fairly common but so far known only to visit flowers of *Heracleum* and *Achillea* (see Gardiner, 1970; Linsley and Chemsak, 1976). Aside from the nominative subspecies, *Trachysida aspera* has two additional subspecies, *T. aspera rufescens* Linsley and Chemsak, 1976, known from Santa Cruz County, California and *T. aspera brevifrons* (Howden), which ranges from New Brunswick to Michigan and New York. The only other species in *Trachysida* is *T. mutabilis*, in Eastern North America. *Trachysida* possesses a pubescent sole on the first segment of its hind tarsi, a trait that is shared by species in *Ortholeptura* and *Dorcasina*, but is more common in the tribe Rhagiini.

***Lepturopsis*** Linsley & Chemsak, 1976

Type species: *Leptura dolorosa* LeConte (by original designation)

Linsley and Chemsak (1976) separated this genus, which consists of the two North American species *L. biforus* (Newman) and *L. dolorosa* (LeConte), on the basis of the longitudinally impressed pronotum and biolobed base of the elytra. *Lepturopsis dolorosa* is fairly common in the Cascades and Coast range of Washington and Oregon, and may be easily recognized among other Pacific Northwestern lepturines by the shape of its pronotum.

The original specimen of *L. dolorosa* was collected on the Northwest Boundary Survey (1857-1861), “East of Fort Colville” on the Columbia River, Washington and was described by the famous entomologist John LeConte. LeConte’s (1961) article is available on the [Biodiversity Heritage Library](#), and a photograph of the holotype specimen is viewable at Harvard’s [MCZ Museum of Comparative Zoology](#) website. Hardy and Preece (1926) note that on Vancouver Island “the adults are most frequently taken in flight, but are also found frequenting the flowers of *Spiraea* [= *Holodiscus*] *discolor* Pursh and sunning themselves on large leaves such as those of *Acer macrophyllum* Pursh.



**Figure 2.12.** *Lepturopsis dolorsa* (LeConte, 1861).

OSAC\_0000597099

***Pygoleptura*** Linsley & Chemsak, 1976

Type species: *Leptura nigrella* Say (by original designation).

Three species of this genus are known. All are restricted to the North American continent and all can be found in the Pacific Northwest, though they appear to be rarely collected. Relatively little is known about the life histories of *Pygoleptura* species, and flower records are only available for *P. nigrella nigrella*.

*Pygoleptura nigrella oregonensis* and *P. brevicornis* are found along the same range in the central Oregon cascades. Females of the two species are easily separated on sight—the outer antennal segments of *P. brevicornis* females are as broad as they are long, and the antennae barely extend past the pronotum, while the antennae of *P. n. oregonensis* females extend well past the pronotum, and the outer segments are longer. The males of the two species, however, may be difficult to distinguish definitely on their own without a series of both species for comparison. In the small amount of material available at OSAC, the posterior apices of the elytra are the most reliable character for separating the two species, and are given first in the key. The relative size and density of the elytral punctuation, the antennal length, and the degree to which the male antennal segments are serrate, or sub-serrate will be more difficult to judge when only a single specimen is available.

**Diagnosis of *Pygoleptura* in the Pacific Northwest**

The species of *Pygoleptura* are similar in appearance to other common species in the genera *Stictoleptura*, *Brachyleptura*, and *Lepturopsis*, but may be readily separated by the hind angles of the pronotum, which are flattened and produced outwards along the humeral angles of the elytra. In both *Pygoleptura* and in the genera just mentioned, the area behind the eyes (the temporal region) is prominently produced with a sharp constriction, forming a distinct “neck.” This character separates *Pygoleptura* from the all-black species *L. anthracina*, in which the head narrows gradually behind the eyes.

<sup>9</sup>Key to Species of *Pygoleputra* in the Pacific Northwest

1. Pronotum densely, closely punctate at middle; elytra with apices obliquely truncate..... 2  
 Pronotum sparsely punctate at middle; elytra with apices transversely truncate. Length 14-20 mm. Brit. Columbia to Idaho and Calif. ....***P. carbonata***
2. Elytra with apices obliquely emarginate, outer angles dentate. Elytra coarsely punctate at base, punctures large. Female antennae with segments 8-10 as broad as long; male antennae with segments 5-10 strongly produced apically, often backwards-pointing. Color always black; Length, 11-21 mm. Sierra Nevada to southern California and central Oregon.....***P. brevicornis***  
 Elytra with apices narrow, shallowly, obliquely truncate. Elytra finely, densely punctate at base, color often reddish testaceous with apical dark margins; female antennae with outer segments elongate; male antennae with segments 5-10 sub-serrate..... 3
3. Elytra usually brownish to reddish with dark lateral bands at apices. Pronotum moderately coarsely, densely, confluent punctate, basal glabrous area small. Elytra finely separately punctate at base, punctures smaller than those of pronotum. Length, 11-23 mm. Alaska to Newfoundland, south to Oregon and northern United States.....***P. nigrella subsp. nigrella***  
 Elytra black in both sexes. Pronotum rather coarsely, separately punctate on disk, punctures fairly sparse at middle. Elytra moderately coarsely, contiguously punctate at base, punctures about as large as those on pronotum. Length, 13-23 mm. Crater Lake and Cascades of Oregon.....***P. nigrella subsp. oregonensis***

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<sup>9</sup> Modified from Linsley and Chemsak (1976). The key provided by Linsley and Chemsak (1976) indicates that the basal elytral punctures in *P. brevicornis* are always larger than those of the pronotum. This may be true for the females, however the male specimens present at OSAC have a tendency for very large pronotal punctures, some of which are even larger than the large elytral punctures. The strongly produced and dentate elytral apices nevertheless confirm those specimens' identity as *P. brevicornis*.



Figure 2.13a. *Pygoleptura brevicornis* (LeConte, 1873) – male. OSAC\_0000268671





**Figure 2.13b.** *Pygoleptura brevicornis* (LeConte, 1873) – female. OSAC\_0000268673



**Figure 2.13c.** *Pygoleptura carbonata* (LeConte, 1861) – male. OSAC\_0000597220



**Figure 2.13d.** *Pygoleptura carbonata* (LeConte, 1861) – female. OSAC\_0000597219

***Stictoleptura* Casey, 1924:280**

(*Corymbia* Des Gozis, 1886:33; nec Walker, 1865; *Aredolpona* Nakane & N. Ohbayashi, 1957:50; *Melanoleptura* Miroshnikov, 1998:594; *Paracorymbia* subgen. *Batesiata* Miroshnikov, 1998:594)

Type species: *Leptura cribripennis* LeConte (by original designation)

28 *Stictoleptura* species are currently recognized worldwide, which are Holarctic in distribution. Only one species, *S. canadensis* (Olivier, 1795), occurs in North America. One of its three subspecies, *S. canadensis cribripennis* (LeConte, 1859), is found in the Pacific Northwest, ranging from British Columbia, south to California and the Rocky Mountains to New Mexico. The nominative subspecies, *S. c. canadensis* occurs in northeastern United States and Canada, and the subspecies *S. canadensis arizonensis* Linsley and Chemsak, 1976 is restricted to central and southeastern Arizona. Özdikmen and Turgut (2008) recently described a new species *Stictoleptura gevneensis* from Gevne Valley, Turkey, and commented on the taxonomic status of the genus. Cope (1984) reported that throughout Colorado and New Mexico, larvae of *S. canadensis cribripennis* utilize dead standing *Populus tremuloides* Michx.

**Diagnosis of *Stictoleptura* in the Pacific Northwest**

The color of the elytra, combined with the usually black-and-red striped antennae will readily distinguish *S. canadensis cribripennis* from the rest of the Pacific Northwestern lepturine fauna. The black forms are superficially similar to the species of *Pygoleptura* and *Leptura anthacina*, all of which have the posterior pronotal angles expanded apically. According to Linsley and Chemsak (1976), *Stictoleptura* is distinguished among other North American genera by the rounded posterior pronotal angles, the apically and basally impressed disk of the pronotum, the subserrate antennae, and the dentate elytral apices.





**Figure 2.14.** *Stictoleptura canadensis cribripennis* (LeConte, 1859).

OSAC\_0000558294

***Nealosterna*** Podany, 1961

Type species: *Leptura capitata* Newman (monobasic).

Linsley and Chemsak (1976:86) remarked: “Although Podany (1961) considered *Nealosterna* as a subgenus of *Alosterna*, we consider the species of the former as being sufficiently distinct from the type species of *Alosterna*, *Leptura tabacicolor* (Degeer), to warrant generic status. In our opinion *rubida* LeConte is more closely related to *capitata* Newman than to *tabacicolor* and we include that species in *Nealosterna* along with *capitata*.”



**Figure 2.15.** *Nealosterna rubida* (LeConte, 1873). OSAC\_0000597174

***Anastrangalia* Casey, 1924**

Type species: *Leptura sanguinea* LeConte (by original designation).

Two species of *Anastrangalia* occur in the Pacific Northwest, *A. sanguinea* and *A. laetifica*. There are 17 species and subspecies of *Anastrangalia* worldwide. Both Pacific northwestern species are fairly common on flowers in the spring and summer, and both use decaying Pinaceae spp. as larval hosts. Linsley and Chemsak (p.147, fig. 38) provide a range map for *A. sanguinea* but not for *A. laetifica*.

Female *A. laetifica* are easily recognized in the field by their distinctive red elytra marked with black spots. The males of *A. laetifica* are sometimes marked with a brown pattern on their black elytra, and Linsley and Chemsak found that the proportion of males with these markings in local populations varied along a geographical gradient. Tyson (1966) reared adults from *Pinus sabiniana* from Jamestown, Tuolumne Co., Cal., and from *Pinus attenuata* from Santa Cruz Co., Cal. "In both hosts the larvae mined in the rotten heartwood of stumps and limbs that had been dead for about 3 years. The adults emerged in early June" (p. 202). Shoening and Tilden (1959) cut an abundance of adults, pupae and larvae from stumps of *Pinus attanuata* that had been killed in a fire 3 years prior. The specimens were found within 2 feet of the ground, and the authors noted "the larval tunnels are concentrated in the deeper parts of the wood, at a depth of more than one or two inches, and seem to run generally in a longitudinal pattern to the tree." For other references to habits, see Gardiner (1970) and Gosling (1954). New distribution records are reported in MacRae and Rice (2007).

## Diagnosis

According to Linsley and Chemsak (1976:144), *Anastranglia* is characterized as a genus by its unique pronotum, which they describe as “subcylindrical, weakly convex, and shallowly impressed.” Note, for example, the contrast between the shape of the *Anastranglia* pronotum and that of *Nealosterna*, which is bell-shaped and has the posterior angles produced over the humeral angles of the elytra.



**Figure 2.16a.** *Anastranglia laetifica* (LeConte, 1859). Left: male, (OSAC\_0000332288). Right: female (OSAC\_0000273261).

## Key to *Anastranglia* species in the Pacific Northwest

1. Males with basal punctures of the elytra larger than those of the pronotum.  
     Female elytra usually brownish red.....***A. sanguinea***
- Males with basal punctures of the elytra equal in size to those of the  
     pronotum. Female elytra usually red with black spots .....***A. laetifica***





**Figure 2.16b.** *Anastrangalia sanguinea* (LeConte, 1859). *Left:* male (OSAC\_0000593939). *Right:* female (OSAC\_0000593965). This species can be found on a wide variety of flowers from May to August throughout the west coast and in a few scattered localities in the southwestern and northwestern United States. The basal punctures of the elytra are larger than those of the pronotum.

***Brachyleptura* Casey, 1913**

Type species: *Leptura vagans* Olivier (By original designation)

Seven species of *Brachyleptura* may be recognized, all of which exist in North America. Two species occur in the Pacific Northwest. Gosling (1954) records a peculiar instance of two eastern species, *B. rubrica* and *B. champlaini*, having an apparent toxic reaction to the pollen of the introduced ornamental plant species *Euonymus fortunei* var. *radicans*. These two species were the only lepturines in the study to visit the plant, and were stunned and unable to fly for day after feeding on the pollen.

**Diagnosis**

*Brachyleptura* can be distinguished by the strongly convex, seemingly "inflated" pronotum, the narrow intercoxal process of the prosternum, and elytra which are truncate and dehiscent (diverging) at the tips.

**Remarks on Classification**

Miroshnikov (1998) proposed that the species *B. vexatrix* and *B. pernigra* are easily separated as a new genus, *Toxoleptura* Miroshnikov 1998:411, based on the shared, unique structure of the male genitalia of both species, as well as by the placement of the antennal insertions (see Figures 137-145 in Miroshnikov (1998). Bezark and Monné (2013) list *Toxoleptura* as a junior synonym of *Brachyleptura*.

**Key to *Brachyleptura* species in the Pacific Northwest**

1. Elytral apices with inner angle rounded. Antennae with 5 outer segments expanded apically, nearly sub-serrate..... ***B. dehiscens***
- Elytral apices with inner angle acute. Antennae slender, outer segments not expanded. .... ***B. vexatrix***



**Figure 2.17a.** *Brachyleptura dehiscens* (LeConte, 1859). Female, OSAC\_0000593111. *Brachyleptura dehiscens* is brown- to reddish brown with the males being smaller and more lightly colored than the females. The species can be readily distinguished from *B. vexatrix* by the characters listed in the key.



**Figure 2.17b.** *Brachyleptura vexatrix* (Mannerheim, 1853). Male, OSAC\_0000143835. *B. vexatrix* may be distinguished from *B. dehiscens* by its narrower antennae that are not serrate or subserrate. The inner angles of the elytral apices are acute in *B. vexatrix*. North of the Siskiyou, the elytra of this species are generally almost entirely black, and occasionally with yellow spots. From Northern California southward into the Sierra Nevadas the elytra become more prominently yellow with black spots. This latter population was described as *Judolia convolvens* by Casey (1913), who commented that it should be easily distinguishable from Mannerheim's *vexatrix*, which was described from the Kenai Peninsula of Alaska: "The two are very different, as may be seen at once on reading Mannerheim's ample description" (Casey, 1913: 251).

***Ortholeptura* Casey, 1913**

Type species: *Ortholeptura oculea* Casey (by original designation)

Three species in *Ortholeptura* are known, two of which occur in the Pacific Northwest. All three species are nocturnal and apparently do not visit flowers. *Ortholeptura valida* is common and widespread, while *O. obscura* is very rare, known from only a handful of specimens taken from the Wallowa Mountains of Northeastern Oregon and Southeastern Washington (see Penrose, 1979). The third species, *O. insignis*, occurs along the coast of California.

Ray et al. (2011) discovered and synthesized a unique long-range sex pheromone produced by females of *Ortholeptura valida*. The pheromone is likely also used by other members of the genus (see Ray et al., 2006).

**Diagnosis of *Ortholeptura* among Pacific Northwestern genera**

The distinctive pale color and elongate body shape will serve to separate *Ortholeptura* from most Pacific Northwestern genera. The pronotum lacks the lateral tubercles or protrusions found in other similar-looking genera, such as *Centrodera*, and the abrupt constriction of the head behind the eyes will easily distinguish *O. obscura* from *Stenocorus obtusus*.

**Key to *Ortholeptura* species in the Pacific Northwest**

1. Elytra with apices spinose at suture, each with two or three sets of dark spots on disk, color testaceous. Larger species. Length, 12-28 mm. Common. Oregon to southern California along the Sierra Nevada.....***O. valida***
- Elytra with apices without spines, yellow at base and sides, oblique dark spots sometimes reduced to a single median pair. Rare. Smaller species. Length, 12-17 mm. Rocky Mts. of Oregon, Washington and Idaho.....***O. obscura***



**Figure 2.18a.** *Ortholeptura obscura* (Swaine & Hopping, 1928).

OSAC\_0000556500





**Figure 2.18b.** *Ortholeptura valida* (LeConte, 1857). OSAC\_0000583774. Adults are common at higher elevations. Tyson (1966) found larvae of *O. valida* in a rotten stump of *Abies concolor* (white fir) collected in April at Pinecrest, Tuolumne County, California. Larvae “pupated in chambers near the surface, and emerged as adults in late July.”

Tribe Rhagiini Kirby, 1837:178



**Fig. 2.19.** *Rhagium inquisitor* (Linnaeus, 1758).

OSAC\_0000621569.



***Rhagium*** Fabricius, 1775

(*Stenocorus* Geoffroy, 1762:221; *Stencorus*; Lamarck, 1817:312; *Hargium* Samouelle, 1819:210;

*Harpium*; Reitter, 1912:6; *Allorhagium* Kolbe, 1884:270)

Type species: *Cerambyx inquisitor* Linnaeus (Curtis designation, 1839)

*Rhagium*, with its dense short hairs, mottled coloration, and distinctly pronounced elytral costae, is one of the most impressive and recognizable lepturine genera. While at least 23 species are currently recognized in three subgenera worldwide, North America is home to just one of these, the Holarctic *Rhagium inquisitor inquisitor* Linnaeus. Adults of that species are found from late spring through mid summer, but are not known to visit flowers. The larvae bore into a variety of hosts, including *Abies*, *Pinus* and *Picea*, and construct a recognizable broad oval pupal chamber on the wood surface that is stuffed with fiber. Gardiner (1957) notes that adults are readily attracted to turpentine bait. The basic life history of *R. inquisitor* has been described by Gardiner (1970) and Hardy and Preece (1926) (under the junior synonym *R. lineatum* Oliv.).

Recently there has been a fair amount of physiological research using various species of *Rhagium*. In Siberia and Norway, *R. inquisitor*, and several congeners are able to overwinter under bark in areas that reach well below 0 °C, raising the question of how they are able to keep from freezing. In a laboratory setting, Zachariassen et al. (2008) found that *R. inquisitor* is able to supercool to -25°C. This remarkable feat is attributable to a protein in the *Rhagium* hemolymph, aptly named *RiATP*, or *Rhagium inquisitor* Antifreeze Protein, which is now thought to be the most potent antifreeze protein known (Kristiansen et al., 1999, 2011, 2012; Hakim et al., 2012, 2013). Hakim et al. (2012) determined the crystal structure of *RiATP* and used it to elucidate the molecular basis for ice binding in antifreeze proteins, which had been poorly

understood. *Rhagium* larvae have also been of interest to research into digestive enzymes (see Zverlov et al., 2003, and Chipoulet and Chararas, 1984).

*Rhagium inquisitor* (Linnaeus, 1758) is one of the earliest cerambycids to be described by European naturalists. Although Carolus Linnaeus is credited with naming *R. inquisitor* (it appeared in his 1758 *Systemae Naturae* as *Cerambyx inquisitor*), the species had actually already been discussed and illustrated by the German entomologist Johann Leonhard Frisch, in his 1730 *Beschreibung von allerley Insecten in Teutsch-Land* (Tom. 13, tab.14). The plate can be viewed on page 646 of the digital version available from [openlibrary.org](http://openlibrary.org).

*Rhagium* was reviewed by Casey (1913) and Cenek Podany (1964), both of whom recognized several distinct species within our current concept of *R. inquisitor*. Linsley and Chemsak (1972, p. 88) placed Casey's and Podany's names into synonymy and considered our species the same as the European form.

***Pseudogaurotina*** Plavilstshikov, 1958

Type species: *Gaurotes splendens* Jakowleff (by original designation)

Our region's only representative of the genus *Pseudogaurotina* is also one of the most eye-catching of the Pacific Northwest lepturine fauna—the bright metallic blue/green *Pseudogaurotina cressoni* (Bland, 1864). Its two subspecies are distinguished from one another by their elytral setae and punctuation, and their geographic ranges. The nominative subspecies, *P. c. cressoni* ranges along the Rocky Mountains from British Columbia to Colorado where it may be encountered at higher elevations (4,500 – 9000 ft) during the daytime on flowers of *Heracleum*, *Xerophyllum*, *Rosa*, and *Ranunculus*. The subspecies *P. c. lecontei* (Casey, 1913) has only been reported on honeysuckle, which is the host plant of its European and Asian congeners. *P. c. lecontei* occurs as far North as Mount Olympus and the North Cascades, and from the Wallowa Mountains of Northeastern Oregon, southward along the coast ranges to southern California, and in the Sierra Nevada mountains. Some populations contain individuals that are intermediate in their characteristics and may be difficult or impossible to identify without a series of specimens.

Five additional *Pseudogaurotina* species are recognized worldwide, all in the Holarctic. The other North American species, *P. abdominalis* (Bland, 1962), is found in the Northeastern United States and southeastern Canada. The type species, *P. splendens* (Jakowlev, 1893) occurs in southern Europe and Mongolia. *P. excellens* (Brancsik, 1874) occurs throughout Europe, *P. magnifica* Plavilstshikov, 1958 in the far eastern part of Russia, and *P. robertae* Pesarini & Sabbadini, 1997 in Sichuan Province, China. (see Adlbauer et al., 2010:131)

*Pseudogaurotina* is one of several Rhagiini genera that are superficially similar in form and recognizable for their metallic elytra. These genera include *Gaurotes* LeConte, 1850, *Carilia* Mulsant, 1863, *Paragaurotes* Plavilstshikov, 1921, and

*Tomentgaurotes* Podany, 1962. All of the north American forms of *Pseudogaurotina* were originally described within the genus *Gaurotes*, and subsequently referred to the subgenus *Gaurotes* (*Pseudogaurotina*) by Podany (1962). Chemsak and Linsley (1963) raised *Pseudogaurotina* to the status of genus, distinguished from *Gaurotes* by the lack of protuberant mesosternum.

Švácha and Danilevsky (1989), both specialists in the Palearctic Cerambycidae, have since cast doubt on the placement of *P. cressoni* and *P. abdominalis* within *Pseudogaurotina*.

“True affinities of the two North American species assigned to that genus by Linsley and Chemsak (1972) remain to be investigated. I have seen adults of *P. abdominalis* (Bland), and they almost surely do not belong to *Pseudogaurotina*, and may be related to *Carilia*<sup>10</sup>. Also, the adults of *Pseudogaurotina* are most frequently found on their host plants, while the two North American species seem to routinely visit various flowers (however, single flower record for *P. cressoni lecontei* (Casey) is *Lonicera* – Linsley et Chemsak, l.c., and this is the host genus for the European *P. excellens*). If the host plant records for *P. cressoni* (Bland) (*Pseudotsuga* and *Abies*) are correct, then it could be taken as another evidence against classifying them in *Pseudogaurotina*.” (p. 17)

To the best knowledge of the author, no detailed account of the biology of *P. cressoni* exists. The host plant records, *Pseudotsuga* and *Abies*, given for both subspecies of *P. cressoni* appear to have been introduced by Linsley and Chemsak (1972), presumably from specimen label data, but no indication is given as to their source of evidence.

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<sup>10</sup> The type species of *Carilia* Mulsant is *Leptura virginea* Linneaus (monobasic). Starzyk (1977) provided illustrations of the adult, pupae and larvae, and the male genitalia of that species, along with a description of its life history and biology in Europe. A series of 8 specimens in OSAC are determined *Gaurotes virginea* L. by Staudinger & Bang-Haas Co. (Det. 1922).

### Diagnosis of *Pseudogaurotina* in the Pacific Northwest

*Pseudogaurotina* is easily separated from other Pacific Northwest lepturine genera by its robust size and shining blue and green metallic elytra, which have the basal margin strongly elevated around the scutellum. *Brachysomida californica* and some species of *Desmocerus* can be somewhat metallic blue or greenish, but always have the scutellum more or less level with the base (anterior) of the elytra.

### <sup>11</sup>Key to *Pseudogaurotina cressoni* subspecies in the Pacific Northwest

1. Elytra with basal punctures moderately coarse, dense, subcontiguous; pronotum with disk distinctly punctate; pubescence usually evident on head and elytra.  
Length, 9-16mm. Rocky Mountains from Colorado to British Columbia.....

***P. cressoni cressoni***

Elytra with basal punctures usually very fine, sparse, greatly separated; pronotum with disk often impunctate; pubescence obsolete on elytra, very sparse on head.  
Length, 9-15 mm. North Wash. Cascades and Northeastern Oregon to Southern California..... ***P. cressoni lecontei***

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<sup>11</sup> Modified from Linsley and Chemsak (1972).



**Figure 2.20a.** *Pseudogaurotina cressoni cressoni* (Bland, 1864). Female.

OSAC\_0000259953. Note the relatively coarse, subcontiguous punctures at the base (anterior one-third) of the elytra. Unfortunately the very fine elytral pubescence is not visible here. NOTE: Individuals of both subspecies can be either blue, green, or purple.



**Figure 2.20b.** *Pseudogaurotina cressoni lecontei* (Casey, 1913). Female.

OSAC\_0000259953. Note the very finely punctured pronotum and base (anterior one-third) of the elytra. NOTE: Individuals of both subspecies can be either blue, green, or purple.

***Brachysomida* Casey, 1913**

Type species: *Acmaeops tumida* LeConte (by original designation)

There are five species in North America and two in the Pacific Northwest. One of these, *Brachysomida californica* is extremely variable throughout its range, and presents a challenging taxonomic puzzle that is presently open for further study (see extensive remarks by Linsley and Chemsak, 1972). Swift (2008) recently reported that *Brachysomida californica* utilizes the living roots of *Lomatium lucidum* (Torrey and A. Gray) and made further notes on the habits of that species, and its Californian congener *B. vittigera*.

**Diagnosis**

In treating this genus, Linsley and Chemsak (1972:127) remarked “the species presently assigned to this genus appear to represent a heterogenous group. They are placed together for convenience and because they are similar in form and do not fit into the definitions of other genera. The resultant genus may be recognized by the short, stout form, convergent tempora, short, thickened antennae, and transverse pronotum.”

<sup>12</sup>**Key to *Brachysomida* species in the Pacific Northwest**

1. Body subglabrous, usually all-black; pronotum nonpubescent, obtusely tuberculate at sides. Length, 7-13 mm. Northwestern United States to Colorado and Alberta. .... ***B. atra***
- Body distinctly pubescent, coloration variable; pronotum distinctly pubescent, sides sub-angulate; integument often with a metallic lustre, shining; Length, 7-16 mm. Washington to California. .... ***B. californica***

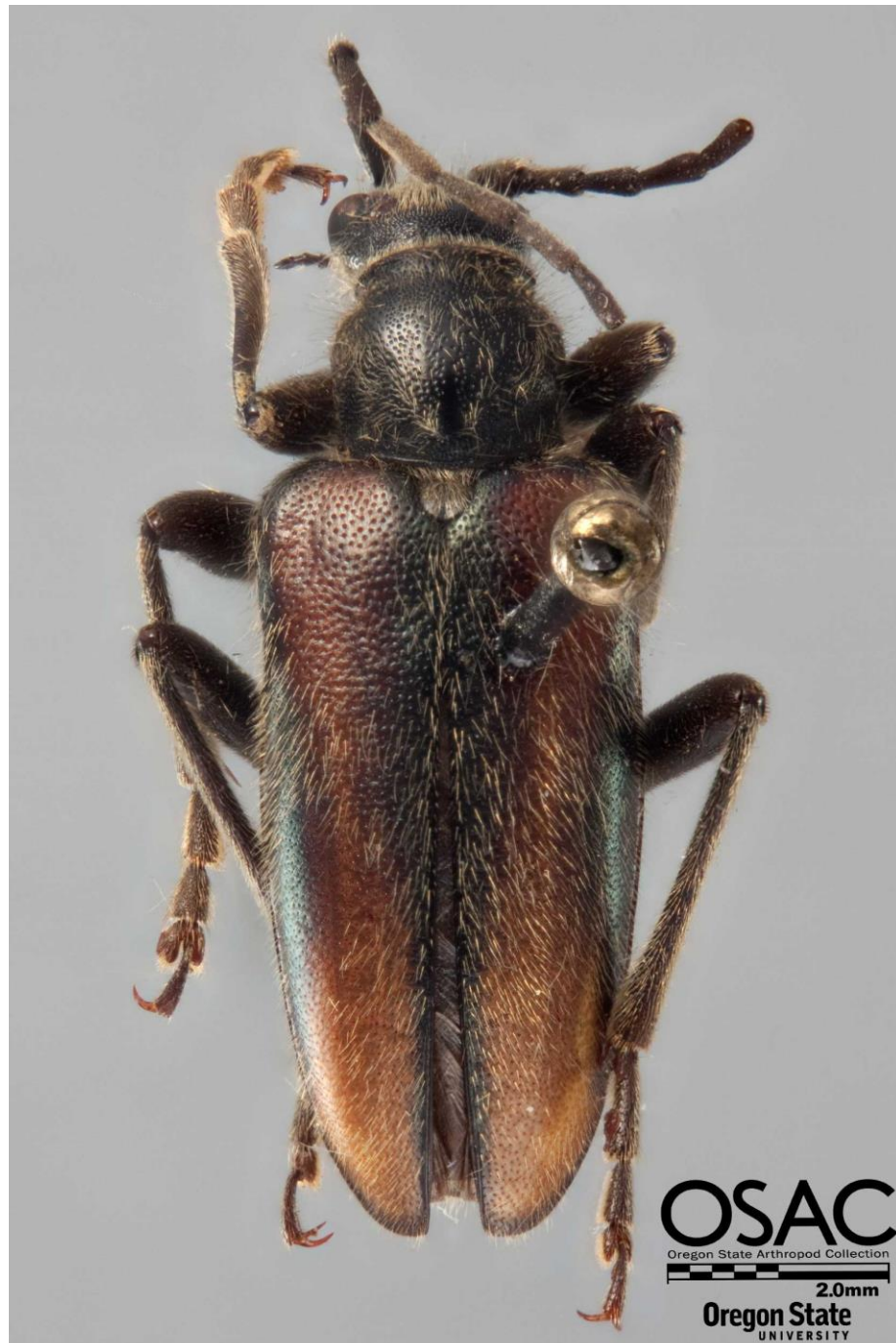
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<sup>12</sup> Modified from Linsley and Chemsak (1972).





**Figure 2.21a.** *Brachysomida atra* (LeConte), female. OSAC\_00000602611. Sanders Co., Montana. 5 mi. S. hot springs. 2900 ft., el. June 23, 1967. L. Russell.



**Figure 2.21b.** *Brachysomida californica* (LeConte). Collected at Monroe, Oregon. June 18, 1930. M. H. Hatch. OSAC\_0000602638

***Cortodera*** Mulsant, 1863

(*Acmaeops* LeConte, 1850:321 (part); *Leptacmaeops* Casey, 1913:219;

*Leptacmaeops* (*Acmaeopsilla*) Casey, 1913:240)

Type species: *Grammoptera spinulosa* Mulsant (= *Leptura humeralis* Schaller)

(Gressitt designation, 1951).

*Cortodera* is a large and taxonomically difficult genus distributed throughout the Northern Hemisphere, the species of which are diurnal, generalist flower feeders. The larvae of several species in both Europe and North America appear to be associated with the roots of *Ranunculus*, although detailed biological information for most of the genus is lacking.

Among the eight species of *Cortodera* in the Pacific Northwest, several display a substantial amount of variation in form and coloration, both within and between geographically disjunct populations. This led previous authors working with more limited specimen material to name a number of species which now appear to be merely varieties of the two common and widespread species *C. longicornis* and *C. subpilosa* (which have 10 and 5 junior synonyms, respectively). Hatch (1971) recognized 12 species of *Cortodera* in the Pacific Northwest, based on an early revision by Hopping (1947). Linsley and Chemsak (1972) synonymized several of Hopping's species, and added one new species and a subspecies, bringing the total to 9. Although still recognized here as a valid species, newly examined specimens from OSAC render the specific status of *C. nitidipennis* somewhat dubious, and these populations may eventually be recognized as varieties of *C. subpilosa*. Re-evaluation of the type specimens, along with a population-level study using DNA would be useful in solving the remaining problems in this genus, and may also restore some of the synonymized names to specific status.

### Diagnosis of the Genus

Unlike some of the charismatic Pacific Northwest lepturines that are readily identified on sight, *Cortodera* fall into a set of genera that can be difficult to distinguish without a microscope. These are typically bean-sized, black, brown, or red/tan-ish species. *Cortodera* may be distinguished by the following characters: eyes entire, finely faceted (diurnal species); antennae filiform, slender; pronotum laterally with slight, obtuse tubercles, the dorsal pronotal surface (disk) convex (not flattened behind nor elevated on each side dorsally into a broad obtuse tubercle, as in *Acmaeops proteus*); head with front short (elongate in *Gnathacmaeops pratensis*), tempora inflated, parallel, abruptly constricted at neck; tibial spurs terminal, inserted at apices of tibiae (subterminal in *Stenocorus* and *Piodes*); prosternum with intercoxal process narrow, not extending beyond coxae (as in *Leptalia*), mesosternum with intercoxal process laying well below margins of coxae.

### The Pacific Northwestern *Cortodera*

Most likely, a specimen caught in the Pacific Northwest and identified to *Cortodera* will turn out to be one of the three common and widespread species in our region, *C. subpilosa*, *C. militaris militaris*, or *C. longicornis*. For the most part, these three species are easily separated using the characters given in the key below. *C. subpilosa* is usually covered in long, thick, golden pubescence, giving the elytra a velvety appearance. Many of our museum specimens of this species are caked in pollen. The relative amount of pubescence varies substantially throughout its range however, sometimes making the species difficult to separate from the more densely pubescent forms of *C. militaris*.

The most reliable character to separate *C. militaris* from *C. subpilosa* is the presence of metasternal tubercles in males, which are lacking in *subpilosa*. In addition, both *C. militaris* and *C. longicornis* “usually” possess distinctly angulate trochanters on

their hind legs, which often form a 90-120 degree angle as they extend out from the coxae to join the femur. In *C. subpilosa* the trochanters are typically more elongate and smoothly rounded on the distal margin. However, in some of the series examined in both *C. militaris* and *C. longicornis* the trochanter angle varied between 90 and 150 degrees, making the distinction between “angled” and “rounded” difficult to judge. In such cases only male specimens provide a definitive identification with reference to the metasternal tubercles.

*Cortodera longicornis* is the most variable in form and coloration throughout its range. The species is most easily identified by the unique characteristics of its pronotum, which is strongly convex and only moderately punctate, usually with a median longitudinal glabrous area on the pronotal disk. Several discrete elytral patterns occur in *C. longicornis*, from tan with a median black stripe, to vittate, or all-black, or (more infrequently) black with humeral angles red.

Of the rest of the 8 Pacific Northwester species, several appear to be quite rare or otherwise restricted in their range. *C. robusta* is apparently known from only 3 female specimens of the type series, from Vantage, Washington, and *C. spuria* is also known from just a small handful of specimens (see Linsley and Chemsak, 1972). The subspecies *C. militaris* ssp. *constans* is restricted to southeastern Oregon and Modoc Co., California. The species *C. impunctata* and *C. coniferae* are only represented in OSAC by a few specimens each, though the latter apparently has a wide geographic range, from British Columbia to Northeastern Oregon and Colorado. Only 30 specimens of *C. impunctata* were available to Hopping (1947), and 29 to Linsley and Chemsak (1972). Three specimens in the OSAC collection from Kittitas Co., Washington, taken on “sunflowers” represent the first known flower record for that species, although it unclear what genus. The species *C. subpilosa*, *C. longicornis* and *C. nitidipennis* are found on *Balsamorhiza* in the sunflower family.

### Key to Species of *Cortodera* in the Pacific Northwest

1. pronotum moderately, to densely pubescent, punctuation either regularly distributed over pronotum, or bisected by a longitudinal glabrous<sup>13</sup> area..... 2
- 1'. pronotum glabrous, shining, punctuation, if present, very sparse and irregularly distributed. Color black, shining, elytra often with two broad, testaceous, longitudinal vittae..... ***C. impunctata***
  
- 2(1). pronotum moderately- to densely covered with long, erect pubescence. elytra never vittate ..... 3
- 2'. pronotum covered with short, appressed pubescence..... 4
  
- 3(2). Hind trochanters distinctly angulate on distal margin (often forming a 90° angle with respect to the femur, but as much as 150° in some specimens); males with metasternal tubercles; Elytra moderately densely pubescent and punctate throughout; punctures fine, dense, contiguous; elytra black or with reddish humeri or tan with suture narrowly black .....***C. militaris***  
(2 subsp.)
- 3'. Hind trochanters typically evenly rounded on distal margin (angle with respect to the femur usually more than 150°) males without metasternal tubercles; elytra densely, irregularly punctate, usually densely covered with long, flowing pubescence, in males sometimes completely reduced on the disk with only the sides and suture pubescent and elytra glabrous, shining. Elytra either black or tan/testaceous .....  
***subpilosa* or *nitidipennis*<sup>14</sup>**

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<sup>13</sup> *glabrous* – “smooth, hairless and without punctures or structures” (Torre-Bueno, 1937: *A glossary of entomology*)

<sup>14</sup> *subpilosa* is older and preferred name when ID is ambiguous. See discussion in Species Notes section.

- 4'. Hind trochanters usually distinctly angulate on distal margin, sometimes rounded.  
 Body elongate. Pronotum shining, punctures only moderately dense, disk strongly convex. Elytra with punctures at base separate, irregularly spaced. Males with metasternal tubercles. Elytra color usually one several patterns: all-black or dark brown, tan with black and brown vittae, or tan with black suture, or occasionally black with humeral angles red..... ***C. longicornis***
- 4(2'). Hind trochanters always evenly rounded to apex; otherwise not as in above..... 5
- 5(4). Elytra with punctures behind base rather fine, separate, often contiguous but not transversely confluent..... 6
- 5'. Elytra with punctures behind base coarse, transversely confluent; elytra all-black or vittate ..... 7
- 6(5). Elytra testaceous with suture narrowly black, basal punctures as large as those on pronotum, separated, becoming obsolete towards apex; pubescence short, subdepressed, and suberect; apices subtruncate ..... ***C. barri***
- 6'. Elytra testaceous, punctures at base slightly larger and denser near basal 1/3 then much finer and sparser toward apex; pubescence rather sparse, fairly long, subdepressed, erect hairs absent; apices rounded. .... ***C. spuria***
- 8(6). Elytra with hairs short, half the length of the second antennal segment (extremely rare species). .... ***C. robusta***
- 8'. Elytra with hairs long, at least the length of the second antennal segment.  
 Punctures at base of elytra larger than those of the pronotum, separated, becoming denser behind scutellum and transversely rugose, punctures becoming finer and shallower toward apex ..... ***C. coniferae***



**Figure 2.22.** *Cortodera longicornis* (Kirby in Richardson, 1837), male, displaying one of several possible elytral patterns. OSAC\_0000607133

#### **Notes on species of *Cortodera***

*C. barri* - In their original description, Linsley and Chemsak mentioned specimens from Harper, OR and Keerin's Ranch, Izee, OR. A third Oregon locality may be added from 1 female specimen, Sucker Creek Canyon, Malheur Co., Oregon, June 15-18, 1951 (Borys Malkin).



*C. coniferae* - Linsley and Chemsak (p. 120) note “this species differs from *C. spuria* primarily by the color of the elytra.” The two specimens at OSAC assignable to this species were taken at Mt. Rainier, Washington, VII-30-41, on frying-pan glacier (R.L. Furniss) and Flathead L., MSU Biol. Station, Montana, VII-31-1965 (Mary Richardson).

*C. impunctata* - New flower record: “Sunflowers,” from three OSAC specimens with label data: W[ashingto]n, Kittitas Co., Taneum Cr. Cutoff, 16 May, 1970. (Norma Berona).

*C. longicornis* (Fig. 2.22) - Considerable taxonomic confusion has resulted from the wide variation in size and coloration of this species, which led to the description of ten species now recognized as variants of *C. longicornis*. An additional point of confusion arises from the shape of the hind trochanter, which was described as distinctly angled by Linsley and Chemsak (1972). However, several series are present at OSAC in which individuals have trochanters ranging from very distinctly angled to more or less rounded (particularly demonstrated in series of 4 specimens from Bozeman, MT).

Individual populations of *C. longicornis* may be dominated by just one or two of the several possible phenotypes for elytral coloration. There is a marked tendency for vittate individuals near The Dalles, Oregon, and a series of 30 specimens from Creston, BC has only tan individuals. Of the 450 specimens available for study, only one series, from Durkee, Oregon (Wallowa Mtns.) has several individuals with elytral red humeral angles. The rest from that locality are either black or tan with a sutural black stripe.

A unique phenotype from Pipestone Pass, Montana, was identified by Loren Russell (1968) as *C. robusta*, which has contributed to that species being incorrectly reported from Montana by Hart et al. (2013).

OSAC is in possession of 1 paratype specimen of *C. oregonensis* Hopping & Hopping, 1947, and 1 paratype specimen of *C. harneyensis* Hopping & Hopping, 1947.

*C. militaris militaris* - Individuals have elytra either all-black, light brown with a narrow black sutural vittae, or black with red humeri. According to Penrose (1979), “an interesting phenomenon is found in the distribution of local populations with red and black individuals within the range of the nominate subspecies. All bicolored specimens seen are from Washington (Tacoma, Olympia and Chehalis), and Linsley and Chemsak’s statement that black *C. militaris* tend to have reddish humeri would seem to be valid only as regards specimens from the northern portions of the subspecies range.”

*C. militaris constans* - When Linsley and Chemsak described this subspecies from northeast California, the authors noted that the population was “remarkably constant” in its coloration (“color black, moderately shining, humeri always reddish...” Shortly after this description, Rick Penrose discovered several new populations from Lake Co. in SE Oregon which were anatomically similar to *constans*, but included specimens which deviated from the typical coloration. According to Penrose (1979):

“In the Lake County material ... 60 specimens (86%) are typical *constans*, 9 (13%) have elytra brown/vittate and 1 (1%) is wholly black. Inclusion of Oregon populations would therefore require a redefinition of *constans* to encompass predominantly black populations in which the red humeral condition is *usually* expressed. It should also be noted that four of the six specimens from Quartz Mt., in marked contrast to other Lake County specimens, have the reddish mark vaguely defined and restricted to the humeral angle. This reduction in maculation size, combined with the occurrence of a wholly black individual could indicate that transitional populations between *constans* and typical *militaris* remain to be discovered in the Klamath Basin. “

*C. nitidipennis* - Both Hopping and Hopping (1947) and Hatch (1971) expressed reservations regarding the specific delimitation of *nitidipennis*. Linsley and

Chemsak (1972), whose characterization was based on just 42 specimens stated “the irregularly punctate basal half of the elytra and very short discal pubescence will readily separate *C. nitidipennis* and *C. subpilosa*.” OSAC is in possession of 15 specimens studied by those latter authors, taken at three localities in the vicinity of The Dalles, Oregon. The specimens, which are all male, generally agree with the above description, as well as the original description by Casey.

However, in sorting through the unidentified *Cortodera* in OSAC, some difficulty arose in trying to segregate certain populations into the species *nitidipennis* and *subpilosa*. Several series with glabrous, *C. nitidipennis*-like males were accompanied by densely pubescent females, indistinguishable from the typical *subpilosa* (as described in Linsley and Chemsak, 1972). This may suggest that the females of *C. nitidipennis* have been historically mischaracterized<sup>15</sup>. Furthermore, the hind trochanters of *C. nitidipennis* specimens identified by Hopping, Hatch, and Chemsak are indistinguishable from those of *C. subpilosa*, and not distinctly angled as stated in Linsley and Chemsak’s description and key. Although I have not had the opportunity to inspect the type specimens of either species, the material in OSAC determined as *C. nitidipennis* by J. Chemsak is clearly unique in elytral punctuation and pubescence compared to those he determined as *C. subpilosa*, so I have retained both species as valid. Below I describe the populations which appear to represent transitions between *C. nitidipennis* and *C. subpilosa* which future revisionary work will need to address.

A series of 25 specimens from Kellogg, Idaho (June 17, 1935, Mrs. A. E. Griffin, collector) has 3 specimens determined as *nitidipennis* by Ralph Hopping, and a specimen labeled “*nitidipennis* Csy., compared with type, M.H. Hatch, 1968.” Both the males and females of this series have the relatively dense punctuation typical of *C. subpilosa*, but vary considerably in their amount of pubescence, with some

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<sup>15</sup> Casey described the female elytra as “nearly as in the [male], but with the rather coarse punctures very widely spaced, being separated by nearly three to five times their own diameters, becoming but slightly smaller apically but notably smaller and closer on the basal swelling near the scutellum.”

specimens appearing almost entirely glabrous and others, particularly the females, being indistinguishable from *C. subpilosa*, with long flowing golden hairs covering the entire elytra. Intermediates between the two extremes are also included, but in all cases the specimens have the thick hair line along the elytral suture typical of *C. nitidipennis*. A similar situation also exists in a large series taken at the Moiese National Bison Range in Montana.

In the Oregon and Washington material, several series have typical *C. nitidipennis* males that are more glabrous and shining than the Montana series, but the females, presumably of the same species, are larger and even more densely pubescent. Series with both males and females present include six specimens from Mosier Cr., Wasco Co., Oregon (IV-23-73, S. G. Jewett, Jr.), eight from Rowena Crest, Wasco Co., Oregon (4 May, 1973, Oman), and eight from 3 mi. S. Husum, Klickitat Co., Washington (24 May, 1977, Oman). The females of these series all appear to have the same dense, regular elytral punctuation of *C. subpilosa*, in contrast to Casey's description of widely separated punctures. I have only seen this latter characteristic in some of the males collected around The Dalles, Oregon, perhaps indicating that Casey incorrectly diagnosed the sex of his specimens.

Finally, it should be noted that the type specimen of *C. subpilosa* LeConte was collected in Oregon or Washington Territory, and based on the photograph available from Harvard's MCZ website, appears to be more or less glabrous on the elytral disk. Two male specimens at OSAC, taken at Olympia, Washington (June 10, 1935), having shining glabrous elytra, very much in agreement with Linsley and Chemsak's description of *nitidipennis*. One is determined "*subpilosa*, compared with type, M. H. Hatch, 1968." Due to this confusion, therefore, a conservative approach in applying names to any of the above-mentioned ambiguous populations would be simply to use the older name, *C. subpilosa* (LeConte, 1850).

*C. robusta* - At the time of Linsley and Chemsak's (1972) revision, *C. robusta* was known only from the type series consisting of three females from Vantage, Washington. Recently Hart, Cope and Ivie (2013) reported the species occurring in three localities in western Montana. One record is based on a male specimen at MTEC identified as *C. robusta* by those authors, and two records are from an M.S. thesis by Russell (1968), who surveyed the Coleoptera of Montana. Russell's specimen from "Pipestone Pass: Silver Bow Co.: eWn: 6000' el.", now at OSAC, is a relatively rare morph of *C. longicornis* with reddish humeral angles. The MTEC specimen, an all-black male with prominent metasternal tubercles and glabrous pronotal vitta, also appears to be a misidentified *C. longicornis* based on photos sent to me by Charles Hart. The second Russell specimen, from "Sanders Co: Hot Springs – National Bison Refuge", may have been lost, since a large portion of that collection was destroyed by dermestids before being transferred to OSAC (Loren Russell, personal communication).

*C. spuria* - No specimens present at OSAC.

*C. subpilosa* - Linsley and Chemsak (1972) note a population at Yellowstone National Park in which the elytral pubescence is reduced. This also occurs in a large series from the Moiese National Bison Range in Montana. See additional comments on *C. nitidipennis*.

***Acmaeops* LeConte, 1850**( *Gnathacmaeops*, Linsley and Chemsak, 1972:137)Type species: *Leptura proteus* Kirby (Casey designation, 1913)

*Acmaeops* consists of 10 species worldwide. Linsley and Chemsak (1972) considered one of the two northwestern species, *A. pratensis*, to be distinct enough to erect a new monotypic genus, *Gnathacmaeops* Linsley and Chemsak (1972:135).

“it differs markedly from *Leptura proteus* Kirby (the type of *Acmaeops*) and relatives in the short body form, elongate head, wide genal area below the eyes, and absence of pronotal tubercles.”

Following Sama (2002), *Gnathacmaeops* is normally treated as either a subgenus or junior synonym of *Acmaeops*. At the time of writing, *Gnathacmaeops* is still occasionally used as a valid genus by North American authors, as well as on BugGuide.net. (Accessed October 10, 2014).

**Key to the species of *Acmaeops* in the Pacific Northwest**

1. Pronotum with disk convex, not flattened behind nor elevated on each side  
into a broad, obtuse tubercle; Head with front longer than broad..... ***A. pratensis***
- Pronotum with disk flattened behind and elevated on each side into a broad,  
obtuse tubercle; head with front short, not longer than broad.....***A. proteus***



**Figure 2.23a.** *Acmaeops proteus proteus* (Kirby in Richardson, 1837). Note each side of the posterior dorsal surface of the pronotum is expanded into a large tubercle.

OSAC\_0000266588



**Figure 2.23b.** *Acmaeops pratensis* (Laicharting, 1784).  
OSAC\_0000609018



***Evodinus*** LeConte, 1850( *Brachyta* Fairmaire in Jacquelin du Val, 1864:185)Type species: *Leptura monticola* Randall (monobasic)

According to Linsley and Chemsak, “this Holarctic genus is closely related to *Stenocorus*. The two may be separated by the longer front of the head, different proportions of the antennal segments, apical spurs of the tibiae, and broad, less elongate form of *Evodinus*.”

Six species are recognized worldwide, with two species in North America, *E. lanhami* Lewis and *E. monticola* (Randall). *Evodinus monticola* is further divided into two subspecies. The nominative subspecies, *E. monticola monticola* is distributed throughout the eastern half of the continent, while *E. monticola vancouveri* occurs west of the Rocky Mountains. Authors prior to Linsley and Chemsak (1972) had *E. m. vancouveri* as a distinct species, *E. vancouveri*.

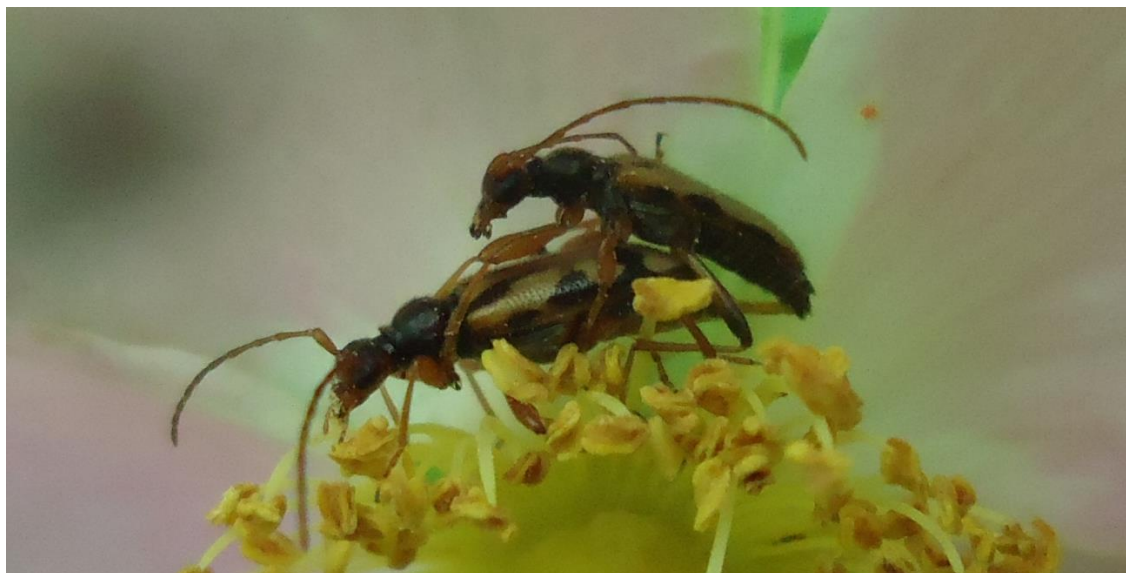
Gardiner (1970) summarized the habits of the eastern subspecies as follows:

“Adults fly in late May and throughout June in Ontario and Quebec, visiting flowers of *Trilium*, *Cornus*, *Viburnum*, *Ledum*, etc. Eggs are laid under bark scales of dead *Pinus*, *Picea*, and *Tsuga*. The larvae feed in the phloem for 12 to 14 months, then drop to the soil in which they pupate at the onset of cold weather. It is not known if they pass the second winter as adults or pupae. Occasionally this species is infected with *Isaria farinose* in the soil. It is also parasitized by the ichneumonid *Rhyssa persuasoria* (L.).” According to Craighead (1923), the earthen pupal chamber is constructed about 6 inches below the surface of the ground.

***Pidonia*** Mulsant, 1863

(*Grammoptera*; Thomson, 1864:141 (not Audinet-Serville, 1835); *Pseudopidonia* Pic, 1900:81; *Hapalosalia* Casey, 1913:200; *Pidnota*; Bayer & Shenefelt, 1969:5)

Type species: Of *Pidonia*, *Leptura lurida* Fabricius (Swaine and Hopping designation, 1928) (Pic designation?); of subgenus *Ceratopidonia* Linsley & Chemsak, 1976:119, *Pidonia quadrata* Swaine and Hopping (by original designation); of subgenus *Thesalia* Casey, 1891:36, *Acmaeops lisa* Leng (by original designation).



**Fig. 2.24.** *Pidonia scripta* pair copulating on blossom of Nootka Rose, *Rosa nootkana*, in Corvallis Oregon. May 30, 2014.

According to Mikio Kuboki (1981), who revised the genus on a global basis, “the genus *Pidonia* Mulsant is one of the most interesting genera of cerambycid beetles in the world.” Linsley and Chemsak (1976) recognized three subgenera in *Pidonia* and remarked that “most of the species which we have assigned to *Pidonia* s. str. are related to Asiatic forms and would fall in *Pseudopidonia* Pic as defined by Plavilstshikov (1936).”

### Key to the Pacific Northwestern subgenera and species of *Pidonia*

\*The following key is only slightly modified from Linsley and Chemsak (1976), and contains their original description (in quotations) of the subgenus *Ceratopidonia*.

1. Antennae with third antennal segment shorter than the scape..... 2  
 Antennae long and filiform in both sexes, outer segments at most feebly enlarged toward their apices, third segments distinctly longer than scape (***Pidonia s. str.***).  
 1 PNW species: Elytra pale, irregularly or obsoletely maculate, not vittate.  
 Length, 6-9 mm. Pacific Coast from southern Alaska to Central California

#### ***P. scripta***

- 2(1). Pronotum feebly constricted at base and apex, distinctly longer than broad in the male, less so in the female, surface coarsely, deeply punctate, including constricted areas; antennae thickened, with third and fourth segments subequal, those of male attaining apical one-fifth or one-sixth of elytra, outer segments not flattened and without poriferous areas, those of female heavier, attaining middle of elytra (**subgenus *Thesalia***). 1 PNW species: Elytra rufotestaceous with a small spot on each side of the elytra fuscous or blackish. Length, 7-9 mm. Western Washington and Oregon to Central Coastal California and the southern Sierra Nevada..... ***P. gnathoides***

“Pronotum strongly constricted at base and apex, wider than long in both sexes, finely, shallowly punctate; antennae short in both sexes, barely surpassing middle of elytra in male, scarcely attaining middle in female, those of male with segments six to ten flattened, expanded, bearing shallow elongate poriferous areas, those of female with outer segments thickened but not flattened nor bearing poriferous areas,” (**subgenus *Ceratopidonia***). 1 PNW species: Form moderately slender; integument pale testaceous, elytra with a faint brownish spot on each side near middle. Length, 6-7 mm. Coastal Pacific Northwest from Southern British Columbia to northwestern California ..... ***P. quadrata***

***Pachyta*** Dejean, 1821

(*Argaleus* LeConte, 1850:319; *Acmaeops*; Thomson, 1866:55 (not LeConte, 1850) ;  
*Anthophylax*; Blessig, 1873:232 (not LeConte, 1850); *Neopachyta* Bedel, 1906:93;  
*Pachyta* (*Linsleyana*) Podany, 1964:43)

Type species: *Leptura 8-maculata* Fabricius (=4-*maculata* Linnaeus)  
 (Westwood designation, 1840)

Ten species are presently assigned to *Pachyta* worldwide, most of them in Europe and Asia. Both of the North American species, *P. armata* and *P. lamed liturata*, occur in the Pacific Northwest and are easily recognized among our regional lepturine fauna. *P. lamed lamed* Linnaeus is found in Europe and Asia. The most recently described species is *P. gorodinskii* Rapuzzi, 2013, from western China.

**Diagnosis of *Pachyta* in the Pacific Northwest**

*Pachyta* is recognized by its robust form, broad, strongly tuberculate pronotum, elytra prominently raised around the scutellum, and eyes notched behind the antennae.

**Key to *Pachyta* species in the Pacific Northwest**

1. Elytra brownish to infuscated, about twice as long as broad, tapering apically.  
     Length, 10-17 mm. Alaska to Labrador and mountains of western North  
     America ..... ***P. lamed liturata***
- Elytra yellow except for narrow or broad black lateral stripes at apical half;  
     Elytra less than 1 ½ times as long as broad, strongly tapering posteriorly.  
     Length, 13-17 mm. Pacific Coast to California. .... ***P. armata***

***Stenocorus*** Geoffroy, 1762

Type species: *Leptura meridiana* Linnaeus (Plavilstshikov designation, 1936).



**Figure 2.25a.** Hind leg of *Stenocorus nubifer*, showing sub-terminal tibial spurs characteristic of the genus. OSAC\_0000621677

Four *Stenocorus* species occur in the Pacific Northwest. All the species can be quite variable in size, form, and coloration, but are reliably separated by the characters given in the key below. There are presently thought to be 30 species in the genus worldwide, 12 of which occur in North America.



**Figure 2.25b.** *Stenocorus obtusus* (LeConte, 1873), female.  
OSAC\_000602700

### Key to Species of *Stenocorus* in the Pacific Northwest

1. Pronotum with basal margin slightly sinuate, not broadly lobed at middle, disk densely punctate and pubescent ..... 2  
 Pronotum with basal margin strongly sinuate, broadly lobed at middle, disk sparsely punctate, shining; elytra with longitudinal yellow vittae or concolorous black. 17-27 mm. British Columbia to California ..... ***S. flavolineatus***
  
- 2(1). Elytra with apices rounded, occasionally feebly transversely truncate ..... 3  
 Elytra with apices obliquely truncate, very finely, densely punctate, often with larger punctures superimposed over minute ones; color variable. 9-21 mm. British Columbia to Montana, Southeast Oregon, Utah, and southern California ..... ***S. nubifer***
  
- 3(2). Elytra densely clothed with appressed pubescence, concolorous or margined with black, not longitudinally vittate; abdomen with last tergite notched at apex in females. 9-12 mm. British Columbia to southern California and Utah ..... ***S. vestitus***  
 Elytra sparsely pubescent, pubescence short and suberect or very short and depressed; males black or with pale longitudinal vittae, females usually pale reddish testaceous. 10-17 mm. Rocky Mountains from Colorado to British Columbia, and Nevada..... ***S. obtusus***



**Figure 2.25c.** *Stenocorus flavolineatus* (LeConte, 1854). OSAC\_143933





**Figure 2.25c.** *Stenocorus nubifer* (LeConte, 1859): one of many phenotypic variants. OSAC\_0000621677. (See also Fig. 2.25d.) This large and magnificent *Stenocorus* is usually quite easy to recognize on sight due to its size and striped elytral pattern. Some specimens however may lack the typical elytral stripes, or “vittae,” and occasionally small and narrow specimens appear similar to *S. vittiger*. According to L&C’72, *S. flavolineatus* can be distinguished from *S. vittiger* “by the minutely punctate, shining pronotal disk, strongly lobed basal margin of the pronotum, and narrower head.”





**Figure 2.25d.** Two more phenotypic variants of *Stenocorus nubifer*.  
(OSAC\_0000621647, \_0000621675)

### Taxonomic History of *Stenocorus*

*“Antennae a vasi ad apicem decrescentes, ante oculos positae. Elytra apice angustiora,”*

- (Geoffroy, 1762)

Geoffroy's original (1762) concept of *Stenocorus* was fairly different from our modern use of the term. His twelve species, which had antennae '*smaller from the base towards the tip, and positioned before the eyes*' included not only the familiar *Rhagium inquisitor* (Linnaeus, 1758) but also Linnaeus' *Leptura aquatica*, which today we recognize as *Donacia aquatica* in the family Chrysomelidae. Geoffroy's 3rd species, described as new (p. 223), appears to be the same as Linnaeus' *Leptura meridiana* (see reference in Latreille, 1758 p. 310). Fabricius (1775), who was the first to characterize *Stenocorus* in the standard Latin binomial format, included *L. meridiana* as his first species, but made no reference to Geoffroy.

Geoffroy used polynomial, rather than binomial taxonomic terms, and for this reason was placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature. The type for *Stenocorus* was later designated by Plavilstchikov (1936) as *Leptura meridiana* Linnaeus, 1758. The International Commission on Zoological Nomenclature (ICZN, 1994: Opinion 1754) later upheld this type designation, when it decided that 24 of Geoffroy's genus names, and *only* his genus names, could be considered available to taxonomy.

### Etymology

*Stenos* (narrowed) + *coros* (particularly), after the particularly narrowed elytra in some species.

***Piodes*** LeConte, 1850

Type species: *Piodes coriacea* LeConte (monobasic)

*Piodes* consists of a single species worldwide, *Piodes coriacea*, that is associated with sagebrush (*Artemisia*) in the Pacific Northwest, but the species is not commonly collected and little is known about its biology and life history. No specimens of this species are present in OSAC. Several photographs (#381604 - #381606) of a pinned specimen were posted to BugGuide.net by Andrew McKorney with the following data: Dalles, Oregon, USA. At Deschutes river around the sage bushes. March 27, 2010. Size: 17 mm.

Westcott et al. (2006) recently recorded a specimen of *P. coriacea* from Malheur Co., Adrian, 23-V-72; Wasco Co., Warm Springs Indian Res., 29-VI-76, both KJG. They remark that “apparently the few published references to this species occurring in Oregon originated from the type locality, "Or". However, when LeConte (1850) described this beetle Oregon was not a state. His reference can refer only to the Oregon Territory.”

**Diagnosis**

The following features distinguish *Piodes* from other Pacific Northwestern genera: Tibial spurs subterminal, inserted into an emargination near apex of tibiae. Antennae with segments very short, stout, almost subequal in length from third segment, not extending beyond middle of elytra; tempora subparallel; eyes entire.

*Tribe Oxymirini Danilevsky (in Althoff & Danilevsky, 1997)*

The taxonomic status of the tribe Oxymirini was recently discussed by Özdikmen (2010).

***Neanthophylax* Linsley & Chemsak, 1972**

(*Anthophilax* Horn in Leng, 1890:98 (part))

Type species: *Anthophilax tenebrosus* (LeConte) (By original designation).

**Key to *Neanthophylax* species in the Pacific Northwest**

1. Disk of pronotum convex, not longitudinally impressed, never densely pubescent.  
(*tenebrosus* ssp.)..... 2  
Disk of pronotum deeply, longitudinally impressed with a longitudinal callus on  
each side or pubescence dense..... 4
- 2(1). Elytra coarsely punctate and rugose..... 3  
Elytra rather finely punctate, rugae not coarse. Length, 13-18 mm. Wallowa Mtns.,  
Oregon. .... ***N. tenebrosus orientalis***
- 3(2). Pronotum with punctures on disk fine, separated, not rugose; lateral tubercle of  
pronotum obtuse. Elytra moderately coarsely punctate and rugose; pubescence very  
obscure. Length, 11-18 mm. Sierra Nevada Mts. to southern Oregon.  
***N. t. tenebrosus***  
Pronotum with disk densely, confluent, rugosely punctate; lateral tubercles of pronotum  
acute. Elytra coarsely punctate and rugose, pubescence pale, visible. Length, 11-17 mm.  
Cascade Range of Oregon and Washington to British Columbia.....***N. t. nigrolineatus***
- 4(1). Pronotum not densely clothed with depressed pubescence; elytra black and rugose or  
black and red, opaque and finely punctate at base only. Length, 12-19 mm. Rocky Mts.  
***N. mirificus***  
Pronotum densely clothed with short, depressed pubescence, surface subopaque; elytra  
vittate, finely, separately punctate over entire length. Length, 10-12 mm. Idaho.  
***N. pubicollis***

*Tribe Rhamnusiini Sama, 2009*

***Enoploderes*** Falderman, 1837

(*Pyrotrichus* LeConte, 1862)

Type species: *Enoploderes sanguineus* Faldermann, 1837

One species of this unusual, and probably very ancient genus occurs in the Pacific Northwest. *Enoploderes vitticollis* ranges from British Columbia to southern California and western Nevada, and is easily recognizable for its parallel form and the bright yellow stripes of thick pubescence adorning its head and pronota. Adults are active as early as February to June, but their activity is apparently confined to their host plants, as no flower records exist. The other two species are *E. bicolor* Ohbayashi, endemic to Japan, and *E. sanguineum* Faldermann, found in the Caucasus, Balkan Peninsula (Albania), Northern Iran, and Turkey (see Miroshnikov, 2000).

#### **Taxonomic status**

North American taxonomists (e.g., Linsley and Chemsak, 1972; Bezark and Monné, 2013) have historically placed *E. vitticollis* in the monotypic genus *Pyrotrichus* LeConte, 1862, although Kasuma & Hayashi (1971) demonstrated convincingly some time ago that *Pyrotrichus* was a synonym of *Enoploderes*. The placement of *Pyrotrichus* in the tribe Encyclopini LeConte, 1873, also followed by North American authors, is a relict of LeConte's original characterization of that tribe. Švácha and Danilevsky (1989, p. 14) separated *Enoploderes* and the Palearctic genus *Rhamnusium* Latreille as an informal tribe ("Tribe II") in the Lepturinae based on a series of unique larval characters<sup>16</sup>. Recently Sama, in Sama & Sudre (2009, p. 383) validly established the tribe Rhamnusiini based on the observation that the adult anatomy of the two genera was also distinct,

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<sup>16</sup> "Tribe II: Differs from Xylosteini as follows: Urogomphi (in the form of two spines) absent, but the caudal armature might have originated from the urogomphi (?). Lateral furrows nearly absent (A). Mandibular type II does occur, although not in its "classical" form. Mala broad (?A). Pleural lobes separate (P). Ampullae primitively seven." (Švácha and Danilevsky (1989, p. 14)

“chiefly the mandible without or with strongly reduced membranous setose area in front of the prostheca.” See also Cebeci & Özdikmen (2010).



**Figure 2.26.** Four specimens of *E. vitticollis* in the OSAC. The species is easily recognized among the PNW genera by the distinct yellow stripes on its head and pronotum, as well as its parallel form.

### Notes on species

The unusual life history of *E. vitticollis* may account for its scarcity in collections. The most detailed account of the behavior of *E. vitticollis* was made by Hardy (1944:16), who reared a number of specimens from the decaying heartwood of a dead maple, *Acer macrophyllum*, in January, 1935. Hardy found the larvae and pupae “in some numbers in a spot twelve feet from the ground.” Upon rearing his specimens in the lab, Hardy observed that “the adults, all females, evinced a decided aversion to daylight; as soon as exposed to its influence they burrowed into the friable rotten wood.” Jim Labonte (personal communication) reports finding adults in rotting portions of willow trees (*Salix* sp.) at Willamette Park, in Corvallis, Oregon, and similar observations have been made by Hovore and Giesbert (1976:350) and Cope (1984). The larvae are also reported from the following host plants: *Anus*, *Populus*, *Umbellularia*, *Ulmus procera* Salsib (see Cope, 1984).

The species’ distribution has not been reported in detail. No map is given by Linsley & Chemsak (1972), and OSAC holds just 5 specimens with vague locality information.

Tribe *Encyclopini* LeConte, 1873

***Encyclops* Newman, 1838**

Type species: *Encyclops pallipes* Newman (= *Leptura caerulea* Say) (monobasic).

The genus consists of 10 species worldwide. Two of these are endemic to North America, including the type, *E. caeruleus* (Say, 1826), and *E. californicus* (Van Dyke, 1920). The eight Palearctic species are *E. concinna* Holzschuh, 1991, *E. hubeiensis* Ohbayashi & Wang, 2004, *E. luteoscelis* Chou & Ohbayashi, 2010, *E. macilenta* (Kraatz, 1879), *E. olivacea* Bates, 1884, *E. ussuricus* Cherepanov & Cherepanova, 1975, *E. viridipennis* Makihara, 1978, and *E. x-signata* Chiang, 1981.

A single species, *Encyclops californicus* (Van Dyke, 1920) is thought to occur in the Pacific Northwest, but the majority of its range is in Coastal northern California. The PNW record is based on the existence of a single museum specimen (**Fig. 2.27**) taken in central Oregon in 1972 (see Penrose and Westcott, 1974b). The larvae of *E. californicus* are known to develop in *Rhamnus* and *Neolithocarpus*. No flower records have been reported.

**Diagnosis.**

The deeply emarginated eyes and narrow, elongate body, which is at least 4 times as long as broad will separate *Encyclops* from most Pacific Northwestern lepturine genera. In addition to the eyes, in *Encyclops californicus* the area between the front of the eyes and the mandibles is shorter than the width of the first antennal segment, serving to distinguish the species from the paler forms of *Leptalia macilenta*.

**Nomenclatural Act:**

*E. californicus* and *E. caeruleus* agree with the masculine gender of *Encyclops* Newman, and should be changed from *E. californica* and *E. caerulea*. (IZCN 30.1.4.3; ICZN 31.2)



**Figure 2.27.** *Encyclops californicus* Van Dyke, 1920. A single specimen at OSAC (shown above) has the following label data: "Lane Co., Blue River, H. J. Andrews Experimental Forest, mid-age Douglas-fir stand, 10-VII-1972, IBP Biome Survey, beating *Tsuga*." OSAC\_0000579556



***Leptalia* LeConte, 1873**

Type species: *Anoplodera macilenta* Mannerheim (by original designation)

*Leptalia* LeConte, 1873 is a monotypic genus consisting of the type species, *L. macilenta* Mannerheim, which is found in Montana, and in the Pacific Northwest from Alaska southward along the Cascade and Coastal ranges to Central California. According to Linsley and Chemsak (1972:99), *Leptalia* "is closely related to *Encyclops* and may be separated by the very feebly emarginate eyes, more strongly tuerculate sides of the pronotum, and arcuately constricted head behind the eyes." *Leptalia* was one of the three genera, including *Encyclops* and *Pyrotrichus* (now *Enoploderes*) to comprise LeConte's original concept of the tribe Encyclopini (see LeConte, 1873b).

Specimens of *L. macilenta* are abundant in OSAC. The life history and mating behavior of *L. macilenta* was described in detail by Chemsak and Powell (1971). Since the species was last reviewed by Linsley and Chemsak (1972), Penrose and Westcott (1974b) found teneral adults and pupae of *L. macilenta* in mid April "boring under the bark of decaying logs of bitter cherry, *Prunus emarginata* (Dougl.) Walp.," at Salem, Oregon, and also reared adults "from portions of a dead trunk section of big leaf maple, *Acer macrophyllum* Pursh., in McDonald Forest, near Corvallis, Benton Co." Recently Swift (2008) reared specimens from dead logs of *Quercus agrifolia* from Marin County, California.



**Figure 2.28.** *Leptalia macilenta* (Mannerheim, 1853).

OSAC\_0000 584281

*Tribe Xylosteini Reitter, 1913*

The tribe Xylosteini presently includes around 8 genera, which are parallel in form and usually have prominently spined pronota. These include (from [Wikispecies](#)): *Caraphia*, *Centrodera*, *Formosotoxotus*, *Leptorhabdium*, *Noctileptura*, *Palaeoxylosteus*, *Pseudoxylosteus*, and the type genus, *Xylosteus*. *Centrodera* is placed in Xylosteini based on larval characters discussed in Svacha and Danilevsky (1989:15), but the genus grouped closely with *Rhagium* in a molecular phylogenetic study by Sýkorová (2008, thesis in Czech). (See also: Sama, 1993)

***Pseudoxylosteus* Sama, 1993**

Type species: *Xylosteus ornatus* (LeConte) (Monotypie)

*Pseudoxylosteus* is a monotypic genus established by Sama (1993) for *Xylosteus ornatus* LeConte. *Pseudoxylosteus ornatus* is a nocturnal species found only in North America, where it ranges from the Siskiyou Mountains of southern Oregon to California. The species is instantly recognizable for its sharply-spined pronotum, and parallel black elytra with four inward-pointing white or reddish lines, that form an 'X' with the middle erased. An apparent mimic of *P. ornatus* in the subfamily Cerambycinae is also found in the Pacific Northwest. *Phymatodes obliquus* has the same elytral markings but does not have lateral spines on the pronotum.

*Pseudoxylosteus ornatus* is rare in collections, and very little is known about its habits. Linsley and Chemsak (1972) report *Abies* as a host, presumably based on specimen label data. Two specimens are currently posted to BugGuide.net which indicate an association with deer brush. Brady Richards' photo (#632217) was found on deer brush (*Ceanothus integerrimus*) at West Branch Feather River along Humbug Summit Road, Butte County, CA, July 10, 2010. Richard Waldrep's photo (#857948) was taken at Nevada City, 20 km E, Nevada County, CA, June 2, 2013; with note: "3 specimens found on the same Buckbrush at 1524 m. No others seen in the next week."

Hovore & Giesbert (1976: 350) report a specimen “beaten by E. F. Giesbert from dead portions of a living Elderberry bush (*Sambucus* sp.) in company with *Desmocerus auripennis auripennis* Chevrolat in July, near Buck’s Summit, Plumas County, California.”



**Figure 2.29.** *Pseudoxylosteus ornatus* (LeConte, 1873). A single specimen in OSAC, pictured here, has the following label data: OR: Josephine Co., Flat Top. T.36S-R.9W-sec.19. 4300'. Aug. 5, 1999. Dana Ross, leg. (42.425°N, -123.795°W). Dr. Paul Hammond, a Lepidopterist at OSAC, recalls having noticed the unusual lepturine specimen and deciding to preserve it while he was assisting Mr. Ross with moth specimens taken from a blacklight trap.

***Centrodera* LeConte, 1850**

(*Rhamnusium*; Haldeman, 1847; *Centrodera* (*Apatophysis*); Gressitt, 1947;  
*Parapachyta* Casey, 1913)

Type species: *Rhagium decoloratum* Harris (Thompson designation, 1864).

*Centrodera* has 13 species and subspecies worldwide, all species are nocturnal and restricted to the North American continent. Three species occur in the Pacific Northwest. The most common species, *C. spurca* is found from British Columbia to southern California and Utah, and is known from a variety of host plants, including *Quercus*, *Amelanchier*, *Shepherdia*, and *Arbutus* (see Linsley & Chemsak, 1972). *Centrodera dayi* Leech ranges from the Cascade Mountains of Washington to central California. Leech's (1963) original description of *C. dayi* includes figures and discussion on its biology. The host plant for that species is unknown. *Centrodera nevadica nevadica* ranges along the east side of the Sierra Nevada mountains, and was previously thought to extend as far north as southeastern Oregon and Idaho. Four specimens present at the OSAC now extend the range of *C. n. nevadica* to the eastern flank of the central Oregon Cascades. Label data are as follows: 2 males—Redmond, Oreg., August 13, 1930; 1 male and 1 female—Oregon, Deschutes Co., 13 mi. S. E. Sisters, July 24, 1965 bl. lt. (C. W. Baker, J. Cornell, and N. Virkii).

**Diagnosis.**

Brown or pale-colored insect with eyes deeply notched and coarsely faceted. The lateral spines of the pronotum and proportions of the antennal segments separate *Centrodera* from the nocturnal genus *Ortholeptura* and other pale-colored species, such as *Stenocorus obtusus*. In *Centrodera* the first antennal segment is always longer than the fourth, and the third longer than fourth.

### Taxonomic Status

*Centrodera* is atypical and difficult to classify among other lepturine genera. Based on larval characters, Švácha and Danilevsky (1987: 15) state, “the North American genus *Centrodera*... is a true Lepturine, belonging into the tribe Xylosteini.” Others, however, treat *Centrodera* in Rhagiini (see Özdikmen, 2010). Gressitt (1947, p. 191) thought *Centrodera* was subgenerically related to the Palearctic genus *Apatophysis* Chevrolat, 1860, however, Adlbauer et al. (2010) follow Danilevsky (1979) in treating *Apatophysis* within a separate subfamily, the Apatophysinae Lacordaire, 1869 (see also Rapuzzi & Sama, 2013).

### Key to *Centrodera* species in the Pacific Northwest

1. Elytra coarsely, closely punctate near base, surface never partially obscured by pubescence..... 2  
     Elytra finely, shallowly punctate near base..... ***C. nevadica nevadica***
  
2. Elytra with vestiture not conspicuous, hairs on basal half suberect, apices not dentate at suture; antennae of males with pubescence of outer segments bristling. Length 13.5-20.5 mm. Washington to central California. .... ***C. dayi***  
     Elytra with hairs at basal portion depressed, recurved, apices dentate at suture; males with pubescence of outer antennal segments smooth, satiny. Length 19-30 mm. British Columbia to southern California and Utah..... ***C. spurca***



**Figure 2.30.** *Centrodera dayi* Leech, 1963 – paratype female. Hood River, OR, “Mid. Col. Expt. Sta.” OSAC\_000061835 (one of 18 paratype specimens at OSAC).



*Tribe Desmocerini Blanchard, 1845*

***Desmocerus* Dejean, 1821**

Type species: *Stenocorus cyaneus* Fabricius (monobasic)

The tribe Desmocerini comprises just one genus, *Desmocerus*, the elderberry-boring longhorn beetles. *Desmocerus* is entirely restricted to the North American continent, and has no obvious sister group among the world's Lepturinae. The genus is anomalous in that its species have an obligate relationship with a living host plant, elderberry (*Sambucus*). Following Linsley and Chemsak (1972), *Desmocerus* is typically considered to consist of three species, and several subspecies. These are the eastern North American species, *Desmocerus palliatus*, and two western species, *D. californicus* (2 subspecies in central and southern California), and *D. aureipennis*, with four subspecies in the Pacific Northwest and California.

The following chapter presents two new species of *Desmocerus* from the Pacific Northwest, along with a revised taxonomy and phylogenetic analysis of the genus.



**Figure 2.31.** *Desmocerus aureipennis* Chevrolat, 1855. Taken in late July at approximately 7000 feet at the summit of Mt. Ashland, Oregon.



## REFERENCES – Chapter 2

- Althoff, J. & Danilevsky, M. L. 1997. A Check-List of Longicorn Beetles (Coleoptera, Cerambycoidea) of Europe. Slovensko Entomološko Društvo Štefana Michielija. Ljubljana, 64 pp.
- Adlbauer, K., Danilevsky, M.L., Drumont, A., Hubweber, L., Komiya, Z., Löbl, I., Morati, J., Rapuzzi, P., Sama, G., Smetana A., and A. Weigel. 2010. In: I Lobl & A. Smetana (ed.): *Catalogue of Palearctic Coleoptera. Vol. 6*. Stenstrup: Apollo Books, 924 pp.
- Bezark, L. G. 2012. Especies presentes en Brasil de la familia Cerambycidae: Lepturinae (Cerambycidae: Lepturinae species from Brasil). Website accessed August 27, 2014. [http://www.coleoptera-neotropical.org/paginas/2\\_PAISES/Brasil/Cerambycidae/lepturinae-brasil.html](http://www.coleoptera-neotropical.org/paginas/2_PAISES/Brasil/Cerambycidae/lepturinae-brasil.html)
- Bezark, L. G. and M. A. Monné. 2013. Checklist of the Oxypeltidae, Vesperidae, Disteniidae and Cerambycidae, (Coleoptera) of the Western Hemisphere. Available from: [plant.cdfa.ca.gov/byciddb/documents.html](http://plant.cdfa.ca.gov/byciddb/documents.html)
- Bily, S. and O. Mehl. 1989. Longhorn beetles (Coleoptera, Cerambyciae) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica. Vol. 22: 1-203.
- Böcher, J. 1988. *The Coleoptera of Greenland*. Nyt Nordisk Forlag Arnold Busck. Gressitt, J. L. 1951. Longicorn beetles of China. Longicornia, Paris. 2: 1-667. 22 pl.
- Bond, W.B. and T.K. Philips. 1999. Diversity, phenology, and flower hosts of anthophilous long-horned beetles (Coleoptera: Cerambycidae) in a southeastern Ohio forest. Entomological News. 110: 267-278.
- Bousquet Y, Heffern DJ, Bouchard P, Nears EH. 2009. Catalogue of family-group names in Cerambycidae (Coleoptera). Zootaxa 2321: 1–80. (22 Dec 2009)
- Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Ślipiński, S.A., and Smith, A.B.T. (2011). "Family-Group Names in Coleoptera (Insecta).", ZooKeys, 88, pp. 1-972. doi : 10.3897/zookeys.88.807
- Casey, T. L. 1913. Further studies amongst the American Longicornia. Memoirs on the Coleoptera, 4:193-388.
- Cebeci, H. & Özdikmen, H. 2010. A synopsis on the genus Rhamnusium Latreille, 1829 with a new record (Coleoptera: Cerambycidae) for Anatolian fauna from a new host plant, Liquidambar orientalis Miller (Hamamelidaceae). Munis Entomology & Zoology 5 (1): 131-139

- Chemsak, J.A. and J.A. Powell. 1971. Behavior of *Leptalia macilentata* (Mannerhiem), with a description of the pupa (Coleoptera: Cerambycidae). *The Pan-Pacific Entomologist* 47(2):101-104.
- Cherepanov, A. I. 1990. Cerambycidae of northern Asia. Volume 1 Prioninae, Disteniinae, Lepturinae, Aseminae, Brill, Leiden, 105-109.
- Craighead, F. C. 1923. North American cerambycid larvae. A classification and the biology of North American cerambycid larvae. Canada Department of Agriculture, Bulletin (new series) 27:1-239.
- Cope, J. 1984. Notes on the ecology of western Cerambycidae. *Coleopterists Bulletin* 38:27-36.
- Danilevsky, M. L. 2014a. A check-list of Longicorn Beetles (Coleoptera, Cerambycoidea) of Europe. Available from: <http://www.cerambycidae.net/> (Updated 17.01.2014)
- Danilevsky, M. L. 2014b. A check list of the longicorn beetles (Cerambycoidea) of Russia, Ukraine, Moldova, Transcaucasia, Central Asia, Kazakhstan and Mongolia. Available from: <http://www.cerambycidae.net/> (Updated 17.01.2014)
- Di Iorio, Osvaldo. 1998. Redescriptions, new combinations, synonymies, and new records of South American Lepturini (Coleoptera: Cerambycidae: Lepturinae). *Insecta Mundi*. Paper 365. <http://digitalcommons.unl.edu/insectamundi/365/>
- Galbreath, K. E., D. J. Hafner, K. R. Zamudio, and K. Agnew. 2010. Isolation and introgression in the Intermountain West: contrasting gene genealogies reveal the complex biogeographic history of the American pika (*Ochotona princeps*). *Journal of Biogeography*, 37:344-362.
- Gardiner L. M. 1970. Biological Notes on some Nearctic Lepturinae (Coleoptera: Cerambycidae), *The Pan-Pacific Entomologist*, San Francisco 46 (4): 284-288.
- Garnett, R. T. 1918. An annotated list of the Cerambycidae of California. *Canadian Entomologist*, 50:172-178, 205-213, 248-252, 281-284. <[archive.org](http://archive.org)>
- Geoffroy, E. L. 1762. Histoire abrégée des insectes qui se trouvent aux environs de dans laquelle ces animaux sont rangés suivant un ordre méthodique. Durand. 1: xxviii + 523 pp., pls I-X.
- Gosling, D. C. L. 1986. Ecology of the Cerambycidae (Coleoptera) of the Huron Mountains in northern Michigan. *GT Lakes Entomol.* 19:153-162.
- Gressitt, J. L. 1953. Notes on nomenclature and relationships of some Palearctic and Nearctic Lepturinae *Pan-Pacific Entomologist*, 29(4): 207

- <sup>17</sup>Gressitt, J. L. & J. A. Rondon. 1970. Cerambycidae of Laos (Disteniidae, Prioninae, Philinae, Aseminae, Lepturinae, Cerambycinae). Pacific Insects Monograph. Bishop Museum, Honolulu. 24:1-314
- Hardy, G. A. 1926. Cerambycidae of Vancouver Island (Preliminary annotated list). B. C. Prov. Mus. Rep., 1925: 24-33, pls. 4-5.
- Hardy, G. A. and W. H. A. Preece. 1927. Further notes on some species of Cerambycidae from the southern portion of Vancouver Island, B. C., with descriptions of some new varieties. The Pan-Pacific Entomologist, 3:34-40.
- Hardy, G. A. 1944. Further notes on the Cerambycidae of Vancouver Island (Coleoptera). Proceedings of the Entomological Society of British Columbia, 41: 15-18 (Dec. 8, 1944) <[PDF](#)>
- Hart, C. J., J. S. Cope and M. A. Ivie. 2013. A checklist of the Cerambycidae (Coleoptera) of Montana with distribution maps. Coleopterists Bulletin 67: 133-148. doi: <http://dx.doi.org/10.1649/0010-065X-67.2.133>
- Hatch, M. H. 1949. A century of entomology in the Pacific Northwest. University of Washington Press. Seattle. 43 pp.
- Hatch, M. 1971. The beetles of the Pacific Northwest. Part V. Rhipicerioidea, Sternoxi, Phytophaga, Rhynchophora, and Lamellicornia. University of Washington Publications in Biology, 16.
- Hayashi, M., K. Morimoto and S. Kimoto. 1984. The Coleoptera of Japan in Color, vol. IV, Hoikusha (Osaka). [ISBN 4-586-30071-X](#).
- Hayashi M. & A. Villiers. 1985. Revision of the Asian Lepturinae (Coleoptera: Cerambycidae) with special reference to the type specimens inspection. Part I. *Osaka Jonan Women's Junior College*, 19-20: 1-75
- Hayashi M. & A. Villiers. 1987. Revision of the Asian Lepturinae (Coleoptera: Cerambycidae) with special reference to the type specimens inspection. Part II. *Osaka Jonan Women's Junior College*, 22: 1-20
- Hayashi M. & A. Villiers. 1989. Revision of the Asian Lepturinae (Coleoptera: Cerambycidae) with special reference to the type specimens inspection. Part III. *Osaka Jonan Women's Junior College*, 24: 1-43

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<sup>17</sup> Includes key to the tribes of Lepturinae.

- Hayashi M. & A. Villiers. 1995. Revision of the Asian Lepturinae (Coleoptera: Cerambycidae) with special reference to the type specimens inspection. Part IV. *Osaka Jonan Women's Junior College*, 30: 1-22
- <sup>18</sup>Heffern, Daniel J. 2005. Catalog and Bibliography of Longhorned Beetles from Borneo (Coleoptera: Cerambycidae). Electronic Version. 2005.1.
- Heffern, Daniel J. 2006. Catalog and Bibliography of Longhorned Beetles from the Hawaiian Islands (Coleoptera: Cerambycidae). Electronic Version. 2006.1.
- Hopping, R. 1937. The Lepturini of America North of Mexico. Part II. National Museum of Canada. (Biological Series) (22)85:1-27, 6 pls.
- Hopping, R. and G. R. Hopping. 1947. The Lepturini of America North of Mexico. Part III. Cortodera. Entomol. Agric., 27:220-236, 6 figs.
- Hovore, F.T. & E.F. Giesbert. 1976. Notes on the ecology and distribution of western Cerambycidae. Coleop. Bull., 30(4): 349 - 360.
- ICZN, 1994. Opinion 1754, (Case 2292). Histoire abrégée des insectes qui se trouvent aux environs de Paris (Geoffroy, 1762): some generic names conserved (Crustracea, Insecta). Bulletin of Zoological Nomenclature, 51(1):58. [[Biodiversity Heritage Library](#)]
- Kadlec, S. and J. Hájek. 2005. Xestoleptura nigroflava, a new genus of longhorn beetles for Europe (Coleoptera: Cerambycidae: Lepturinae). 1 colour plate, 6 pp. [FHC207] Folia Heyrovskyana 12(A)(4): 161-166.
- Kakutani, T., Inoue, T., Kato, M., and H. Ichahashi. 1990. Insect-flower relationship in the campus of Kyoto Japan: An overview of the flowering phenology and the seasonal pattern of insect visits. Contrib. Biol. Lab. Kyoto Univ. 27:465-522.
- Kasuma, K. and M. Hayashi. 1971. Generic names and type species applied to Japanese Cerambycidae (Coleoptera). Reports Facul. Sci.Shizuoka Univ. 6: 95-126.
- LeConte, J. L. 1850. An attempt to classify the longicorn Coleoptera of the part of America, north of Mexico. Journal of the Academy of Natural Sciences of Philadelphia, (2)1: 311-340; 2:5-38. <[Biodiversity History Library](#)> <[PDF-1](#)> <[PDF-2](#)>

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<sup>18</sup> According to Heffern (2005): "The cerambycid fauna of Borneo is closely related to the fauna of the Malaysian Peninsula, Sumatra and Java, with a distinct overlap of species and a strong commonality of tribes and genera. ... nearly all tribes and many genera which occur in Southeast Asia are found in Borneo. ... The cerambycid fauna of Borneo is also closely related to the Philippine island of Palawan, since it was part of the Sunda Shelf around 160,000 years ago when sea levels were at their lowest, permitting dispersion of ancestral fauna to that island via a land bridge."

- <sup>19</sup>LeConte, J. L. 1851. An attempt to classify the longicorn Coleoptera of the part of America, north of Mexico. *Journal of the Academy of Natural Sciences of Philadelphia*, (2)2:99-112. <[Biodiversity History Library](#)>
- LeConte, J. L. & G. H. Horn. 1883. Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution. *Smithson. Misc. Coll'ns.*, 26(507): xxxvii + 1-567
- Leech, H. B. 1963. *Centrodera spurca* (LeConte) and two new species resembling it, with biological and other notes. *Proceedings of the California Academy of Sciences*, 32:149-218, 28 figs.
- Linsley, E. G. 1958a. Geographical origins and phylogenetic affinities of the cerambycid beetle fauna of western North America. In Hubbs, C. L. ed. *Zoogeography*, Amer. Assoc. Adv. Sci., Washington, pp. 299-320. [Openlibrary.org](#).
- Linsley, E. G. 1958b. The role of Cerambycidae in forest, urban and agricultural environments. *Pan-Pacif. Ent.*, 34(3): 105-124.
- Linsley, E. G. 1959. Ecology of Cerambycidae. *Annual Review of Entomology* 4: 99-138. <[PDF](#)>
- Linsley, E. G., and J. A. Chemsak. 1972. Cerambycidae of North America. Part VI. No. 1. Taxonomy and Classification of the Subfamily Lepturinae. University of California Publications in Entomology 69, xiii+138 pp, 2 pl.
- Linsley, E.G. and J.A. Chemsak. 1976. Cerambycidae of North America. Part VI, No.2. Taxonomy and Classification of the Subfamily Lepturinae. University of California Publications in Entomology 80, 186 pp.
- Lobanov, A.L., M.L.Danilevsky, S.V.Murzin. 1981. Systematic list of longicorn beetles (Coleoptera, Cerambycidae) of the USSR I. *Revue d'Entomol.*, LX, 4, 1981: 784-803.
- Lobanov, A.L., M.L.Danilevsky, S.V.Murzin. 1982. Systematic list of longicorn beetles (Coleoptera, Cerambycidae) of the USSR II. *Revue d'Entomol.*, LXI, 2, 1982: 252-278.
- MacRae, T. C. and Rice M. E. 2007. Biological and Distributional observations on North American Cerambycidae (Coleoptera). *The Coleopterists Bulletin*, 61(2):227–263.
- Miroshnikov, A. I., 1998: A new classification of longicorn beetles of the *Anoplodera* complex, tribe Lepturini Coleoptera, Cerambycidae of Holarctic fauna. I. *Entomologicheskoe*

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<sup>19</sup> *G. molybdica* (LeConte, 1851("1850")) and *B. californica* (LeConte, 1851 ("1850")). The ("1850") is due to an appendix (on page 101) that amends pages from LeConte (1850) and inserts original descriptions. Although the article was published 1852, the reference is cited as 1851 because, in a footnote in the table of contents, it is indicated that LeConte had pre-prints in December of 1851,

- Miroshnikov A.I., 2000. On taxonomy of the genus *Enoploderes* Faldermann and distribution of its congener *Enoploderes sanguineum* Faldermann (Coleoptera Cerambycidae). *Entomologia Kubanica*, 1: 55-59.
- Özdikmen, H. 2010. Turkish Oxymirini Danilevsky in Althoff & Danilevsky, 1997 with zoogeographical remarks (Coleoptera: Cerambycidae: Lepturinae). *Munis Entomology & Zoology* 5 (1): 52-59
- Ödikmen, H. 2011. A propose for acception of a single genus as *Judolia* Mulsant, 1863 instead of the genera *Judolia* Mulsant, 1863 and *Pachytodes* Pic, 1891 (Coleoptera: Cerambycidae: Lepturinae: Lepturini) *Munis Entomol. Zool.* 6(2): 900-904.
- Ohbayashi, N., M. Satô and K. Kojima, 1992. An Illustrated Guide to Identification of Longicorn Beetle of Japan, Tokai University Press (Tokyo). [ISBN 4-486-01181-3](#).
- Okutaner, A. Y., Özdikmen, H., Yüksel, E., Koçak, Y., 2012. "Cytogenetic observations of *Pachytodes erraticus* (Coleoptera: Cerambycidae: Lepturinae: Lepturini). *Florida Entomologist*, 95 (3): 731-736 (2012) (SCI). <http://dx.doi.org/10.1653/024.095.0323>
- Penrose, R. L. and Richard L. Westcott. 1974a. Lepturine longhorns collected on chinquapin bloom (Coleoptera: Cerambycidae). *The Pan-Pacific Entomologist* 50(1):72.
- Penrose, R. L. and Richard L. Westcott. 1974b. Notes on the Distribution, Hosts and Bionomics of Some Pacific Northwest Cerambycidae (Coleoptera). *The Coleopterists Bulletin*, Vol. 28, No. 4 (Dec.), pp. 233-236
- Penrose, Richard. L. 1979. Notes on three Oregon Lepturine Cerambycidae. *Pan-Pacific Entomologist*. 55(2): 159-160.
- Plavilstshikov, N. N. 1936. Fauna SSSR. Nasekomye zhestokrylye. T. XXI. Zhukidrovoseki (ch. 1). Moskva – Leningrad: Izdatel'stvo Akademii Nauk SSSR, 612 + [1] pp.
- Rapuzzi, P. & Sama, G. 2013. A new species of *Apatophysis* Chevrolat, 1860 from Jordan (Coleoptera: Cerambycidae). *Munis Entomology & Zoology*, 8 (2): 682-684
- Ray, A. M., Lacey, E. S., and Hanks, L. M. 2006. Predicted taxonomic patterns in pheromone production by longhorned beetles. *Naturwissenschaften* 93:543–550.
- Ray, A. M., Zunic, A., Alten, R. L., McElfresh, J. S., Hanks, L. M., and Millar, J. G. 2011. cis-Vaccenyl acetate, a sex attractant pheromone of *Ortholeptura valida*, a longhorned beetle in the subfamily Lepturinae. *J. Chem. Ecol.* 37:172–178.

- Ribardo, K., & J. Cope, 2000. "Checklist of the Cerambycidae of Madagascar and Adjacent Islands. Website Accessed August 27, 2014.  
[http://researcharchive.calacademy.org/research/entomology/Entomology\\_Resources/Faunal\\_Projects/Madagascar\\_Cerambycidae/Index.htm](http://researcharchive.calacademy.org/research/entomology/Entomology_Resources/Faunal_Projects/Madagascar_Cerambycidae/Index.htm)
- Robertson, J. A. 1988. Descriptions of the immatures of *Typocerus serraticornis* (Coleoptera: Cerambycidae), and new observations on biology, including "Varnish" production and usage by larva. *The Pan-Pacific Entomologist*. 64(3), 228-242.
- Russell, L. K. 1968. The faunal relationships of the Coleoptera of Montana, west of the Continental Divide, with a list of the species known to occur there. MSc thesis, University of Washington, Seattle, WA.
- Sama, G. 1993. Notes sur les Xylosteini Reitter. *Biocosme Mésogéen*, Nice, 10(1): 7-15, 6 figs.
- Sama, G. 2002. Atlas of the Cerambycidae of Europe and the Mediterranean Area. Volume 1: Nothern, Western, Central and Eastern Europe. British Isles and Continental Europe from France (excl. Corsica) to Scandinavia and Urals. Nakladatelstvi Kabourek, Zlin, 173 pp.
- Shoening, E. H. and J. W. Tilden. 1959. *Anoplodera laetifica* (LeConte) and *Ergates spiculatus* LeConte from knob-cone pine [*Pinus attenuata*] (Coleoptera: Cerambycidae). *The Pan-Pacific Entomologist*, 35: 167-168.
- Švácha P., Danilevsky M. L., 1989. Cerambycoid larvae of Europe and Soviet Union. (Coleoptera, Cerambycoidea). Part III. *Acta Univ. Carol. (Biol.)* 32[1988]: 1–205.  
 <PDF>
- Swaine, J. M. & R. Hopping. 1928. The Lepturini of America North of Mexico. Part I. *Bull. Nat. Mus. Canada, (Biol. Serv.)* (14)52:1-97, 13 pls.
- Swift, Ian. 2008. Ecological and biogeographical observations on Cerambycidae (Coleoptera) from California, USA. *Insecta Mundi*, 0026: 1-7.
- Sýkorová, M. 2008. Molecular phylogeny of the subfamilies Spondylidinae and Lepturinae (Coleoptera: Cerambycidae) based on mitochondrial 16S rDNA. Bachelor's thesis, Faculty of Natural Sciences, South Bohemian University, Ceske Budejovice. <http://www.entu.cas.cz/popevol/lide/sykorova.pdf>
- Tyson, W. H. 1966. Notes on reared Cerambycidae (Coleoptera). *The Pan-Pacific Entomologist*, 42(3): 201-207.
- Westcott, R. L., J. R. LaBonte, G. L. Parsons & P. J. Johnson. 2006. New records and other notes for Oregon Coleoptera. *Zootaxa* 1142:1-33

## APPENDIX A – CHECKLIST AND BIBLIOGRAPHY FOR PACIFIC NORTHWEST LEPTURINAE

The present checklist is adapted, with additions and corrections from Bezark and Monné (2013). Two genera, *Cosmosalia* Casey and *Pyrotrichus* LeConte are listed as junior synonyms of *Lepturobosca* Linnaeus, and *Enoploderes* Faldermann, respectively, following Miroshnikov (1998), and Miroshnikov (2000). *Encyclops californicus* is masculine, and returned to its original spelling, and the species of *Desmocerus* reflect the findings in the following chapter. Other minor deviations from Bezark and Monné (hereafter referred to as “B&M”) are noted in the footnotes, and other notes are made in reference to the revision by Linsley and Chemsak (1972; 1976), hereafter “L&M.” Valid names are in bold, with junior synonyms listed in italics.

### Tribe Desmocerini Blanchard, 1845: 163

#### **Desmocerus** Dejean, 1821:111

**aureipennis** Chevrolat, 1855: 187

*auripennis*; LeConte, 1857:23

**cribripennis** Horn, 1881:vii

**lacustris** Linsley and Chemsak, 1972:11

**piperi** Webb, 1905: 104

### Tribe Lepturini Latreille, 1802: 218.

#### **Anastrangalia** Casey, 1924:280

**laetifica** (LeConte, 1859:89)

*lugens* LeConte, 1859:89

**sanguinea** (LeConte, 1859:89)

*boulderensis* Casey, 1913:252

*apicata* Casey, 1924:280

#### **Brachyleptura** Casey, 1913:247

*Toxoleptura* Miroshnikov, 1998:411

**dehiscens** (LeConte, 1859:89)

**vexatrix** (Mannerheim, 1853:250)

*quadrillum* LeConte, 1859:88

*convolvens* Casey, 1913:250

#### **Dorcasina** Casey, 1913:269

**matthewsii** (LeConte, 1869:384)

*macrocera* Casey, 1913:270

#### **Grammoptera** Audinet-Serville, 1835:215

*Parallelina* Casey, 1913:247

**molybdica** (LeConte, 1851

[“1850”]:101)

**rhodopus** (LeConte, 1874:68)

*campanifera* Casey, 1913:256

**subargentata** (Kirby in Richardson, 1837:184)

*similis* Kirby in Richardson, 1837:185

*rufibasis* LeConte, 1862:40

*quebecensis* Couper, 1864:88

*filicornis* Casey, 1913:255

#### **Judolia** Mulsant, 1863:496

**gaurotoides gaurotoides** (Casey, 1893:592)

*vivarium* Casey, 1924:282

*knilli* Swaine & Hopping, 1928:46

**gaurotoides auripilis** Linsley & Chemsak, 1976:50

**impura** (LeConte, 1857:64)

**instabilis** (Haldeman, 1847:64)

*convexa* LeConte, 1850:332

*quadrata*; Horn, 1886:xiii (not LeConte, 1873)

*flaviventris* Schaeffer, 1908:342

*pacifica* Casey, 1913:249

*trajecta* Casey, 1913:250



- montivigans montivigans** (Couper, 1864:87)  
*sexmaculata*; Kirby in Richardson, 1837:182 (not Linnaeus, 1758)  
*seminigra* Casey, 1924:283  
**montivigans barberi** (Fall, 1907:250)  
**scapularis** (Van Dyke, 1920:43)  
*isabellae* Hopping, 1922:162
- Leptura (Leptura)** Linnaeus, 1758:397  
*Stenura* Haldeman, 1847:62 (part)  
*Strangalia*; LeConte, 1850:327 (part)  
*Nakanea* Ohbayashi, 1963:9  
**anthracina** LeConte, 1875: 174  
*subcostata* Fall, 1907: 249  
**kerniana** Fall, 1907: 249  
**obliterata obliterata** (Haldeman, 1847:62)  
*vitiosa* LeConte, 1854:18  
*perductor* Walker in Lord, 1866:333  
*idahoensis* Casey, 1913:259  
**plagifera** LeConte, 1873:224  
**propinqua** Bland, 1865:384  
*regularis* Casey, 1913:259  
*miniscula* Casey, 1913:260
- Lepturobosca** Reitter, 1913:17  
*Cosmosalia* Casey, 1913:267  
**chrysocoma** (Kirby in Richardson, 1837:179)  
*auripilis* LeConte, 1850:339  
*aureola* Casey, 1913:268  
*auripilis densepilosa* Casey, 1924:281
- Lepturopsis** Linsley & Chemsak, 1976:158  
**dolorosa** (LeConte, 1861:355)
- Neostalosterna** Podany, 1961:27  
**rubida** (LeConte, 1873:224)  
*keeni* Casey, 1913:257
- Neobellamira** Swaine & Hopping, 1928:15  
**delicata delicata** (LeConte, 1874:68)
- Ortholeptura** Casey, 1913:204  
**obscura** (Swaine & Hopping, 1928:56)  
**valida** (LeConte, 1857:64)  
*oculea* Casey, 1913:204
- Pygoleptura** Linsley & Chemsak, 1976:59  
**brevicornis** (LeConte, 1873:226)  
**carbonata** (LeConte, 1861:355)  
**nigrella nigrella** (Say, 1826:279)  
*lacustris* Casey, 1891:43  
*praestans* Casey, 1913:267  
*serricornis* Casey, 1924:279  
**nigrella oregonensis** Linsley & Chemsak, 1976:62
- Stenostrophia** Casey, 1913:248  
**amabilis** (LeConte, 1857:64)  
**tribalteata serpentina** (Casey, 1891:41)  
**tribalteata sierrae** Linsley & Chemsak, 1976:113
- Stictoleptura** Casey, 1924:280  
*Corymbia* Des Gozis, 1886:33; nec Walker, 1865  
*Aredolpona* Nakane & N. Ohbayashi, 1957:50  
*Melanoleptura* Miroshnikov, 1998:594  
*Paracorymbia* subgen. *Batesiata* Miroshnikov, 1998:594  
**canadensis cribripennis** (LeConte, 1859:21)  
*coccinea* LeConte, 1873: 226
- Strophiona** Casey, 1913:248  
**laeta** (LeConte, 1857:64)  
*ostenta* Casey, 1913:265  
**tigrina** Casey, 1913:266  
*reducta* Casey, 1913:266

**Trachysida** Casey, 1913:271

**aspera aspera** (LeConte, 1873:228)

<sup>20</sup>var. *parkeri* Hippisley, 1922:66

<sup>21</sup>**Typocerus** LeConte, 1850:333

<sup>22</sup>**serraticornis** Linsley & Chemsak,  
1976:69

**Xestoleptura** Casey, 1913:248

<sup>23</sup>**behrensii** (LeConte, 1873:227)

**crassicornis** (LeConte, 1873:227)

*corusca* Casey, 1913:261

**crassipes** (LeConte, 1857:65)

<sup>24</sup>*xanthogaster* LeConte, 1859:88

*fasciventris* LeConte, 1861:355

*crassipes shastana* Casey, 1913:263

*muliebris* Casey, 1913:263

*vancouveri* Casey, 1913:263

**tibialis** (LeConte, 1850:236)

*hirtella* LeConte, 1873:226

*columbica* Casey, 1913:261

*miquelonensis* Pic, 1922:11

*pictipennis* Casey, 1924:285

Tribe Rhagiini Kirby, 1837

**Acmaeops** LeConte, 1850: 235

**proteus proteus** (Kirby in Richardson,  
1837: 186)

*sublineata* Haldeman, 1847:60

*gibbula* LeConte, 1861:356

*pinicola* Schaeffer, 1908:341

*parkeri* Casey, 1913:242

*lacustrina* Casey, 1913:242

*obsoleta* Casey, 1913:243

*puncticeps* Casey, 1913:243

*aurora* Casey, 1913:244

*coloradensis* Casey, 1913:244

*cavicollis* Casey, 1913:244

*scutellata* Casey, 1924:276

**pratensis** (Laicharting, 1784:172)

*strigilata* Fabricius, 1792:341

*longiceps* Kirby in Richardson, 1837:187

*semimarginata* Randall, 1838:30

*fulvipennis* Mannerheim, 1853:251

**Brachysomida** Casey, 1913:219

**atra** (LeConte, 1850:323)

*morata* Casey, 1913:222

*aterrima* Casey, 1924:276

**californica** (LeConte, 1851[“1850”]:101)

*subaeneus* LeConte,

1851[“1850”]:101

*tumida* LeConte, 1857:63

*fusca* LeConte, 1857:62

*subcyanea* LeConte, 1857:63

*lugens* LeConte, 1857:62

*viola* LeConte, 1860:321

*mollipilosa* LeConte, 1860:321

*pinguis* LeConte, 1873:210

*celestina* Casey, 1913:222

*corpulenta* Casey, 1913:222

*lanatula* Casey, 1913:224

*francisca* Casey, 1913:225

*californica proxima* Casey, 1913:225

*brevicornis* Casey, 1913:226

*trinitatis* Casey, 1913:226

*tumidiceps* Casey, 1913:227

*caerulea* Casey, 1913:227

*caerulea chalybea* Casey, 1913:228

*robustula* Casey, 1913:228

*protensicollis* Casey, 1913:228

*hirsuta* Casey, 1913:228

*lepidula* Casey, 1913:229

*versicolor* Casey, 1913:229

<sup>20</sup> Incorrectly spelled “Hippisly” in B&M (2013) and L&C (1976).

<sup>21</sup> There is a genus *Pseudotypocerus* Linsley & Chemsak, 1971 with 8 species in South America.

<sup>22</sup> Paratype male and female are in Westcott private collection, currently housed at Oregon Dept. Agric. in Salem, Oregon.

<sup>23</sup> Original spelling with two ‘i’s. Appears in many publications, including L&C’76 as *behrensi* with one ‘i.’

<sup>24</sup> L&C give *xanthogaster* LeConte, 1860.

**Centrodera** LeConte, 1850:325  
*Rhamnusium*; Haldeman, 1847:58  
*Centrodera (Apatophysis)*; Gressitt, 1947:191  
*Parapachyta* Casey, 1913:216  
**dayi** Leech, 1963:178  
**spurca** (LeConte, 1857:63)  
*cervinus* Walker, 1866:332  
**nevadica nevadica** LeConte, 1873:205

**Cortodera** Mulsant, 1863: 572  
*Acmaeops* LeConte, 1850:321 (part)  
*Leptacmaeops* Casey, 1913:219  
*Leptacmaeops (Acmaeopsilla)* Casey, 1913:240  
**barri** Linsley & Chemsak, 1972:120  
**coniferae** Hopping & Hopping, 1947:233  
**impunctata** Hopping & Hopping, 1947:222  
**longicornis** (Kirby in Richardson, 1837: 185)  
*dorsalis* LeConte, 1859:21  
*vincta* LeConte, 1861:356  
*ligata* LeConte, 1873:211  
*marginalis* LeConte, 1857:23  
*punctiventris* Casey, 1913:238  
*alticola* Casey, 1913:239  
*suturalis* Casey 1924:277  
*oregonensis* Hopping & Hopping, 1947:227  
*harneyensis* Hopping & Hopping, 1947:228  
*bakeri* Hopping & Hopping, 1947:229  
**militaris militaris** (LeConte, 1850: 322)  
**militaris constans** Linsley & Chemsak, 1972:110  
**nitidipennis** (Casey, 1913:236)  
**robusta** Hopping & Hopping, 1947:234  
**spuria** (LeConte, 1873:228)  
**subpilosa** (LeConte, 1850:322)  
*intermedia* Casey, 1913:236  
*lupina* LeConte, 1860:321

*pugetana* Casey, 1913:237  
*quadriceps* Casey, 1913:237

**Evodinus** LeConte, 1850:325  
*Brachyta* Fairmaire in Jacquelin du Val, 1864:185  
**monticola vancouveri** Casey, 1913: 216

**Pachyta** Dejean, 1821:112  
*Argaleus* LeConte, 1850:319  
*Acmaeops*; Thomson, 1866:55 (not LeConte, 1850)  
<sup>25</sup>*Anthophylax*; Blessig, 1873:232 (not LeConte, 1850)  
<sup>26</sup>*Neopachyta* Bedel, 1906:93  
*Pachyta (Linsleyana)* Podany, 1964:43  
**armata** LeConte, 1873:207  
**lamed liturata** Kirby in Richardson, 1837:178  
*nitens* LeConte, 1850:319  
*conflagrata* Motschulsky, 1860:147  
*lamed americana* Podany, 1964:50

**Pidonia (Ceratopidonia)** Linsley & Chemsak, 1976:119  
**quadrata** (Hopping, 1931:233)

**Pidonia (Pidonia)** Mulsant, 1863:570  
*Grammoptera*; Thomson, 1864:141 (not Audinet-Serville, 1835)  
*Pseudopidonia* Pic, 1900:81  
*Hapalosalia* Casey, 1913:200  
<sup>27</sup>*Pidnota*; Bayer & Shenefelt, 1969:5  
**scripta** (LeConte, 1869:384)

**Pidonia (Thesalia)** Casey, 1891:36  
**gnathoides** (LeConte, 1873:228)  
*lisa* Leng, 1890:108  
*rubriceps* Casey, 1913:198

<sup>25</sup> This reference is missing both in L&C and B&M.

<sup>26</sup> This reference is missing in B&M.

<sup>27</sup> Reference missing.

**Piodes** LeConte, 1850:318

**coriacea** LeConte, 1850:318

**Pseudogaurotina** Plaviltstshikov, 1958:720

*Gaurotus* Lacordaire, 1869:442 (part)

**cressoni cressoni** (Bland, 1864:69)

ab. *howdeni* Podany, 1962:237

ab. *amethystina* Podany, 1962:238

ab. *nigrita* Podany, 1962:238

**cressoni lecontei** (Casey, 1913:219)

**Rhagium** Fabricius, 1775:182

*Stenocorus* Geoffroy, 1762:221

*Stenocorus*; Lamarck, 1817:312

*Hargium* Samouelle, 1819:210

*Harpium*; Reitter, 1912:6

<sup>28</sup>*Allorhagium* Kolbe, 1884:270

**inquisitor inquisitor** (Linnaeus, 1758:393)

*lineatus* Olivier, 1795:13

*investigator* Mannerheim, 1852:283

*californicum* Casey, 1913:195

*crassipes* Casey, 1913:195

*parvicorne* Casey, 1913:195

*boreale* Casey, 1913:195

*cariniventre* Casey, 1913:196

*thoracicum* Casey, 1913:196

*montanum* Casey, 1913:197

*mexicanum* Casey, 1913:197

*canadense* Podany, 1964:30

*americanum* Podany, 1964:32

*quadricostatum* Podany, 1964:34

*nigra* Podany, 1978:4

**Stenocorus** Geoffroy, 1762:221

*Stenochorus*; Reitter, 1912:6

*Toxotus* Dejean, 1821:112

*Anisorus* Mulsant, 1863:467

*Minaderus* Mulsant, 1863:467

*Toxotochorus* Reitter, 1907:208

*Stenocorus (Toxotopsis)* Casey, 1913:206

*Stenocorus (Eutoxotus)* Casey, 1913:206

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<sup>28</sup> Reference missing.

**flavolineatus** (LeConte, 1854:18)

*flavolimbatus*; LeConte, 1857:23

<sup>29</sup>**nubifer** (LeConte, 1859:80)

*lateralis* Casey, 1891:37

*pacificus* Casey, 1913:209

*tenellus* Casey, 1913:210

*hesperus* Casey, 1913:210

*parviceps* Casey, 1913:210

*truncatulus* Casey, 1913:211

*apiciventrus* Casey, 1913:211

*rufipennis* Casey, 1913:212

*plagiatus* Casey, 1924:273

*marginellus* Casey, 1924:274

*spinosus* Hopping, 1940:32

<sup>30</sup>**uteanus** Casey, 1924:273

*morio* Casey, 1924:274

**obtusus** (LeConte, 1873:206)

*brevicollis* Casey, 1913:214

**vestitus** (Haldeman, 1847:59)

*vestitus* var. *ater* Leng, 1890:68

*virgatus* LeConte, 1874:67

*aureatus* Casey, 1913:213

*aureatus gilvicornis* Casey, 1913:213

*sericatus* Casey, 1913:213

*subpinguis* Casey, 1913:213

*oregonensis* Casey, 1913:214

*flaccidus* Casey, 1913:212

Tribe Oxymirini Danilevsky, 1997

**Neanthophylax** Linsley & Chemsak, 1972:78

*Anthophilax* Horn in Leng, 1890:98 (part)

**mirificus** (Bland, 1865:382)

*venustus* Bland, 1865:383

*costaricensis* Bates, 1885:277

**pubicollis** Linsley & Chemsak, 1972:81

**tenebrosus tenebrosus** (LeConte, 1873:208)

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<sup>29</sup> L&C give *Toxotus nubifer* LeConte, 1860

<sup>30</sup> *uteanus* Casey and *morio* Casey are treated as junior synonyms of *S. nubifer* in Bezark and Monné (2013)

**tenebrosus nigrolineatus** (Van Dyke,  
1917:36)

**tenebrosus orientalis** Linsley &  
Chemsak, 1972:81

Tribe Encyclopini LeConte, 1873:326

**Encyclops** Newman, 1838:392

**californicus**<sup>31</sup> Van Dyke, 1920: 45

**Leptalia** LeConte, 1873:204

**macilenta** (Mannerheim, 1853: 253)

*frankenhaeuseri* Mannerheim, 1853

*fuscicollis* LeConte, 1857

<sup>32</sup>Tribe Rhamnusiini Sama, 2009:383

**Enoploderes** Faldermann, 1837:309<sup>33</sup>

*Pyrotrichus* LeConte, 1862:41

*Xylostylon* Reitter, 1879:82

**vitticollis** LeConte, 1862:41

*cribripennis* Casey, 1913:198

Tribe Xylosteini Reitter, 1913:5

**Pseudoxylosteus** Sama, 1993:12

**ornatus** (LeConte, 1873:205)

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<sup>31</sup> *Encyclops* is masculine. Bezark and Monné (2013) lists *E. californica* Van Dyke introduced by Linsley and Chemsak (1972).

<sup>32</sup> See Cebeci & Özdikmen (2010).

<sup>33</sup> Bezark and Monné (2013) give *Pyrotrichus*.

*References for Original Descriptions of Taxa*

- Audinet-Serville, J. G. 1835. Nouvelle classification de la famille des longicornes (suite). Ann. Soc. Entomol. France, (1)4:5-100.
- Bates, H. W. 1885. Biologia Centrali-Americana, Insecta; Coleoptera, suppl. to Longicornia, London, 5:249-436, pls. 17-24.
- Bedel, L. 1906. Synonymes de coléoptères palearctiques. Bull. Soc. Entomol. Fr., 1906:91-93.
- Blanchard, C.E. 1845. Histoire des insectes, traitant de leurs mœurs et de leurs métamorphoses en général, et comprenant une nouvelle classification fondée sur leurs rapports naturels. 2:163. <http://archive.org/details/histoirenaturell02blan>
- Bland, J. H. B. 1862. Descriptions of several supposed new species of Cerambycidae in the collection of the Entomological Society of Philadelphia, with observations of some already described. Proceedings of the Entomological Society of Philadelphia, 1:267-276.
- Casey, T. L. 1891. Coleopterological notices III. Annals of the New York Academy of Sciences, 6:9-214. <[Biodiversity History Library](#)>
- Casey, T. L. 1893. Coleopterological notices V. Annals of the New York Academy of Sciences, 7:281-606, 1 pl.
- Casey, T. L. 1913. Further studies amongst the American Longicornia. Memoirs on the Coleoptera, 4:193-388. <[Link to Biodiversity Heritage Library](#)> <[PDF](#)>
- Casey, T. L. 1924. Additions to the known Coleoptera of North America. Memoirs on the Coleoptera, 11:1-347. <[Openlibrary.org](#)> <[PDF](#)>
- Chevrolat, L. A. A. 1855. Description de vingt et une espèces nouvelles de coléoptères longicornes. Revue et Mag. Zool., (2)7:178-187
- <sup>34</sup>Couper, W. 1864. List of Coleoptera and Diptera taken at Quebec, and other parts of lower Canada. Trans. Lit. Hist. Soc. Quebec, (n.s.) 3:27-36.
- Danilevsky ML (1997) [new taxa] In: Althoff J, Danilevsky ML: Seznam kozličev (Coleoptera, Cerambycoidea) Europe. A check-list of longicorn beetles (Coleoptera, Cerambycoidea) of Europe. Slovensko Entomološko Društvo Štefana Michielija, Ljubljana, 64 pp.

---

<sup>34</sup> This reference to the description of *Judolia montivigans* was missing in Bezark and Monne (2013).

- Dejean, P. F. M. A. 1821. Catalogue de la collection de coléoptères de M. le baron Dejean. Crevot Libr., Paris, France. viii + 136 pp. + 11 pp.
- Des Gozis, M. 1886. Recherche de l'espèce typique de quelques anciens genres rectifications synonymiques et notes diverses. 36 pp. Montlucon-Imprimerie Herbin.
- Fabricius, J. C. 1775. Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. Flensburgi et Lipsiae, 832 pp.
- Fabricius, J. C. 1792. Entomologia systematica, emendata et aucta. Secundum classes ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus. Hafniae, 1: xx + 538 pp.
- Fairmaire, L. 1864. In P. N. Jacquelin du Val, Genera des Coléoptères d'Europe comprenant leur classification en famille naturelle. 4:1-295, 376 figs., 78 pls.
- Faldermann F. 1837. Fauna entomologica transcaucasica. Coleoptera. II. // Nouv. Mém. Soc. Nat. Mosc. 1837. Vol. 5. P. 1–433 + tab. 1–15.
- Fall, H. C. 1907. Descriptions of new species. Transactions of the American Entomological Society, 33: 218-272. <[Biodiversity History Library](#)>
- Geoffroy, E. L. 1762. Histoire abrégée des insectes qui se trouvent aux environs de dans laquelle ces animaux sont rangés suivant un ordre méthodique. Durand. 1: xxviii + 523 pp., pls I-X.
- Gressitt, J. L. 1947. Notes on the Lepturinae (Coleoptera: Cerambycidae). Proceedings Ent. Soc. Wash. 49 (7), 190-192.
- Haldeman, S. S. 1847. Material towards a history of the Coleoptera Longicornia of the United States. Transactions of the American Philosophical Society, 10:27-66. <[Biodiversity History Library](#)>
- Hippisley, W. W. 1922. Notes on northern British Columbian Coleoptera. The Canadian Entomologist, 54: 63-66. <[Biodiversity History Library](#)> <[PDF](#)>
- Hopping, R. 1922. New species of the old genus Leptura and allied genera. Can. Entomol., 54(7): 162 – 166. <[Biodiversity History Library](#)>
- Hopping, R. 1928. Some notes on examination of types of Coleoptera in the LeConte and Casey collections. Can. Entomol., 60(1):6-8.
- Hopping, R. 1931. New Coleoptera from Western Canada III. The Canadian Entomologist, 63(10):233-238.

- Hopping, R. 1937. The Lepturini of America North of Mexico. Part II. National Museum of Canada. (Biological Series) (22)85:1-27, 6 pls.
- Hopping, R. 1940. New Lepturini. Pan-Pacific Entomologist, 16(1):32-4
- Hopping, R. and G. R. Hopping. 1947. The Lepturini of America North of Mexico. Part III. Cortodera. Entomol. Agric., 27:220-236, 6 figs.
- Horn, G. H. 1881. In *Monthly Proceedings*. Two new species of *Desmocerus*. Transactions of the American Entomological Society, 9: vii-viii.
- Horn, G. H. 1884. In C. W. Leng, Synopses of Coleoptera. Bull. Brooklyn Entomol. Soc., 7(1):7-11.
- Horn, G. H. 1886. Notes from the Museum at Cambridge. Trans. Amer. Entomol. Soc., 13: xi-xvi, 12 figs.
- Horn, G. H. 1890. In C. W. Leng, Synopses of Cerambycidae. Entomologica Amer., 6(5):97-98.
- Kirby, W. 1837. The Insects. Coleoptera. In J. Richardson, W. Swainson, and W. Kirby, Fauna Boreali Americana; or the Zoology of the Northern Parts of British America: containing descriptions of the objects of natural history collected on the Late Northern Land Expedition, under the command of Captain Sir John Franklis, R. N. Norwich, Josiah Fletcher. 249 pp. <[Biodiversity History Library](#)>
- Lacordaire, T. 1869. Histoire Naturelle des Insectes. Genera des coléoptères, vol. 8, 552 pp.
- Laicharting, J. N. von. 1784. Verzeichniss und Beschreibung der Tyroler-Insecten. II Theil. Zürich. Johann Caspar Füessly, pp. 1-176.
- Lamarck, Jean-Baptiste. 1817. Histoire naturelle des animaux sans vertèbres...l'exposition des principes fondamentaux de la Par M. de Lamarck. Tome 4. March, 1817. pp. 1-603. <[Biodiversity History Library](#)> <[PDF](#)>
- Latreille, P. A. 1802. Histoire naturelle, générale et particulière des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres. Tome troisième. F. Dufart, Paris, xii + 13-467 + [1] pp. [An X (title page, =1802); Nov 1802 (Evenhuis 1997)]
- Latreille, P. A. 1829. Crustacés, Arachnides et Insectes. In Cuvier, G. L. C. D. Le Règne Animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux, et d'introduction à l'Anatomie comparée, deuxième édition, 4: 28 + 584 pp., 4 pls.



LeConte, J. L. 1850. General remarks upon the Coleoptera of Lake Superior. pp. 201-242. In: Agassiz, J.L.R. *Lake Superior: its physical character, vegetation, and animals, compared with those of other and similar regions, with a narrative of the tour, by J. Elliott Cabot. And contributions by other scientific gentlemen.* Boston: Gould, Kendall and Lincoln. x + 428 pp. + 8 pl.

LeConte, J. L. 1850. An attempt to classify the longicorn Coleoptera of the part of America, north of Mexico. *Journal of the Academy of Natural Sciences of Philadelphia*, (2)1: 311-340; 2:5-38. <[Biodiversity History Library](#)> <[PDF-1](#)> <[PDF-2](#)>

<sup>35</sup>LeConte, J. L. 1851. An attempt to classify the longicorn Coleoptera of the part of America, north of Mexico. *Journal of the Academy of Natural Sciences of Philadelphia*, (2)2:99-112. <[Biodiversity History Library](#)>

LeConte, J. L. 1854. Descriptions of some new Coleoptera from Oregon, collected by Dr. J. G. Cooper on the North Pacific R. R. expedition under Gov. J. J. Stevens. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 7:16-20. <[Biodiversity History Library](#)> <[PDF](#)>

LeConte, J. L. 1857. Report upon Insects collected on the survey. In, Report of Explorations and Surveys to ascertain the most practicable and economical route for a railroad from the Mississippi river to the Pacific Ocean. Made under the Direction of the Secretary of War, in 1853-5, according to Acts of Congress of March 3, 1853, May 31, 1854 and August 5, 1854, 12:1-72, 2 pls. <[Making of America Books](#)> <[pg.64.gif](#)> <[pg.65.gif](#)>

LeConte, J. L. 1859. The Coleoptera of Kansas and eastern New Mexico. *Smithsonian Contributions to Knowledge*, 11(6):1-58. <[Biodiversity History Library](#)> <[PDF](#)>

LeConte, J. L. 1859. Catalogue of the Coleoptera of Fort Tejon, California. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 11:69-90. <[Biodiversity History Library](#)> <[PDF](#)>

LeConte, J. L. 1860. Notes on Coleoptera found at Fort Simpson, Mackenzie River, with remarks on northern species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 12:315-321.

LeConte, J. L. 1861. New species of Coleoptera inhabiting the Pacific District of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 13:338-359. <[Biodiversity History Library](#)> <[PDF](#)>

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<sup>35</sup> *G. molybdica* (LeConte, 1851("1850")) and *B. californica* (LeConte, 1851 ("1850")). The ("1850") is due to an appendix (on page 101) that amends pages from LeConte (1850). The reference is cited as 1851 because, in a footnote in the table of contents, it is indicated that LeConte had pre-prints in December of 1851, although the article was published 1852.

- LeConte, J. L. 1862. Note on the classification of Cerambycidae with descriptions of new species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14:38-43.
- LeConte, J. L. 1869. List of the Coleoptera collected in Vancouver's Island by Henry and Joseph Matthews with descriptions of some new species. *The Annals and Magazine of Natural History*. (4)4:369-385. [<Biodiversity History Library>](#) [<PDF>](#)
- LeConte, J. L. 1873a. New species of North American Coleoptera. Prepared for the Smithsonian Institution. Part II. *Smithsonian Miscellaneous Collections*. 11(264):169-240. [<Biodiversity History Library>](#) [<PDF>](#)
- LeConte, J. L. 1873b. Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution. Part II. *Smithsonian Miscellaneous Collections*. 11(265):279-348. [<Biodiversity History Library>](#) [<PDF>](#)
- LeConte, J. L. 1874. Descriptions of new Coleoptera chiefly from the Pacific slope of North America. *Transactions of the American Entomological Society*, 5:43-72. [<Biodiversity History Library>](#) [<PDF>](#)
- LeConte, J. L. 1875. Descriptions of new Coleoptera of the United States with notes on geographical distribution. *Transactions of the American Entomological Society*, 5:169-176.
- Leech, H. B. 1963. *Centrodera spurca* (LeConte) and two new species resembling it, with biological and other notes. *Proceedings of the California Academy of Sciences*, 32:149-218, 28 figs.
- Leng, C. W. 1890. Synopses of Cerambycidae. *Entomol. Americana*, 6: 9-13, 65-69, 97-98, 104-110, 156-160, 185-200, 213-214.
- Linnaeus, C. (Carl von Linné). 1758. *Systema Naturae per regna tria naturae secundum classes, ordines, genera, species. cum characteribus, differentiis, synonymis, locis*. (ed. 10). Holmiae. Laur. Salvius. 1: iii + 824 pp.
- Linsley, E. G., and J. A. Chemsak. 1972. Cerambycidae of North America. Part VI. No. 1. Taxonomy and Classification of the Subfamily Lepturinae. University of California Publications in Entomology 69, xiii+138 pp, 2 pl.
- Linsley, E.G. and J.A. Chemsak. 1976. Cerambycidae of North America. Part VI, No.2. Taxonomy and Classification of the Subfamily Lepturinae. University of California Publications in Entomology 80, 186 pp.
- Mannerheim, C.G. von. 1852. Zweiter Nachtrag zur Käfer-Fauna der Nord-Amerikanischen Länder des Russischen Reiches. *Bull. Soc. Imp. Natur. Moscou*, 25(2):283-387.

- Mannerheim, C. G. von. 1853. Dritter Nachtrag zur Käfer-Fauna der Nord-Amerikanischen Länder des Russischen Reiches. Bull. Soc. Imp. Natur. Moscou, 26(2):96-273.
- Miroshnikov, A. I., 1998: A new classification of longicorn beetles of the Anoplodera complex, tribe Lepturini Coleoptera, Cerambycidae of Holarctic fauna. I. Entomologicheskoe Obozrenie 77(2): 384-420. [English Translation: *Entomological Review*, Vol. 78, No. 4, 1998, pp. 437--465.]
- Moltschulsky, V. von. 1860. Coléoptères de la Sibérie orientale et en particulier des rives de l'Amour, in Schrenk, Reisen und Forschungen im Amurlande, 2:77-257.
- Mulsant, E. 1863. Histoire naturelle des Coléoptères de France. Longicornes. 2e. ed. Ann. Soc. Imp. Agric Hist. Nat. Industrie, Lyon, p. 1-590. <[Hathitrust](#)> <[PDF](#)>
- Newman, E. 1838. Entomological notes. Entomol. Mag., 5: 168-182; 372-402; 483-500, 3 figs.
- Nicolay, A. S. 1917. A synopsis of the Anthophylax of North America. Journal of the New York Entomological Society, 25(1):38-44. <[Biodiversity History Library](#)>
- Olivier, A. G. 1795. Entomologie, ou Histoire Naturelle des Insectes, avec leurs Caractères Génériques et Spécifiques, leur Description, leur Synonymie et leur Figure Illuminée. Coléoptères. 4:1-519, 72 pls.
- Pic, Maurice. 1900. Contributions à l'étude des Longicornes. L'Échange, No. 191: 81-83.
- <sup>36</sup>Pic, Maurice. 1922. Diagnoses de coléoptères exotiques (suite). L'Échange, 37(405):11.
- Plavilstshikov, N. N., 1958. Novyi dalnevostochnyi vid *Gaurotes* J. Lec. (Coleoptera, Cerambycidae). Entomologicheskoe Obozrenie, 37:720-723.
- Podany, C. 1961. Monographie der Gattung Alosterna Muls. (Stenocorini). Mitt. Entomol. Ges., (N. F.) 11:27-33
- Podany, C. 1962. Monographie des genus Gaurotes J. Lec. Mitt. Müncher Entomol. Gessels., 52:219-252, pls. 4-5
- Podany, C. 1964. Monographie des genus Rhagium Fabricius (Stenocorini). Acta zool. Mex., 7(1 3):1-55, 7 pls.

---

<sup>36</sup>Unverified. **Appears in L&C (1976) as:** *Leptura miquelonensis* Pic, 1922, L'Échange, 37(405):11.  
**B&M (2013):** Pic, M. 1921. Diagnoses de coléoptères exotiques (suite). L'Échange, 37(409):10-12.

- Randall, J. W. 1838. Description of new species of coleopterous insects inhabiting the State of Maine. Boston J. Nat. Hist., 2(1):1-33.
- Reitter, E. 1913. Fauna Germanica. Die Käfer des Deutschen Reiches. Nach der analytischen Methode bearbeitet. IV. Band. K. G. Lutz, Stuttgart, 236 pp. + pls. 129–152. [1912 (title page); 1913 (Zool. Record; Arch. Naturg. 80B); Feb 1914 (Ent. Litteraturbl.); 1 Mar 1914 (Ent. Bericht. 4 (76): 62)]
- Sama, G. 1993. Notes sur les Xylosteini Reitter. Biocosme Mésogéen, Nice, 10(1): 7-15, 6 figs.
- Say, T. 1826. Descriptions of new species of coleopterous insects inhabiting the United States. Journal of the Academy of Natural Sciences of Philadelphia, 5(2):237-284. <[Biodiversity History Library](#)> <[PDF](#)>
- Schaeffer, C. F. A. 1908. List of the longicorn Coleoptera collected on the Museum expedition to Brownsville, Texas and the Huachuca Mts., Arizona, with descriptions of new genera and species and notes on known species. Sci. Bull. Mus. Brooklyn Inst. Arts Sciences, 1(12):325-352.
- Swaine, J. M. & R. Hopping. 1928. The Lepturini of America North of Mexico. Part I. Bull. Nat. Mus. Canada, (Biol. Serv.) (14)52:1-97, 13 pls.
- Thomson, J. 1864. Systema cerambycidarum où expose de tous les genres compris dans la famille des cérambycids et familles limitrophes. Mem. Soc. R. Sci. Liège, 19: 1-540.
- Thomson, C.G. 1866. Skandinaviens Coleoptera, 8. 409 + 75 pp. Lund.
- Van Dyke, E. C. 1917. A new species of the genus Anthophilax LeC. Journal of the New York Entomological Society, 25(1):36-37. <[Biodiversity History Library](#)> <[PDF](#)>
- Van Dyke, E. C. 1920. Description of new species of Cerambycidae from the Pacific coast of North America, with notes concerning others. Bull. Brooklyn Entomol. Soc., 15(2-3):33-48.
- Walker, F. 1866. Appendix, in J. K. Lord, The Naturalist in Vancouver Island and British Columbia. London, Richard Bentley, 2: x + 375 pp., 4 pls. (Walker's Appendix, p. 289-375).
- Webb, J. L. 1905. Description of a new species of Desmocerus with a synoptic table of the genus. Proc. Entomol. Soc. Wash., 7(2-3):104-105.

CHAPTER 3: Phylogenetic Observations on *Desmocerus* Dejean (Cerambycidae: Lepturinae), taxonomic implications and the descriptions of two new species.

## ABSTRACT

A phylogenetic analysis of *Desmocerus* (Coleoptera: Cerambycidae: Lepturinae) is performed based on two genes, mt-CO1 and 28S rDNA, using parsimony, likelihood, and Bayesian methods. The resulting topologies were largely concordant across the separate approaches and character sets, and are also concordant with morphological evidence. The new genetic evidence, and characters from the male genitalia and hindwings, are used to assess prior hypotheses about the species boundaries within *Desmocerus*. Two new species are described from Western North America and a revised taxonomy is proposed. New distributional records are given for the western species and the type locality of *D. aureipennis* Chevrolat is clarified. Finally, new observations on the life history of *Desmocerus* are presented along with a review of existing literature. Implications for the conservation and further study of *Desmocerus* are discussed.

## INTRODUCTION

The longhorn beetle genus *Desmocerus* Dejean, 1821, comprises a small group of charismatic species that bore exclusively into the living roots and stems of elderberry (*Sambucus* Linnaeus) in North America. The genus is often placed within the monotypic tribe Desmocerini Blanchard, 1845, due to a series of unique anatomical features that make *Desmocerus* difficult to place among the world's lepturine genera. The diversity of forms in *Desmocerus* range from small and cryptic, to several large, and brightly colored, probably aposematic, species. The eastern North American species *D. palliatus* (Forster, 1771) is prized among collectors—the large blue-and-yellow lycid mimic has appeared on a 1999 American postal stamp and is currently the subject of a large-scale population study involving citizen scientists, organized by Dr. Daniel Durran at Drexel

University. Members of *Desmocerus* have never been considered major economic pests, and historically very little has been published about the group in general. The listing of *D. californicus dimorphus* Fisher, 1921 from the Sacramento Valley of California as a federally threatened species in 1981 (USFWS, 1980) has led to a surge of research into that species' life history and ecology (Barr, 1991; Huxel, 2000; Collinge et al., 2001; Talley et al., 2007), distribution (Halstead and Oldham, 1990; Halstead and Oldham, 2000), and physiology, including the synthesis of a novel female-produced sex pheromone in *D. c. dimorphus* (Ray et al., 2012). The pheromone, R-Desmolactone, is now known to be used by several additional species in the genus, and holds potential to assist in conservation efforts to track *D. c. dimorphus* and other *Desmocerus* species that are otherwise quite elusive (Ray et al., *in prep*).

The behavior of the larvae, pupae, and adults of the various *Desmocerus* species have been described by Burke (1921), Craighead (1923), Davis (1931), Davis and Comstock (1924), Halstead and Oldham (1990:26), Hardy (1926), Hardy and Preece (1927), Herrick (1902), Gardiner (1970), and others. In general, *Desmocerus* larvae spend one to three years boring within the elderberry plants, both in the roots and in the central pith of the living stems. Adults emerge around the time the elderberry flowers are in bloom, and may live up to two months (Halstead and Oldham, 1990:25). Males are usually smaller in size and will fly to find the relatively larger and more sedentary, pheromone-producing females. Shortly after mating, the females search for oviposition sites in crevices in the elderberry bark, and may crawl or fly short distances to oviposit as many as a hundred or more eggs on multiple trees (Halstead and Oldham, 1990). Unlike the majority of lepturines that feed on flowers, *Desmocerus* adults appear to feed only on the leaves of the elderberry plant (Schapker, personal observations; D. Duran, personal communication; but *cf.* Halstead and Oldham, 1990:4).

A review of lepturine specimens from the Pacific Northwest revealed *Desmocerus* specimens inconsistent with already described species. Additional specimens were obtained from throughout the known distribution of *Desmocerus* to clarify species limits and to construct a preliminary phylogenetic analysis for the genus. The author examined approximately 1350 specimens, and made observations of hindwing venation and male genitalia on a subset of those. Additionally, two genes, mitochondrial CO1 and nuclear 28S rDNA, were sequenced. Based on the accumulated evidence, two new species are proposed in the Pacific Northwest, along with a revised taxonomy for the genus.

*Background – classification of Desmocerus species*

The complexity involved in assigning species boundaries among North America's diverse and widespread *Desmocerus* populations is demonstrated by the multiple, sometimes competing systems of nomenclature that have been applied by taxonomic experts over the last century. Up to the 1970's, as many as six distinct species of *Desmocerus* were recognized worldwide, all occurring in America north of Mexico. In their authoritative revision of the Lepturinae of North America, Linsley and Chemsak (1972) (hereafter: L&C) noticed that the five *Desmocerus* species west of the Rocky Mountains could be separated into two distinct groups based on a number of shared morphological features. Within each of those groups, however, L&C found specimens they regarded as representing transitions between otherwise distinct populations. Thus, the authors recognized just two species in western North America, each with multiple subspecies. These were *D. californicus* Horn, 1881, comprising two subspecies in California, and *D. aureipennis* Chevrolat, 1855, with four markedly divergent subspecies ranging from British Columbia to the Sierra Nevada mountain range of California. The description of *D. aureipennis lacustris* L&C, from Crater Lake, Oregon, as part of that revision brought the total number of validly recognized species-level names in *Desmocerus* to seven. Figure 3.1 shows the geographic distributions of the

subspecies of *D. aureipennis* as conceived in the classification by Linsley and Chemsak (1972, p. 6., Fig. 1), which remained the dominant classification to the present day.

Two things are notable in this treatment of *the D. aureipennis* subspecies. First, while the differences described in body size, pubescence, and coloration between the supposed *D. aureipennis* subspecies are fairly extreme, the locations of the transitional zones between subspecies are not indicated in the text. More curious however is that several of the subspecies are reported to use different—and seemingly quite divergent—species of *Sambucus* as host plants, even when both elderberry species occur abundantly within the same range. This might suggest a level of ecological niche differentiation that is indicative of species-level segregation.

An alternative hypothesis for the specific limits within *Desmocerus* was proposed by Halstead and Oldham (1990). However, this obscure revision of *Desmocerus*, submitted as a special studies staff report to the Kings River Conservation District of California, is not widely available and has been almost entirely ignored. In addition to providing a substantial number of new distribution records for all the known *Desmocerus* species, they examined characters of the genitalia of both sexes to assess species limits among the western species and subspecies. Figure 3.2 is extracted from Halstead and Oldham (1990, Fig. 23), showing their revised interpretation of the species delimitations among *D. aureipennis* subspecies (*sensu* Linsley & Chemsak; hereafter the *D. aureipennis* species complex). The conclusion reached by those authors was substantially different from that of L&C, namely: (1) *D. aureipennis* Chevrolat, *D. cribripennis* Horn, and *D. piperi* Webb are regarded as three distinct species based on discrete morphological characters and apparent sympatry/overlap of ranges based on museum specimen records; (2) *D. lacustris* Linsley & Chemsak is regarded as a junior synonym of *D. piperi* Webb; and (3) *D. c. dimorphus* is regarded as a junior synonym of *D. c. californicus* (see also Halstead and Oldham, 2000). The last finding was explicitly addressed and rejected



by Barr (1991), who cited a personal communication from J. Chemsak expressing doubt to the proposed synonymy.



**Fig. 3.1:** Detail of distribution map taken from Linsley and Chemsak (1972, p. 6, Fig. 1), showing the geographic ranges of the subspecies of *D. aureipennis* Chevrolat. This map represents the dominant classification of *Desmocerus* up to the present day. **1:** *D. aureipennis aureipennis* Chevrolat. **2:** *D. a. cribripennis* Horn. **3:** *D. a. lacustris* Linsley and Chemsak. **4:** *D. a. piperi* Webb.



**Fig. 3.2:** Detail of distribution map taken from Halstead and Oldham (1990, Fig. 23), showing their interpretation of species within the *D. aureipennis* species complex. **Dark circles:** *D. aureipennis* Chevrolat. **Dark triangles:** *D. cribripennis* Horn. **Empty circles:** *D. piperi* Webb. Halstead and Oldham remark: “due to difficulties in distinguishing between the females of *D. cribripennis* and *D. piperi*, the distribution map is based on male specimens” (p.33).

### *Remarks on nomenclature*

Audinet-Serville, 1835, is often cited as the author for *Desmocerus* (e.g., Linsley & Chemsak, 1972, Halstead and Oldham, 1990; 2000). However, the name was first made available in the published catalogue of the Baron Dejean's personal collection (1821, p. 111), where it was listed in combination with an available species name, *cyaneus* Fabricius, 1775 (see IZCN, 1999, Article 12.2.5, and Silfverberg, 1984).

The Latin root of "*aureipennis*," as originally spelled by Chevrolat (1855: 187) means "golden wing" (the bright red elytra fade to yellow in pinned specimens). The incorrect spelling "*auripennis*" (without an *e*) was introduced early on by LeConte (1857), and repeated by Chevrolat (1858) himself, who mistakenly used '*auripennis*' in the citation to his original description. That misspelling was used by nearly all subsequent authors, including Linsley and Chemsak (1972) and Halstead and Oldham (1990). The mistake was first recognized by Monné and Giesbert (1994: 157).

## **METHODS**

### *Specimens*

Approximately 1350 dried and pinned specimens were borrowed and examined from the following museums:

<b>OSAC</b>	-	Oregon State Arthropod Collection
<b>EMEC</b>	-	Essig Museum of Natural History
<b>CAS</b>	-	California Academy of Sciences
<b>SEMC</b>	-	University of Kansas Snow Entomological Museum
<b>CNC</b>	-	Canadian National Collection of Insects
<b>PMAE</b>	-	Royal Alberta Museum
<b>BMNH</b>	-	Natural History Museum, London
<b>MCZ</b>	-	Museum of Comparative Zoology, Harvard University
<b>WFBM</b>	-	W.F. Barr Entomological Collection, University of Idaho

### Specimen collection

Fresh material, suitable for DNA sequencing, was obtained in 2012 and 2013 by collecting live specimens. Habitat was sought by locating elderberry stands within the known ranges for *Desmocerus* based on records obtained from museum specimens. During the flight season, between March and August when the elderberry hosts were in bloom, adults were obtained either by examining the leaves of the plants for adults or with the use of traps baited with R-Desmolactone, a synthetic *Desmocerus* pheromone developed by Ray et al. (2012). Details of the traps, their location and efficacy in California and Oregon are reported elsewhere (Ray et al., *in prep*). Adults intended for DNA extraction were placed directly into 100% EtOH, while others were kept alive for observation. Living adults were given fresh leaves, stems, and flowers of elderberry, and water. Upon death, specimens were either placed into alcohol or frozen and pinned.

Larvae were also sought when adults were not active, from about the time the elderberry fruits begin to mature until the start of the next spring's bloom. Elderberry plants were examined for signs of *Desmocerus* infestations, both by looking for old exit holes (as described in Barr, 1991, Talley et al., 1997, etc.) and by simply cutting living and dying branches of various thicknesses to check for larval chambers in the pith. *Desmocerus* larval chambers could often be distinguished from those of sawflies and other Hymenoptera by their distinctive crescent shape in the lateral cross-section (Fig. 3.3a). The longitudinal cross section of a *Desmocerus* larval chamber is usually uniformly broad and with characteristic stringy frass (Fig. 3.3b.), while the Hymenoptera chambers frequently encountered were irregular (Fig. 3.3c). In some cases larvae were encountered within their chambers and placed directly into 100% EtOH.

Several attempts were made to rear adults from their host plants. When elderberry plants were about to bloom, samples of stems from infested plants were removed

using pruning shears and/or a small saw, brought indoor, placed into a 10 gallon translucent lidded tub, and monitored daily for any emerging adults.

Voucher specimens were deposited in OSAC under Accession Number 2014-05-19-001-01.



**Figure 3.3a.** Latitudinal cross section of red elderberry stem, *Sambucus racemosa*, showing work of *Desmocerus* larva. Collected with permission, May 2, 2013 at Silver Falls State Park, by the parking lot to South Falls. Photo by Phil Schapker, 2014.



**Figure 3.3b.** Pupal chamber and emergence hole of *Desmocerus lacustris*. Longitudinal cross section of a stem of red elderberry, *Sambucus racemosa*. Collected with permission, May 2, 2013 at Silver Falls State Park. Photo by Phil Schapker, 2014.



**Figure 3.3c.** The work of Hymenoptera larvae in blue elderberry, *Sambucus nigra cerulea*. The top specimen was collected by Little Blitzen Crossing in the Steens Mountains, Oregon. August, 2012. The bottom is from uncertain origin. Photo by Phil Schapker, 2014.



**Figure 3.3d.** The work of woodpecker on blue elderberry. Specimen taken from the H.J. Andrews Experimental Forest in the Cascades of Oregon. Photo by Phil Schapker, 2014.





**Figure 3.4.** Red elderberry, *Sambucus racemosa*, at Crater Lake National Park, Oregon. East Rim Drive. Photo taken by Schapker, September 16, 2012.



**Figure 3.5.** The author examining a flowering blue elderberry, *Sambucus nigra* ssp. *cerulea* in Warner Co., California. Note the flat panicles.

## Identifications

Species identifications were made with reference to their original descriptions and type specimens. Specimens of the holotypes of *D. aureipennis* Chevrolat (BMNH) and *D. cribripennis* Horn (MCZ), and the paratype series of *D. lacustris* Linsley and Chemsak (CAS) were physically examined. Images of the following types were viewable online by their respective institutions: *D. dimorphus* Fisher (NMNH), *D. piperi* Webb (NMNH), *D. lacustris* Linsley and Chemsak (CAS), *D. californicus* Horn (MCZ), and *Stenocorus cyaneus* Fabricius (HMUG). All of the above images are also viewable at Larry Bezark's Photographic Catalogue of the Cerambycidae of the World (Bezark, 2014). An image of the holotype of *D. palliatus* Forster (BMNH) was made available to the author by the Linnaean Society.



**Figure 3.6.** Labels for the male allotype of *Desmocerus piperi* Webb, 1905. Used with permission from the Smithsonian Institution National Museum of Natural History.

Of the *D. piperi* material examined, 17 specimens were found to have the exact same label as the *D. piperi* Webb holotype and allotype, reading “Blue Mts., Wash. July 1896” (Fig. 3.6). Webb (1905) stated that the species had been “collected in numbers” by Piper, but that his type series consisted of only 15 specimens. Since the location and



identity of the type series is presently unknown, I concluded that all of these 17 specimens were potential paratypes of *D. piperi* Webb, and affixed labels reading “Potential Paratype of *Desmocerus piperi* Webb, 1905. Det. P. Schapker, 2014.” The specimens are as follows: (CAS): 3 males and 4 females. Two specimens have the same label “Collector C.V. Piper” as in Fig. 6, four are labeled with “R. Hopping Collection” and one is labeled “Van Dyke Collection;” (ESSIG): EMEC654661 and EMEC654662; (OSAC): 4 males and 3 females with blue barcodes (OSAC\_0000496843, OSAC\_0000496828, OSAC\_0000496845, OSAC\_0000496820, OSAC\_0000496818, OSAC\_0000496844, respectively) indicating that they were part of the Melville Hatch collection. The male OSAC\_0000496873 is determined *Desmocerus piperi* with the trademark Victorian-era handwriting of Orson Bennet ( “Bug”) Johnson<sup>37</sup>.

#### *Morphological Analysis and Species Delimitation*

The external anatomy, hindwings, and male genitalia of adult *Desmocerus* were examined (see *Results*, Table 3.4.) to help evaluate species delimitations in concert with the molecular phylogenetic analyses. The total number of specimens examined for each species are as follows (nomenclature reflects results of present study):

***D. palliatus*** – 64 specimens from USA: PA, NC, VT, Mich., Wisc., NY, Mass., Ill., OH, AK, Georgia; Canada: Quebec. **Genitalia – 1, Hindwings – 1.**

***D. californicus californicus*** – 36 specimens from USA: CA. **Genitalia – 3, Hindwings – 3.**

***D. californicus dimorphus*** – 19 specimens from USA: CA. **Genitalia – 3, Hindwings – 3.**

***D. cribripennis*** – 220 specimens from USA: CA, OR, WA; Canada: BC (mainland and Vancouver Island); Holotype: “W.T.” [=Washington Territory].

**Genitalia – 26, Hindwings, - 26.**

***D. maximus* sp. n** – 242 specimens from USA: CA; Canada: BC (Vancouver Island).

**Genitalia – 10, Hindwings – 10.**

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<sup>37</sup> <http://www.washington.edu/research/pathbreakers/1882a.html>

***D. aureipennis*** – 108 specimens from USA: CA, OR, WA; Holotype: “Mont. Roch.”

**Genitalia – 10, Hindwings – 10.**

***D. piperi*** – 467 specimens from USA: CA, OR, WA, MT, ID; (includes 18 specimens that were collected with the holotype, and are potentially paratypical).

**Genitalia – 11, Hindwings – 11.**

***D. sympatricus*** sp. n. – 10 specimens from USA: WA (Stevens Pass).

**Genitalia – 2, Hindwings – 4.**

***D. lacustris*** sp. n. – 181 specimens from USA: OR; Canada: Haida Gwaii (Queen Charlotte Islands).

**Genitalia – 7, Hindwings – 7.**

### **Species delimitation and species concept**

Initial hypotheses of species delimitations were made with consideration to anatomical, life history, and biogeographical information, and these were then tested using the molecular data, with DNA sequences from true species expected to form monophyletic groups. After discovering conflicts between the gene trees and the initial species delimitation hypotheses, further investigations were made into the anatomy and life history of the populations in question.

For the purpose of this dissertation, species are defined as separately-evolving meta-population lineages, following the General Lineage Species Concept (GLSC) of de Queiroz (1998; 2007). The GLSC is not a specific method for delimiting species based on molecular evidence, but a more general approach to species conception that attempts to unify the majority of existing species concepts that prefer one or another specific criterion for delimiting species, such as mating isolation mechanisms, discrete morphological or ecological differences, or the “3% rule” of genetic divergence. The GLSC asserts that all of these phenomena develop at various points during, or after lineage separation in no particular, predestined order (de Queiroz, 2007; see also Hausdorf, 2010; Alcaide et al., 2014). Thus all available data – morphological,

ecological, behavioral, molecular, etc. – should be taken into account as potential evidence for the divergence of lineages under differential selective pressures. Following this vein, in the present study, robust clades on the tree that were also supported by discrete phenotypic, or other relevant features of the populations in question were cautiously considered as evidence for lineage separation at the species level. The interpretation of this evidence was intentionally conservative, given the uncertainties posed by the relatively small number of populations and genes sampled, and other technical considerations, such as the possibility for phylogenetic breaks to be erroneously inferred from mitochondrial genes even without natural barriers to gene flow (Irwin, 2002).

#### **Preparation and examination of internal anatomy**

Genitalia and hind wings were dissected from pinned specimens using fine forceps after heating the specimens in 5% KOH solution for approximately 10 minutes. Once removed, the genitalia were placed into 10% KOH solution and heated again for 10 minutes to dissolve the remaining muscle tissue. Genitalia were suspended in Safeway brand Lubricating Jelly and photographed with a Canon EOS 40D camera mounted to a Visionary Digital P-51 Camlift. Vertically-layered images were compiled using ZereneStacker. Wings were slide-mounted with Euparal Mounting Medium (BioQuip #6372B) and photographed with the same camera. Finally, genitalia were placed in micro vials in Glycerol and affixed to their respective pinned specimens.

## *Molecular Analysis*

### **DNA extraction, amplification, and sequencing**

The two genes used in the study were the mitochondrial gene Cytochrome Oxidase Subunit 1 (to be abbreviated as “CO1 mtDNA” or just “CO1”), and the nuclear ribosomal RNA-encoding gene 28S (to be abbreviated as “28S ribosomal DNA”, “28S rDNA,” or just “28S”). These genes were chosen to provide differing levels of temporal resolution for inferring relationships among the sampled *Desmocerus*, with the mtCO1 expected to be more rapidly evolving (Avice et al., 1987; Zink, 2008). 28S rDNA on the other hand was expected to be relatively conservative, more appropriate for establishing basal branching patterns (Kjer, 2004; Zink, 2008; Galbreath et al., 2010).

Specimens were stored in alcohol in a -20 °C freezer until genomic DNA was extracted using the Qiagen DNEasy extraction kit and manufacturer-recommended protocol, which has been described in Maddison (2008). Sequence amplification using Polymerase Chain Reaction was conducted on site using an Eppendorf Mastercycler Thermal Cycler, using TaKaRa Ex Taq and the basic protocols recommended by manufacturers. Target gene regions were: (CO1) a 590 bp segment flanked by primers HC2198 and LC1490, and (28S) a 925 bp segment flanked by primers NLF184 and D3aR (for details on primers see Maddison (2012)). The thermal profile for both CO1 and 28S rDNA began with an initial denaturation of 2 minutes at 94°C, followed by 36 cycles of the following: denaturation: 94°C for 20 seconds; annealing: 20 seconds at 52°C; and extension: 70°C for 1 min. PCR product was dyed with SYBR® Green and examined after gel electrophoresis to make sure the reaction had worked.

Raw PCR product was sent to the University of Arizona Genomic and Technology Core Facility, where it was cleaned and sequenced using either a 3730 or 3730 XL Applied Biosystems automatic sequencer. The chromatogram files were processed using the Chromaseq package in Mesquite (Maddison and Maddison, 2011a,b), which

incorporates Phred (Green and Ewing, 2002) and Phrap (Green, 1999) to build contigs of each gene fragment and make initial base calls. Chromatograms were then visually inspected and modified manually.

### **Taxon sampling – ingroup**

**Table 3.1** lists the *Desmocerus* taxa represented by each gene in the analysis, and the number of distinct localities from which each taxon is represented. The details of each *Desmocerus* sequence is given in **Table 3.2**. CO1 mtDNA was sequenced from all previously recognized species and subspecies, with an emphasis on sampling as many geographically distinct populations as possible. In all, 44 mitochondrial CO1 sequences for *Desmocerus* were used in this study, representing 28 localities in North America. Twenty-three of these sequences are from specimens extracted as part of this study and thus have corresponding 28S rDNA sequence data, representative of 18 *Desmocerus* localities. 28S rDNA was obtained for all significant populations except from Haida Gwaii, BC. The CO1 sequence representing that population was produced elsewhere and genomic DNA was not available to us.

Twenty-one additional sequences of *Desmocerus* CO1 were obtained from other sources (marked by asterisks in **Table 3.2**). The CO1 sequences obtained elsewhere are as follows: 12 CO1 sequences were provided by Dr. Patrice Bouchard, sequenced from specimens in the Canadian National Collection (CNC) in collaboration with Dr. Serge Laplante (CNC) and Dr. Paul Hebert (International Barcode of Life Project in University of Guelph, Ontario). Museum specimens corresponding to these sequences were borrowed and examined. One sequence identified as *D. aureipennis* from the Warner Mts., California was not used in the analysis because it was of poor quality. Dr. Leland Humble provided 10 CO1 sequences from the Natural Resources Canada and Canadian Forest Service collections in Victoria (Pacific Forestry Centre), Edmonton (Northern Forestry Centre) and Ste. Foy (Laurentian Forestry Centre). Those specimens were

identified to species by Paul Hebert and were not examined by the authors. None of these samples had corresponding 28S sequences.

Two specimens of *D. palliatus*, barcoded from British Columbia [CERPA324-08|PaA-08-419 and CERPA325-08|PaA-08-420], were handpicked from host plants at a commercial nursery and apparently represent movement of that species from eastern North America with commercial nursery stock (Leland Humble, personal communication).

**Table 3.1.** *Desmocerus* taxa used in the molecular study. Taxon names on the left reflect revisions recommended in the present study, followed by that population's treatment in Linsley and Chemsak (1972) and Halstead and Oldham (1990). The number of sequences (Seqs) of CO1 and 28S representing each taxon is given, followed by the number of distinct localities (Locs) from which sequences are taken. The last column indicates the number of specimens from which both hindwings and genitalia were dissected and examined.

<i>Species Group</i>	<i>Species</i>	<b>Linsley and Chemsak (1972)</b>	<b>Halstead and Oldham (1990)</b>	<b>CO1 Seqs</b>	<b>CO1 Locs</b>	<b>28S Seqs</b>	<b>28S Locs</b>	<b>Hindwing/ Genitalia</b>
<b><i>D. aureipennis</i> species complex</b>	<i>D. aureipennis</i> Chevrolat	<i>D. auripennis auripennis</i> Chevrolat	<i>D. auripennis</i> Chevrolat	1	1	1	1	10
	<i>D. maximus</i> sp. n.	<i>D. auripennis auripennis</i> Chevrolat	<i>D. auripennis</i> Chevrolat	3	2	1	1	10
	<i>D. cribripennis</i> Horn	<i>D. auripennis cribripennis</i> Horn	<i>D. cribripennis</i> Horn	7	4	2	2	26
	<i>D. piperi</i> Webb	<i>D. auripennis piperi</i> Webb	<i>D. piperi</i> Webb	4	3	1	1	11
	<i>D. sympatricus</i> sp. n.	<i>D. auripennis piperi</i> Webb	<i>D. piperi</i> Webb	1	1	1	1	2
	<i>D. lacustris</i> Linsley & Chemsak	<i>D. auripennis lacustris</i> Linsley & Chemsak	<i>D. piperi</i> Webb	15	14	11	9	7
<b><i>D. californicus</i></b>	<i>D. californicus californicus</i> Horn	<i>D. californicus californicus</i> Horn	<i>D. californicus</i> Horn	2	1	2	1	3 (2 Locs)
	<i>D. californicus dimorphus</i> Fisher	<i>D. californicus dimorphus</i> Fisher	<i>D. californicus</i> Horn	3	1	3	1	3 (1 Loc)
<b><i>D. palliatus</i></b>	<i>D. palliatus</i> (Forster)	<i>D. palliatus</i> (Forster)	<i>D. palliatus</i> (Forster)	8	3	1	1	1
<b>Totals</b>				44	28	23	18	82

**Table 3.2.** *Desmocerus* sequences used in the study. Sequence IDs beginning with PAS or KK were used by the author but are not available publically at present. Future publications resulting from this work will have GenBank accession numbers associated with each sequence. Source of sequences were: PS = Present Study/Phil Schapker, 1 = Humble, 2 = Bouchard/CNC.

Species	Specimen #	CO1 Seq ID	28S Seq. ID	Genomic Vial - OSAC	Locality	Source
<i>D. aureipennis</i>	OSAC 0000556816	PAS0008	PAS0001	PAS1112001	USA: OR: Mt. Ashland	PS
<i>D. c. californicus</i>	UCRCENT 293613	PAS0069	PAS0053	PAS0213001	USA: CA: San Bernardino Co.	PS
	UCRCENT 293625	PAS0070	PAS0054	PAS0213002	USA: CA: San Bernardino Co.	PS
<i>D. c. dimorphus</i>	OSAC 0000556491	KK22112	KK22105	PAS0913005	USA: CA: Ord Bend	PS
	OSAC 0000556492	KK22113	KK22106	PAS0913006	USA: CA: Ord Bend	PS
	OSAC 0000556493	KK22114	KK22107	PAS0913007	USA: CA: Ord Bend	PS
<i>D. cribripennis</i>	PFC-2005- 00002	PaA-08- 274	n/a	n/a	CAN: BC: Victoria (1)	1
	PFC-2005- 00004	PaA-08- 276	n/a	n/a	CAN: BC: Victoria (2)	1
	PFC-2005- 00003	PaA-08- 275	n/a	n/a	CAN: BC: Victoria (3)	1
	CNC COLEOPT # 05-312	CNCCB273 6-11	n/a	n/a	CAN: BC: 50 mi. SW of Terrace	2
	CNC COLEOPT #05-321	CNCCB274 3-11	n/a	n/a	CAN: BC: 50 mi. SW of Terrace	2
	OSAC 0000556461	PAS0026	PAS0039	PAS1212017	USA: WA: Steven's Pass Summit	PS
	OSAC 0000555790	KK22111	KK22104	PAS0913004	CAN: BC: Vancouver: Colony Farm Park	PS
<i>D. lacustris</i>	cnc coleopt #05-340	CNCCB274 2-11	n/a	n/a	CAN: BC: Haida Gwaii (Queen Charlotte Islands)	2
	CNC COLEO 00123622	CNCCB274 0-11	n/a	n/a	USA: OR: Crater Lake - Vidae Falls (1)	2
	CNC COLEO 00123623	CNCCB274 1-11	n/a	n/a	USA: OR: Crater Lake - Vidae Falls (2)	2
	OSAC 0000556469	PAS0012	PAS0005	PAS1112005	USA: OR: Crater Lake - East Rim Dr.	PS
	OSAC 0000556456	PAS0019	PAS0032	PAS1212009	USA: OR: Crater Lake - C.C. Meadow	PS
	OSAC 0000524095	PAS0513.1	PAS0513.2	PAS0513002	USA: OR: Silver Creek Falls	PS
	OSAC 0000556474	PAS0018	PAS0031	PAS1212008	USA: OR: Portland	PS
	CNC COLEOPT # 05-322	CNCCB273 7-11	n/a	n/a	CAN: BC: Glacier Cr. 10 mi. N. Terrace	2



Table 3.2. *continued.*

Species	Specimen #	CO1 Seq ID	28S Seq. ID	Genomic Vial	Locality	Source
<i>D. lacustris</i>	OSAC 0000556482	PAS0020	PAS0033	PAS1212010	USA: OR: Tombstone Pr. (1)	PS
	OSAC 0000556484	PAS0021	PAS0034	PAS1212011	USA: OR: Tombstone Pr. (2)	PS
	OSAC 0000555788	KK22110	KK22102	PAS0913002	USA: OR: Monument Peak (2)	PS
	OSAC 0000555787	KK22109	KK22101	PAS0913001	USA: OR: Monument Peak (1)	PS
	OSAC 0000558305	PAS0062	PAS0029	PAS1212006	USA: OR: Logsden	PS
	OSAC 0000558309	PAS0017	PAS0030	PAS1212007	USA: OR: Newport	PS
	OSAC 0000555789	KK22111	KK22103	PAS0913003	USA: OR: Coast Range, Suislaw N.F., Cummin's Peak	PS
<i>D. maximus</i>	CNC COLEO 00123620	CNCCB27 35-11	n/a	n/a	USA: CA: Plumas Co.	2
	OSAC 0000556507	PAS0015	PAS0028	PAS1212001	USA: CA: Tehama Co. (1)	PS
	OSAC 0000556505	PAS0064	n/a	PAS1212003	USA: CA: Tehama Co. (2)	PS
<i>D. palliatus</i>	CNC COLEO 00086445	CNCCB27 34-11	n/a	n/a	CAN: Quebec: Chelsea	2
	PFC-2004-00031	PaA-08- 419	n/a	n/a	CAN: BC: Westbank	1
	PFC-2004-00032	PaA-08- 420	n/a	n/a	CAN: BC: Westbank	1
	LFCa-08-094	LFCa-08- 094	n/a	n/a	CAN: Quebec: Lotbiniere: Sainte-Agathe-de-Lotbiniere	1
	LFCa-08-095	LFCa-08- 095	n/a	n/a	CAN: Quebec: Lotbiniere: Sainte-Agathe-de-Lotbiniere	1
	LFCa-08-096	LFCa-08- 096	n/a	n/a	CAN: Quebec: Sainte-Foy	1
	LFCa-08-097	LFCa-08- 097	n/a	n/a	CAN: Quebec: La Jacques-Cartier: Stoneham	1
	OSAC 0000556524	PAS0013	PAS0006	PAS1212024	USA: MO: (locality not specified)	
<i>D. piperi</i>	NFRC-P-2005- 000043	NoA-08- 010	n/a	n/a	CAN: Alberta: Crowsnest Pass	1
	CNC 61.22	CNCCB27 38-11	n/a	n/a	USA: ID: Clearwater	2
	CNC 61.27	CNCCB27 39-11	n/a	n/a	CAN: Alberta: Tp.6 Rge.3 W.5 Mer.	2
	OSAC 0000556475	PAS0063	PAS0038	PAS1212015	USA: OR: Blue Mtns. - Mt. Emily	PS
<i>D. sympatricus</i>	OSAC 0000556468	PAS12120 18 – CO1	PAS12120 18 – 28S	PAS1212018	USA: WA: Steven's Pass Summit	PS

## Outgroup selection

Although there is no clear consensus in the available literature regarding the phylogenetic placement of *Desmocerus* among the Lepturinae, a recent phylogenetic analysis by Sýkorová (2008) suggests that *Desmocerus* could be closely related to the tribe Lepturini. Lacking an obvious sister taxon to serve as an outgroup for *Desmocerus* in the phylogenetic analysis, an initial set of analyses were conducted using 28S rDNA to compare *Desmocerus* to as many potential lepturine outgroups as were available. These consisted of 5 species from the tribe Rhagiini, and 13 species from the tribe Lepturini (see Table 3.3, and *Results*, Figs. 3.8-18). Ultimately, four genera from the tribe Lepturini, *Trachysida*, *Stictoleptura*, *Xestoleptura*, and *Judolia*, were chosen as outgroups in the subsequent CO1 and combined gene analyses. *Stenocorus* was ultimately removed as a potential outgroup for a variety of reasons, including morphological dissimilarity and suspicions of artificial long branch attraction in the 28S data set (see *Discussion* for more details).

As a rough indicator of the degree to which outgroup choice may have affected the CO1 and combined-gene analyses, each CO1 analysis was conducted under two different outgroup treatments. **Outgroup A** comprised *Trachysida a. aspera*, *Stictoleptura canadensis cribripennis*, *Xestoleptura crassicornis*, and *Judolia instabilis*. **Outgroup B** had only *Judolia instabilis* and *Judolia montivigans* as outgroups. Trees are given for each of the two outgroup treatments and their differences are discussed. Preliminary trials using different subsets of the lepturine taxa in the 28S analysis did not affect the phylogeny within *Desmocerus*, and are not shown in the results.

**Table 3.3.** Outgroup taxa used in analysis of nuclear 28S rDNA. Sequences with asterisks (\*\*\*) in the GenBank Accession # column were produced in the present study, GenBank numbers will be available when this study is published. Sequences with accession numbers beginning with CNE- and DDM- were produced by a different study.

Tribe	Species	GenBank Accession #
Rhagiini	<i>Gaurotes virginea thalassina</i>	CNE1034
	<i>Pachyta bicuneata</i>	CNE1004
	<i>Pidonia gibbicollis</i>	CNE1002
	<i>Pidonia similis</i>	CNE1003
	<i>Stenocorus amurensis</i>	CNE1013
Lepturini	<i>Anastrangalia sequensi</i>	CNE1008
	<i>Judolia instabilis</i>	* * *
	<i>Judolia sexmaculata</i>	CNE1009
	<i>Judolidia bangi</i>	CNE1015
	<i>Leptura aethiops</i>	CNE1006
	<i>Leptura duodecimguttata</i>	CNE1032
	<i>Macroleptura thoracica</i>	CNE1014
	<i>Stictoleptura canadensis cribripennis</i>	* * *
	<i>Stictoleptura variicornis</i>	CNE1012
	<i>Strangalia attenuata</i>	CNE1007
	<i>Strangalia luteicornis</i>	DDM0977
	<i>Trachysida aspera aspera</i>	* * *
	<i>Xestoleptura crassicornis</i>	* * *

## Phylogenetic analysis

Mesquite (Maddison and Maddison, 2011) was used to manage the sequence data, including the alignment, which was done by hand. Once, aligned, the sequence data matrix was analyzed using Bayesian, Likelihood and Parsimony methods, which are discussed in greater detail below. Nucleotide substitution models were chosen separately for four sequence matrices (28S, CO1-(Outgroup A), CO1-(Outgroup B), and a combined-gene matrix) under a Bayesian Inference Criterion (BIC) as employed by jModelTest v.2.1.6 (Guindon & Gascuel, 2003; Darriba et al., 2009). The recommended model for the 28S, CO1-(Outgroup A), and combined-gene matrices was GTR +  $\Gamma$ . The recommended model for CO1-(Outgroup B) was HKY +  $\Gamma$ . The latter model was used in the Bayesian analysis of CO1-(Outgroup B). However, in the Likelihood analysis of the same matrix, the second-best model, GTR +  $\Gamma$ , was used since HKY +  $\Gamma$  is not available in RaxML Blackbox.

### ***Parsimony***

A classical approach to generating phylogenetic hypotheses, using a criterion called *parsimony*, asserts that the best evolutionary hypothesis should be based on a topology that requires the fewest ad hoc assumptions about the homology assessments and character-state transformations in the dataset. The character states under consideration, in this case individual DNA nucleotides, are assumed to be homologous after sequence alignment. The number of character state changes along a given branch is referred to as the branch *length*, and the best parsimony tree is the tree with the smallest overall length. Due to the immense computation time required for an exhaustive comparison of all possible tree topologies for our data set, a heuristic search for the shortest tree(s) was performed using PAUP\* version 4.0 (beta) (Swofford, 2002).

For each gene separately, and in the combined-gene analysis, a heuristic search was first performed with 1000 *random addition search* (RAS) replicates, with each starting tree formed by stepwise addition of taxa chosen in a random order. The initial arrangement of taxa on the starting tree can affect the outcome of a parsimony algorithm by making it more or less likely to arrive at a solution that is optimal only within a subset of the global range of possible tree topologies (see Wiley and Lieberman (2011: 209); Maddison, 1991). All characters were weighted equally, and gaps were treated as missing data. In order to speed up the analysis, PAUP\* was allowed to hold just 25 trees in memory at any time during each search replicate. By default, the searches employed the Tree-Bisection and Reconnection (TBR) method for branch swapping (Wiley and Lieberman, 2011:203-313). Only the shortest tree(s) discovered among all the 1000 replicates were saved, and these were concatenated into a strict consensus tree. This initial set of best trees were then used as starting trees for a final round of heuristic searches. The best tree, or trees returned from that search were finally concatenated into a strict consensus tree.

Each PAUP\* analysis was run by executing a Nexus file with the following commands:

```
begin paup; set torder=right tcompress increase=auto outroot=monophyl
taxlabels=full nowarnreset;
log file = DesmocerusPAUPMPTs.log;
execute charactermatrix.nex;

hsearch addseq=random rstatus nreps=1000 nosavereps nchuck=25
      chuckscore=2; savetrees file=DesmocerusPAUPMPTsInitial.tre;
      contree all/ strict=yes majrule=no
      treefile=DesmocerusPAUPMPTsInitial.con;
38hsearch start=current rstatus nchuck=1000000;
      savetrees file=DesmocerusPAUPMPTs.tre;
      contree all/ strict=yes majrule=no
      treefile=DesmocerusPAUPMPTs.con;
log stop; end;
```

---

<sup>38</sup> Sets the max limit of trees PAUP\* can hold in its memory to an arbitrarily high number.

***Likelihood analysis***

A different approach to forming phylogenetic hypotheses allows the researcher to make inferences based upon the probability of observing the sequence data given a particular tree topology and set of parameters under a stochastic model of nucleotide evolution. Depending on the model, each type of nucleotide state change ( $A \rightarrow T$ ,  $C \rightarrow G$ ,  $C \rightarrow A$ , etc.) may be assumed to occur with equal probability, or the probabilities of each type of substitution can be estimated independently as in the General-Time-Reversible (GTR) model. Branch lengths are also taken into account in the analysis: as the length of a branch increases, the less probable it becomes that two identical character states at the base and tip of a branch are homologous. A likelihood score for a tree is calculated by multiplying all the probabilities at each branch. After calculating likelihood scores for a large number of trees in a heuristic search, the best evolutionary hypothesis is judged to be the tree with the highest overall, or *maximum likelihood* (ML). Likelihood scores are used to compare competing tree topologies given a specific set of parameters and are not directly comparable between analyses of different data sets.

Maximum Likelihood analyses of the CO1 mtDNA and 28S rDNA were performed both separately, and in a combined matrix using RAxML Blackbox (Stamatakis et al., 2008), a free, online server for running phylogenetic analyses. RAxML Blackbox optimized model parameters and performed 100 heuristic search replicates for tree topologies yielding the highest likelihood score. Each replicate proceeds from a random addition maximum parsimony starting tree. The combined-gene matrix was partitioned to allow individual  $\alpha$ -shape parameters, GTR-rates, and base frequencies to be estimated and optimized for each gene separately. (For a discussion on different approaches to gene partitioning and their potential to influence the inferred tree topology see Bevan et al., 2007.)

To assess strength of phylogenetic signal at each node in the best ML tree, a separate set of non-parametric likelihood bootstrap searches were performed on 100 pseudoreplicate data matrices (the maximum allowed in Blackbox). For each pseudoreplicate, a portion of characters from the original matrix are deleted and then replaced by a random subset of the remaining characters, and then a heuristic search is performed. The best tree from each run is saved. The best ML tree from the original character matrix is then labeled at each node, indicating the frequency at which that clade appeared in the 100 bootstrap trees. As a summary of the trees produced by the bootstrap analysis, RAxML Blackbox also produced a strict consensus tree and two types of majority rules consensus trees. In the 50% majority-rules consensus tree, only nodes that appeared in 50% or more of the best trees from each of the bootstrap pseudoreplicate are included, with node values representing the percentage of times that particular node was recovered in the resulting ML tree. The extended consensus tree is formed by adding sets of species to the majority rules tree in the order of the frequency with which they have appeared until the tree is fully resolved.

### ***Bayesian analysis***

The Bayesian approach essentially uses the observed sequence data as a focal point to estimate tree topologies and sequence evolution parameters simultaneously (See Huelsenbeck et al., 2001; 2002; Ronquist and Deans, 2010). According to Bayes' theorem, the posterior probability of a tree (interpreted as the probability the tree is correct) given the sequence data,  $\Pr[Tree|Data]$ , is proportional to the prior probability of the phylogeny,  $\Pr[Tree]$ , multiplied by the likelihood and divided by the overall probability of the data. The standard method assumes the prior probability of the phylogeny to be equal across all possible topologies. Methods exist to produce a single best tree—a tree with highest posterior probability—through Bayesian analysis. A more common application is to produce a 50% majority-rules consensus tree of samples taken from a Bayesian posterior probability distribution on trees, as an

alternative to likelihood bootstrap analysis for the assessment of statistical support for nodes (Douady et al., 2003; Ronquist and Deans, 2010; Holder, 2008; but *c.f.*, Barrett et al., 1991; Wheeler and Pickett, 2008).

The posterior probability distribution was estimated using MrBayes v3.2.1 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). An exact computation of the posterior requires summation over all possible trees and, for each tree, integration over all possible combinations of branch length and substitution model parameter values (Huelsenbeck et al., 2001). For this reason, the posterior probability must be estimated heuristically. In the Metropolis-Coupled Markov Chain Monte Carlo (MCMCMC) method used by MrBayes, several independent algorithms, called Markov Chains, search through parameter space for probable trees, taking samples at regular intervals. By the default setting in MrBayes, in each run 1 *cold* chain is responsible for taking samples of the posterior probability while exploring relatively minor perturbations in parameter space. The cold chain is accompanied by 3 *heated* chains that search more broadly through parameter space, allowing the cold chain to avoid entrapment by local topology. The first 25% of samples visited by the cold chain are discarded from the analysis (also known as *burn-in*) to give some time for the chains to start providing a meaningful sample of the posterior probability distribution. The multiple runs are guaranteed to eventually converge on a stationary distribution, however, this may take an unreasonably long time. In this analysis, the estimate of the posterior was considered sufficiently close, and the analysis stopped after the two runs became arbitrarily close to stasis, as indicated by a convergence diagnostic, *the standard deviation of split frequencies* (SDSF) reaching near or below 0.01 (Lakner et al, 2002). MrBayes reports the SDSF of the multiple runs continuously during the analysis.

In the present study, the CO1 and 28S sequences were first analyzed separately and then combined into a single analysis. Each DNA matrix analyzed was exported



from Mesquite in Nexus format with the following commands, and then executed in MrBayes:

```
outgroup 1; set autoclose=yes nowarn=yes;
lset nst=6 rates=gamma;
mcmcp ngen= 10000000 printfreq=1000 samplefreq=1000 nchains=4
relburnin=yes burninfrac=0.25 savebrlens=yes;
mcmc; sumpt
```

This set the evolutionary model to the GTR +  $\Gamma$ , and directed two sets of four independent MCMC chains to run for ten million generations each, returning a sample every 1000 generations. (nst=2 was used to select the HKY model for CO1-Outgroup B.) The 15000 trees resulting after burn-in were then summarized in a 50% majority-rules consensus tree using Mesquite. On this consensus tree, the node values indicate the proportion of the 15,000 trees in which a given clade was present.

In the combined-gene analysis, the two genes were first concatenated into a single matrix, and exported with the additional following commands, which allow for nucleotide substitution parameters and the gamma-shaped rate distribution to be estimated independently for each gene:

```
charset 28S = 1-1016;
charset Co1 = 1017-1688;
partition favored = 2: 28S, Co1;
set partition=favored;
unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
prset applyto=(all) ratepr=variable;
```

## RESULTS

### *Morphological Analysis*

Below is a summary of morphological characters that were examined for each *Desmocerus* species, and represented in a matrix in **Table 3.4**. The list includes characters that are parsimony-informative, as well as some non-parsimony-informative characters that were useful in species delimitation. Morphological data was not explicitly incorporated into the molecular phylogenetic analysis. Instead, select characters are mapped onto the preferred phylogeny (see *Discussion*, **Fig. 3.22**). The species represented in **Table 3.4** include new species and nomenclatural recommendations given at the end of this chapter (see *Discussion*, pp. 219-244).

**Antennae** - Base of third segment: (0) conical; (1) flattened

**Pronotum** - Dorsal pubescence on males: (0) short; (1) long.

#### **Elytra** -

Punctuation: (0) dense and minute; (1) large, irregular and/or rugose

Dorsal pubescence: (0) short; (1) long

Red pigment in live specimens (fades to yellow in pinned specimens):

(0) absent; (1) present

Extent of dark pigmented area on male elytron: (0) absent; (1) full (2) lycid pattern

Extent of dark pigmented area on female elytron: (0) absent; (1) full; (2) lycid pattern

Color of dark pigmented area on female elytron: (0) monochrome;

(1) dichromatic/semi-metallic

#### **Hind wings** -

Color: (0) partially opaque, often with anal portion transparent; (1) entirely opaque

Color: (0) distal portion gradually or irregularly darkened; (1) distal portion with distinct dark area

**Abdomen** - color of pubescence: (0) brown; (1) white

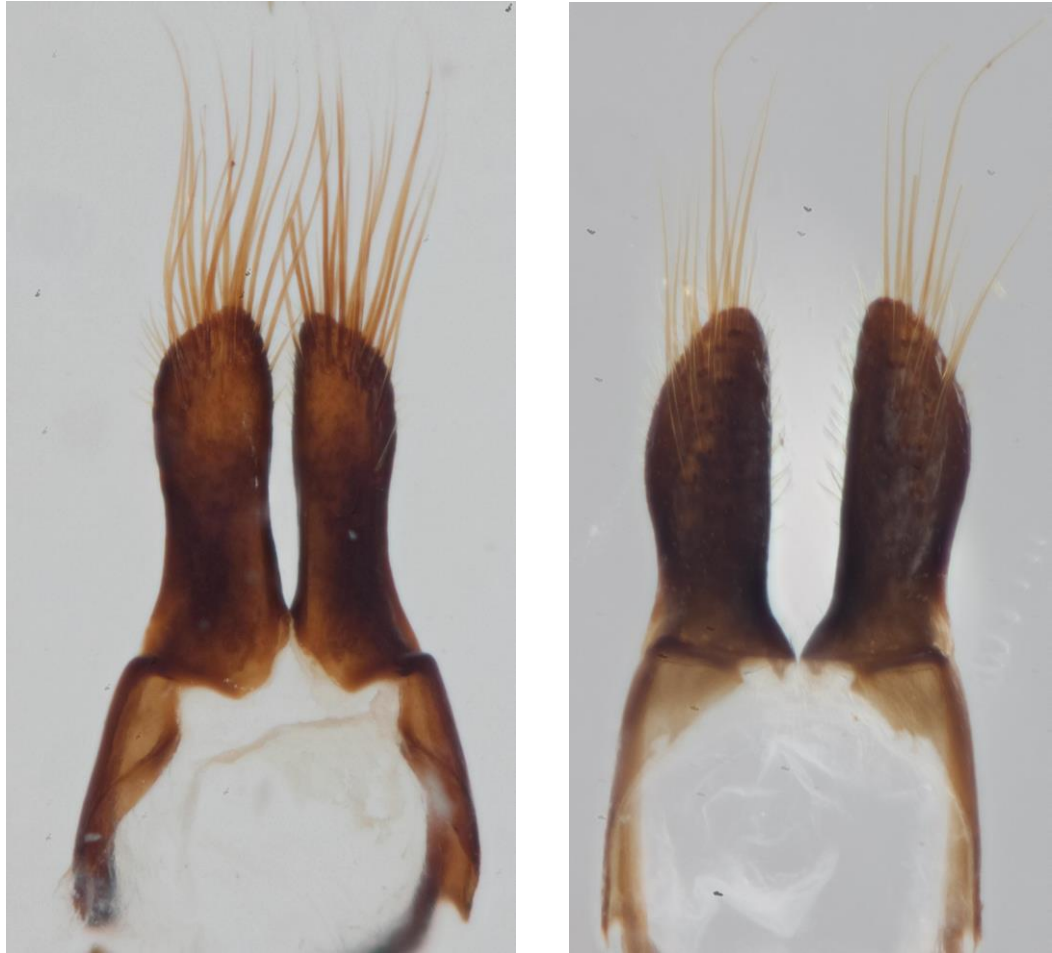
**Hind coxae** - Posterior-ventral margin: (0) smooth; (1) sharply keeled

#### **Male Genitalia, parameres – (Fig. 3.7)**

Posterior apical setae: (0) few, sparse; (1) numerous, dense

Dorsal setae: (0) sparse or absent, never occurring on anterior half of the paramere; (1) thick, prominent, usually forming a line up middle part of paramere.



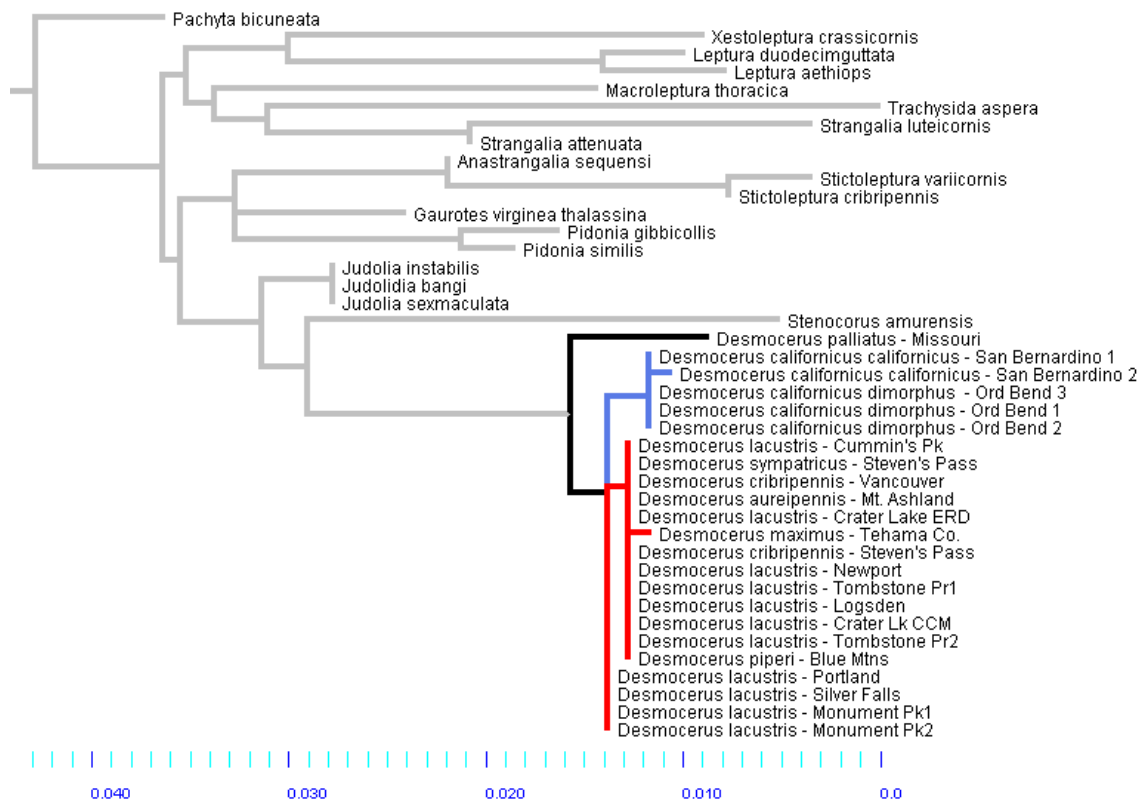


**Figure. 3.7.** Characters of male genitalia. **Left:** *D. palliatus* – dorsal parameres with apical setae dense (OSAC\_0000556523). **Right:** *D. californicus dimorphus* – apical setae are sparse, but dorsal setae are thick, prominent, arranged in a line up the middle of the paramere (OSAC\_0000556491).

*NOTE: character states for these two species are based on observations of very few specimens. See table 3.1.*

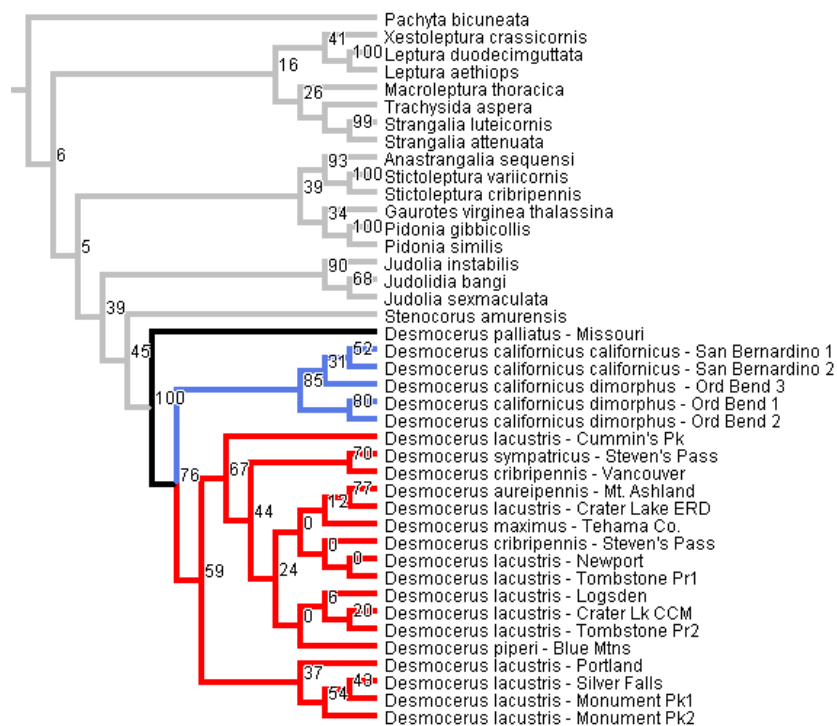
### 28S Analysis

The results of Maximum Likelihood, Parsimony, and Bayesian analyses conducted on the nuclear 28S rDNA gene for *Desmocerus* and 18 lepturine outgroups are given below. In all three approaches: (a) *Desmocerus* is recovered as a clade, (b) the two subspecies of *D. californicus* form a clade, and (c) the two western species groups (*D. californicus* + *D. aureipennis* complex) are a clade that is sister to the eastern *D. palliatus*. The *D. aureipennis* species complex is recovered as a clade only in the Likelihood analysis (Figs. 3.8-3.9).



**Figure 3.8. Nuclear 28S rDNA - Maximum Likelihood (ML) Analysis.** Best tree is shown with branches drawn proportional to lengths. Final ML Optimization Likelihood: -2624.138328. Node values indicate percentage of time a clade was observed in separate analysis of 100 non-parametric bootstrap pseudoreplicate matrices. **Red clade:** *D. aureipennis* species complex.

28S sequence diversity was low among the *D. californicus* subspecies (blue clad), and within the *D. aureipennis* species complex (red clad). This is demonstrated by the best ML tree in Figure 3.8, in which branches are drawn proportional to their lengths. In the *D. aureipennis* complex the majority of 28S sequences were either identical, or differed only in the length of their untrimmed ends. Some of the ends did have an effect on the topology of the ML tree (Fig. 3.9), but those nodes are characterized by low bootstrap values. *Desmocerus maximus* differs from the rest of the *D. aureipennis* complex by a single nucleotide at position 415, and a group of four *D. lacustris* sequences from Northern Oregon (Cascades and Portland) differ only at position 414, where they have a thymine, a symplesiomorphy with *D. californicus*, *D. palliatus*, and all of the lepturine outgroups.

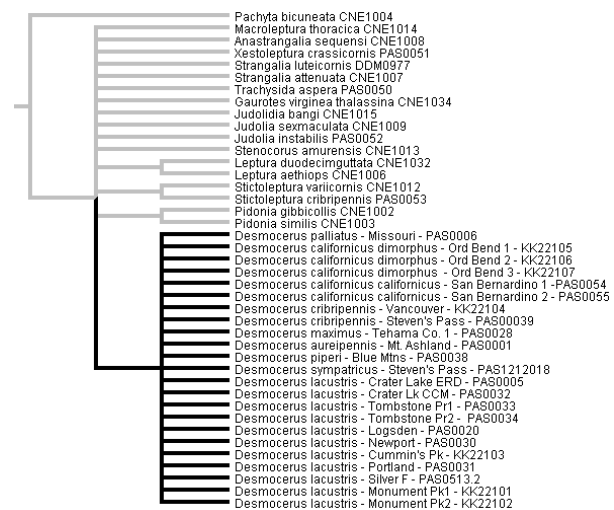


**Figure 3.9. Nuclear 28S rDNA - ML Analysis.** Same tree as Figure2 with branches not shown proportional to lengths for easier viewing of nodes. Best tree with final ML Optimization Likelihood: - 2624.138328. **Red clad:** *D. aureipennis* species complex. Node values are derived from a separate analysis of 100 non-parametric bootstrap pseudoreplicate matrices , and indicate the percentage of matrices from which that clad was recovered.

## Maximum Likelihood

A single best ML tree was generated, with node values mapped on from a separate bootstrap analysis (Figs. 3.8, 3.9). Given the low sequence divergence in 28S, the node support in the best ML tree was correspondingly low (Fig. 3.9), a fact that is well illustrated by a strict consensus tree of the bootstrap analysis trees (**Fig. 3.10**) showing lack of any structure within *Desmocerus*. Still, the ML tree does display a number of clades with support values above 50% (Fig. 3.9), including a monophyletic *Desmocerus* (100%). The western *Desmocerus* species groups form a clade sister to *D. palliatus* with 76% support. The *D. californicus* species group is a clade with 85% support, and the *D. aureipennis* species complex is recovered as monophyletic with 59% bootstrap support. A clade containing all members of the Northern Oregon *D. lacustris* group was discovered in 37% of the bootstrapped matrices. Four clades within the *D. aureipennis* species complex were not present in any of the bootstrap analyses and have node support values of zero. The phylogenetic placement of *Desmocerus* within the Lepturinae is less clear, with low bootstrap values uniting *Desmocerus* with *Stenocorus amurensis* (45% support) and then both clades to a clade containing: *Judolia sexmaculata*, *J. instabilis*, and *Judolidia bangi* (39% support).

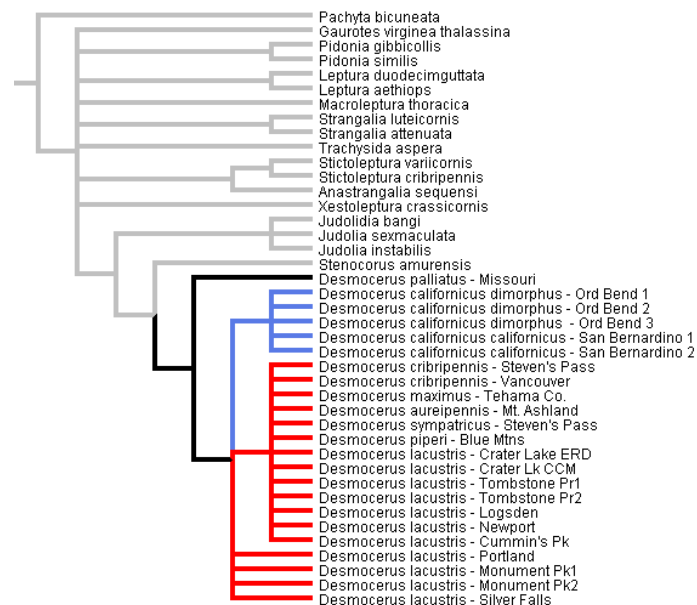
**Figure 3.10. Nuclear 28S rDNA - ML analysis. Strict consensus of 100 trees resulting from maximum likelihood bootstrap analysis in RAxML Blackbox.**



## Parsimony

An heuristic search in PAUP\* yielded 9900 best trees of length 212, which are summarized in a strict consensus tree (**Figure 3.11**). Of 1025 total characters in the 28S matrix, 71 characters were parsimony-informative, 883 were constant, and 71 variable characters included presumptive autapomorphies that were parsimony-uninformative.

*Desmocerus* is recovered as monophyletic among the 18 lepturine outgroups in the parsimony analysis. The western species of *Desmocerus* form a clade that is the sister clade to the eastern species, *D. palliatus*. Sequence divergence in the 28S data was low, resulting in poor support for relationships within, and between, the *D. californicus* and *D. aureipennis* species complexes. Among the outgroup taxa, *Stenocorus amurensis* (tribe Rhagiini) appears to be more closely related to *Desmocerus*, which together form a sister-group relationship to a clade containing *Judolia instabilis*, *J. sexmaculata*, and *Judolia bangi*.



**Figure 3.11. Nuclear 28S rDNA – Parsimony Analysis.** Strict consensus of 9900 best trees of length 212 resulting from a heuristic search in PAUP\*. Branches are not proportional to length. **Red clade:** *D. aureipennis* species complex.



## Bayesian

The Bayesian analysis was terminated after 10 million search replicates. The two runs were judged to be sufficiently close to stationarity, with an average standard deviation of split frequencies of 0.002936 at the end of the analysis. After discarding the initial 25% of trees sampled during the two independent runs, 15002 trees were retained and summarized by a 50% majority-rules consensus tree (**Fig. 3.12**).

The topology of the ingroup taxa in the Bayesian majority-rules consensus tree is identical to the parsimony based strict consensus tree. *Desmocerus* is recovered as a clade in 100% of the trees sampled from the posterior probability distribution. The western North American species groups (*D. californicus* + *D. aureipennis* complex) form a clade (58% support) that is sister to *D. palliatus*. The two subspecies of *D. californicus* were recovered as a monophyletic group in 98% of samples, but the *D. aureipennis* complex was not monophyletic. A clade consisting of the entire *D. aureipennis* species complex except the *D. lacustris* group from Northern Oregon was found in 81% of samples. There is no further resolution of relationships among or within *Desmocerus* species. As in parsimony and ML analysis, Bayesian analysis found *Desmocerus* to be most closely related to *Stenocorus* (67% support) with the next most basal lineage being a clade containing *Judolia sexmaculata*, *J. instabilis*, *Judolidia bangi* 85% of samples from the posterior distribution.



**Figure 3.12. Nuclear 28S rDNA - Bayesian analysis.** 50% Majority-rules consensus tree of 15002 trees. Node values represent proportion of trees having that clade. Model: GTR + Gamma. Branches are drawn proportional to length. MrBayes reported the following summary statistics for partitions with frequency  $\geq 0.10$  in at least one run: Average standard deviation of split frequencies = 0.002936; Max. SD split frequencies = 0.010370; Avg. PSRF for parameter values (excluding NA and  $>10.0$ ) = 1.000; Max. PSRF for parameter values = 1.002.

### mtCO1 Analysis

A number of the sampled specimens had identical mtCO1 sequence data

*D. palliatus*: Westbank, BC and Westbank, BC 2

*D. palliatus*: Quebec 4 and Quebec 5.

*D. maximus*: Tehama Co., Cal 1 and Tehama Co., Cal 2.

*D. piperi*: Alberta 1 and Alberta 2.

*D. lacustris*: ERD, Crater Lake, OR and Vidae F, Crater Lake, OR 1.

Separate sets of Maximum Likelihood, Parsimony, and Bayesian analyses were conducted using two versions of the CO1 matrix: one with four outgroup genera (**Outgroup A**: *Trachysida*, *Xestoleptura*, *Stictoleptura*, and *Judolia*) and one with only *Judolia* (**Outgroup B**). In general, similar topologies were obtained by all analyses, with the most significant differences being the placement of two groups: *D. californicus* sensu lato, and the relative positions of *D. aureipennis* and *D. maximus* nov. sp.

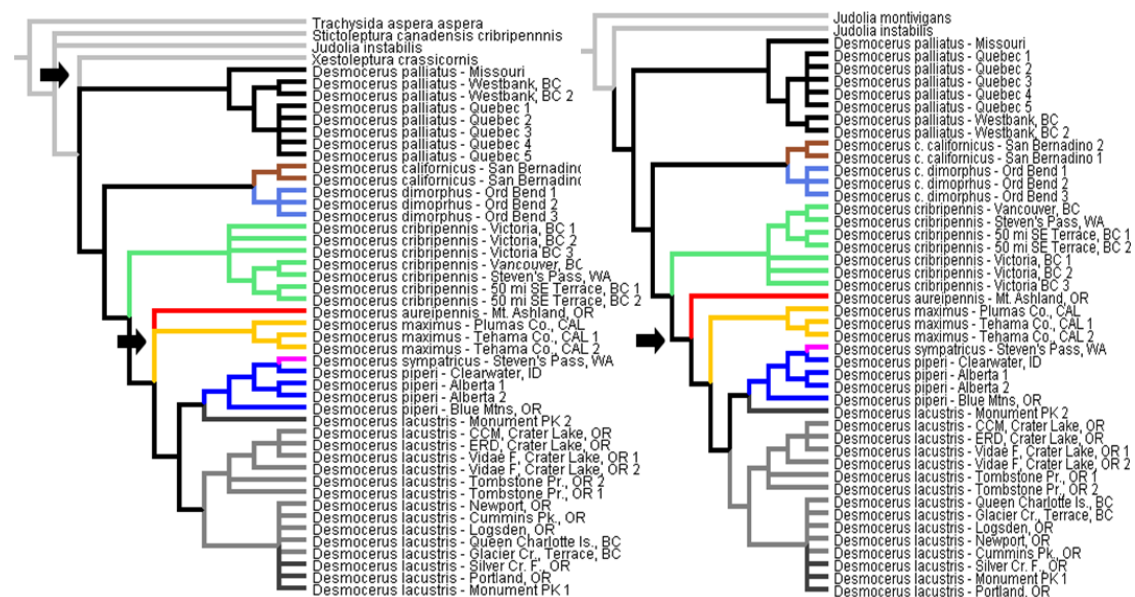
### Parsimony

Two sets of most parsimonious trees were obtained (one for each outgroup set). Outgroup set A yielded 651 MP trees of length 495, which are summarized in a strict consensus tree (**Figure 3.13, left**). Of the 669 total characters, 178 were parsimony-informative, 444 were constant, and 47 variable characters were parsimony-uninformative. The analysis with Outgroup B yielded 130 MP trees of length 370, which are summarized in a strict consensus tree (**Figure 3.14, right**). Of 658 total characters in the CO1 matrix, 157 characters were parsimony-informative, 447 were constant, and 54 variable characters were parsimony-uninformative.

The two MP analyses yielded almost identical topologies with two exceptions: the monophyly of *Desmocerus* is not recovered when using Outgroup set A, but is with Outgroup B (*Judolia*). In the Outgroup set A, *Xestoleptura crassicornis* often appeared inside the *Desmocerus* clade, sister to *D. palliatus*. The relationship between *D.*

*aureipennis* and *D. maximus* are also less resolved in the strict consensus tree using Outgroup set A.

Under both outgroup sets, *D. palliatus*, *D. californicus* (including both subspecies), *D. cribripennis*, *D. maximus*, and *D. aureipennis* are all recovered as clades. *D. sympatricus* arises from within the *D. piperi* clade. *D. lacustris* is monophyletic except for one individual from the Northern Oregon Group, Monument PK 2 (isolated dark grey branch in **Figs. 3.13**), which was taken on the same bush as Monument PK 1 and apparently represents a second haplotype of that population. The Monument PK 2 sequence in both analyses is located at the base of the *D. piperi* clade. Relationships among the other populations identified as *D. lacustris* from western Oregon and the Queen Charlotte Islands in British Columbia are also inconsistent.



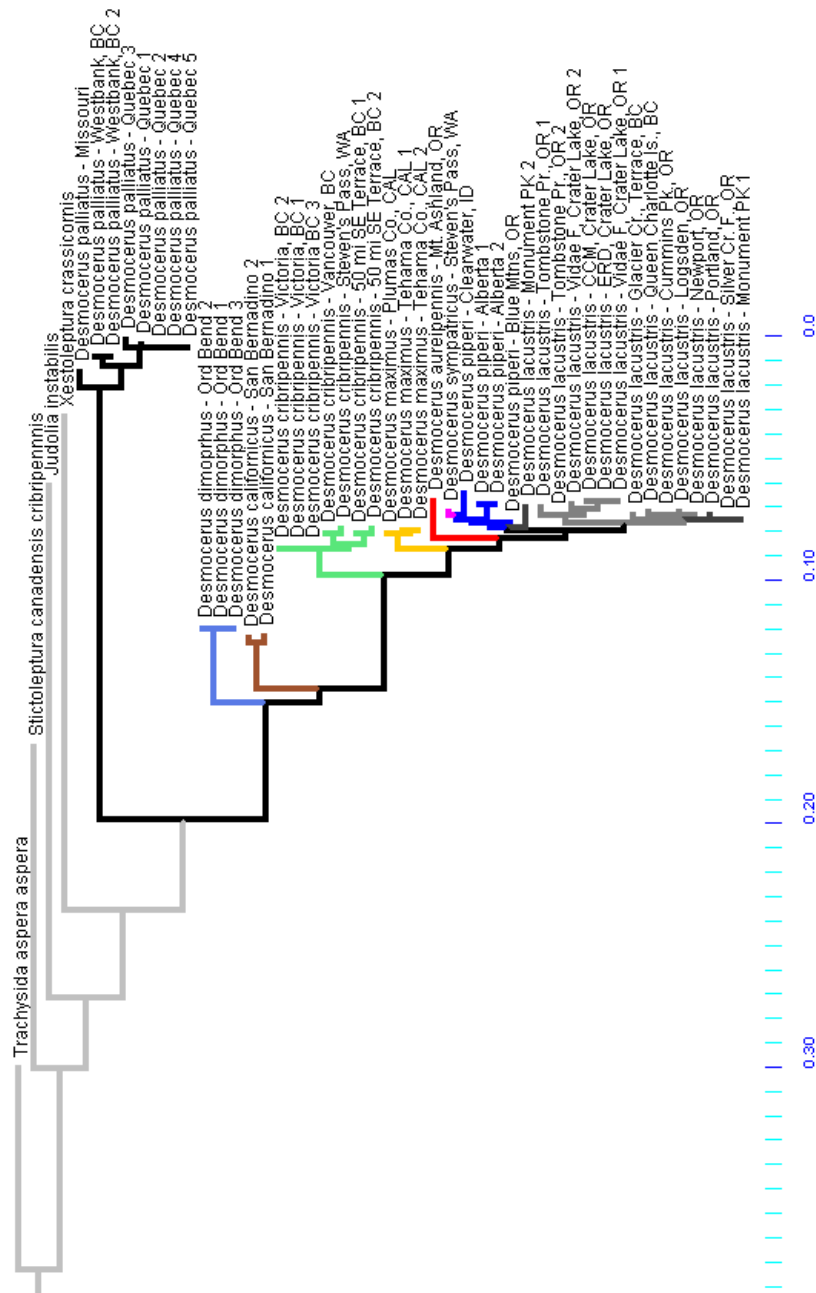
**Figure 3.13. Mitochondrial C01 – Parsimony Analysis. Left: Outgroup A - Four genera.** Strict consensus of 650 best trees of length 495 from PAUP\* heuristic search. **Right: Outgroup B - Judolia.** Strict consensus of 130 best trees of length 370. Branches are not shown proportional to length.

## Maximum Likelihood

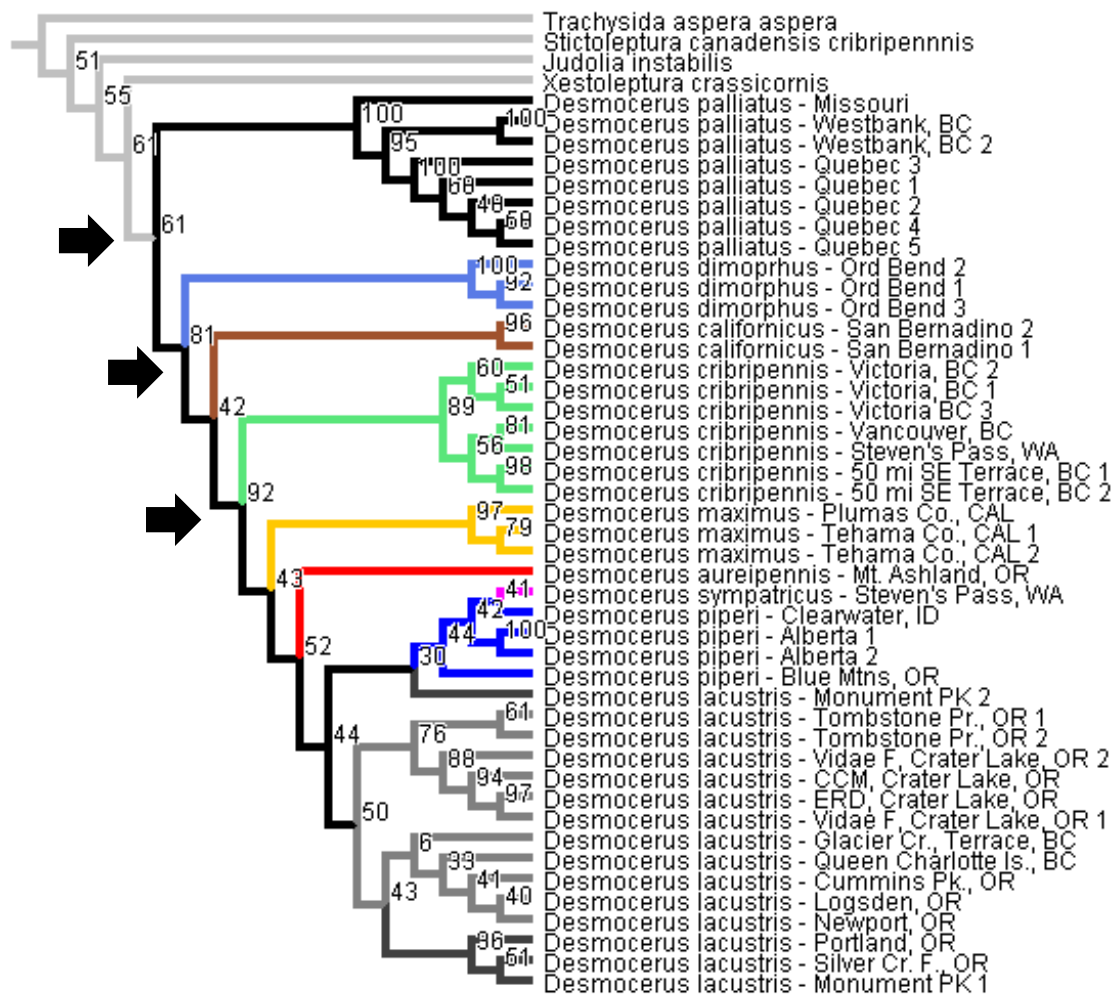
Nearly identical ML tree topologies were obtained under both outgroup treatments (**Figs. 3.14-3.16**). The resulting topologies differed only in the placement of the *D. californicus* subspecies. Despite similar topologies in the ingroup, different outgroups affected node support, especially for basal nodes in the analysis.

Outgroup set A yielded a ML tree with a -log likelihood of 3114.538871 (**Figs. 3.14, 3.15**). *Xestoleptura crassicornis* appears as the sister group to *Desmocerus* with weak bootstrap support (61%). As was seen in the parsimony analysis, similarities between *Xestoleptura* and *D. palliatus* sequences are likely the cause of the reduced bootstrap support for a monophyletic *Desmocerus* (also 61% top arrow). *D. palliatus* forms a well-supported clade (100% support), and the western species groups (*D. californicus* sensu lato and the *D. aureipennis* complex – middle arrow) also form a well supported clade with 81% support. Notably, *D. californicus* s.l., which was monophyletic in the parsimony analysis, is weakly supported as paraphyletic (45% bootstrap), with *D. c. californicus* more closely allied to the *D. aureipennis* species complex than to *D. c. dimorphus*. The *D. aureipennis* complex (bottom arrow) is a relatively well-supported clade (92%), with several short-lengthed, but well-resolved subclades concordant with observable morphological and geographical relationships. *D. cribripennis* is basal to the rest of the *D. aureipennis* species complex, forming a distinct, well-supported clade (89%). The three sequences representing *D. maximus* (monophyletic with 97% support) are basal to the single *D. aureipennis* sequence (unresolved in parsimony analysis). As in the parsimony analysis, *D. sympatricus* arises within *D. piperi* clade, which is itself sister to one of the *D. lacustris* haplotypes from Monument Peak, Oregon (dark grey). Within *D. lacustris*, the most well-supported clade consisting of geographically-disjunct populations (with 96% support) are three sequences from the Northern Oregon group (Portland, Silver Falls, and Monument Peak, Oregon) that also shared a synapomorphy in the 28S gene.

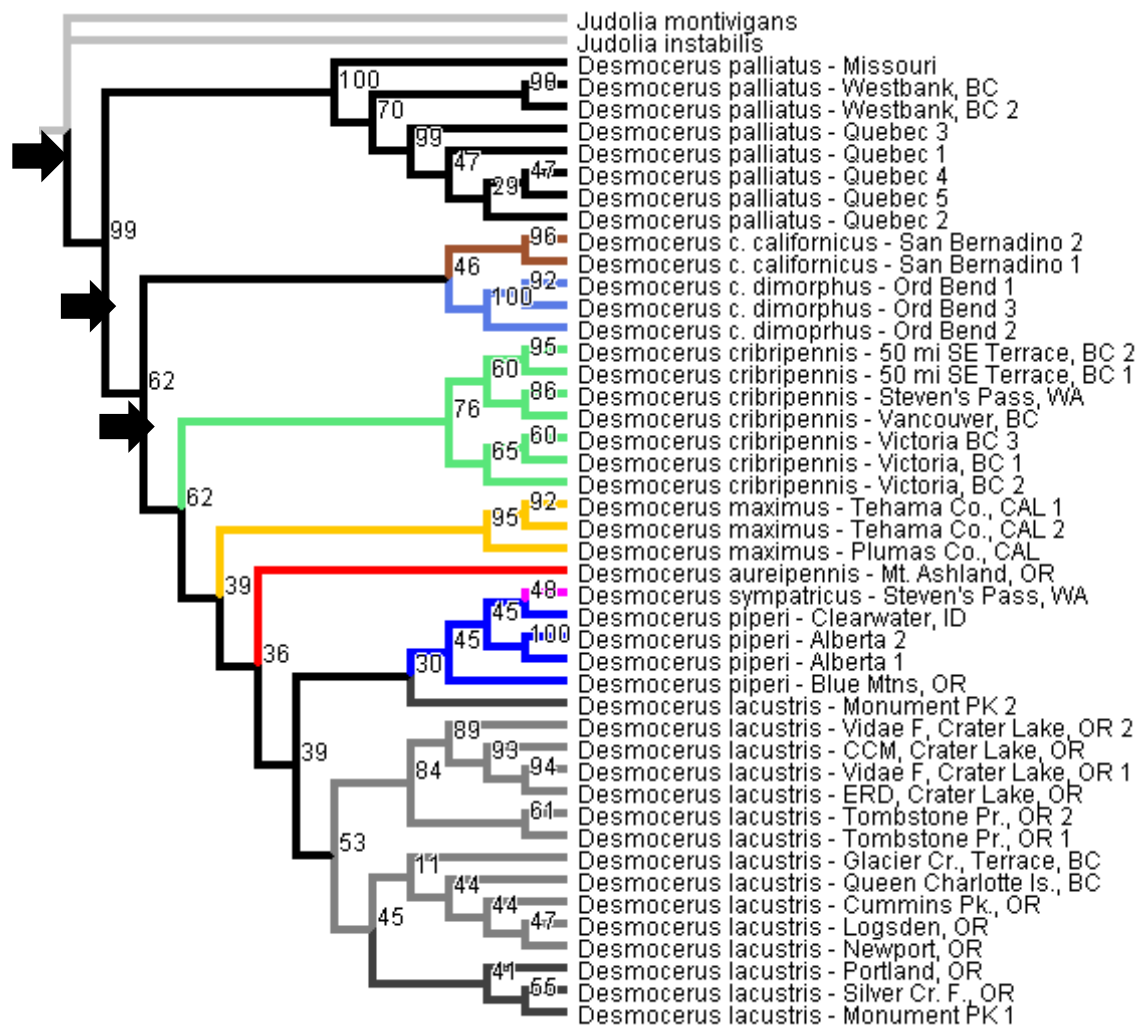
The ML tree obtained using Outgroup set B (**Figure 3.16**) has a negative log likelihood score of 3114.538871. *D. californicus* is monophyletic, but with only 46% support, and the monophyly of the *D. aureipennis* complex is supported in only 62% of bootstrap replicates.



**Figure 3.14. Mitochondrial CO1 - Maximum likelihood (ML) Analysis, Outgroup A - Four genera.** Best tree with final ML Optimization Likelihood: -3114.538871. Branches drawn proportional to lengths. Node values are derived from a separate analysis of 100 non-parametric bootstrap pseudoreplicate matrices, and indicate the percentage of matrices from which that clade was recovered.



**Figure 3.15. Mitochondrial CO1 - ML Analysis, Outgroup A - Four genera.** Same tree as Figure 9 except branches are not drawn proportional to lengths. Best tree with final ML Optimization Likelihood: -3114.538871. Node values are derived from a separate analysis of 100 non-parametric bootstrap pseudoreplicate matrices, and indicate the percentage of matrices from which that clade was recovered.



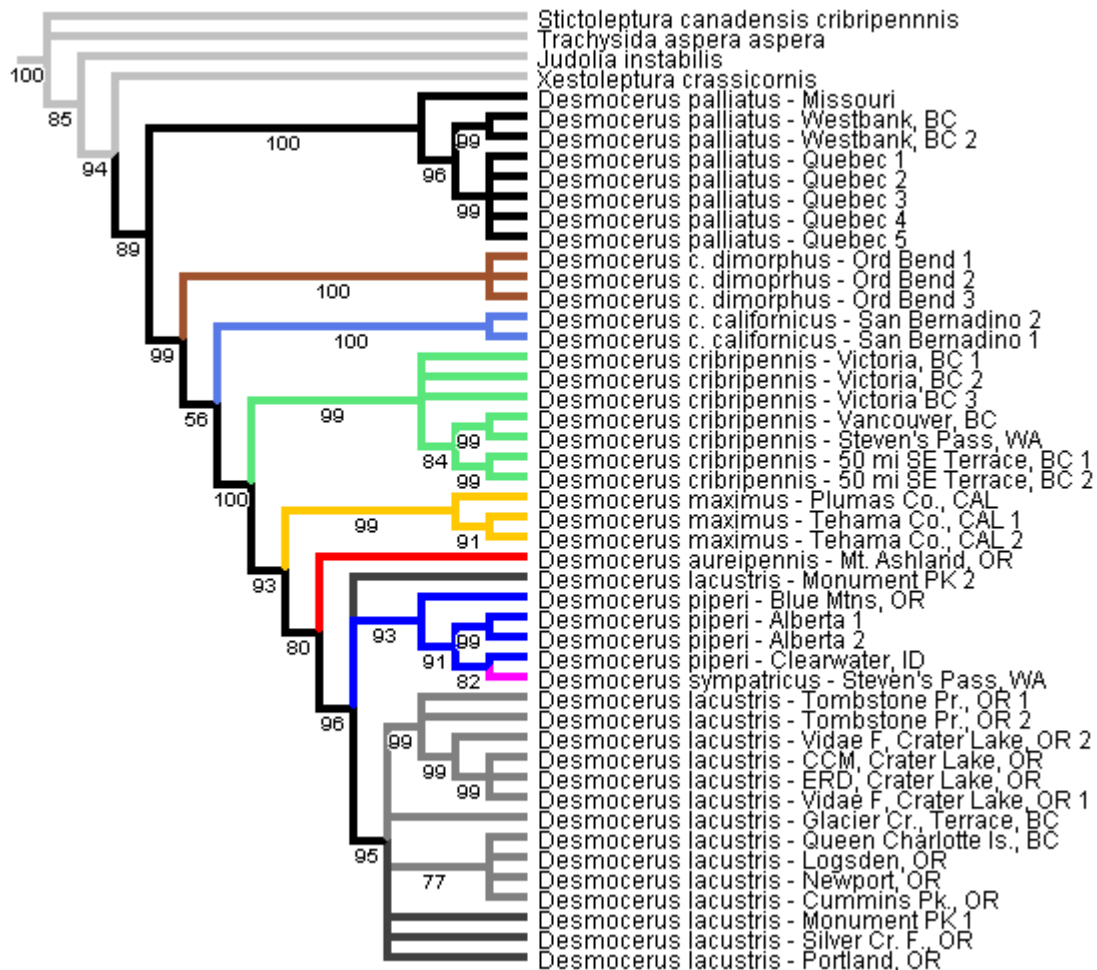
**Figure 3.16. Mitochondrial CO1 – ML Analysis, Outgroup B - *Judolia*.** Best tree with final ML Optimization Likelihood: -2644.399220. Branches not drawn proportional to lengths. Node values are derived from a separate analysis of 100 non-parametric bootstrap pseudoreplicate matrices, and indicate the percentage of matrices from which that clade was recovered.



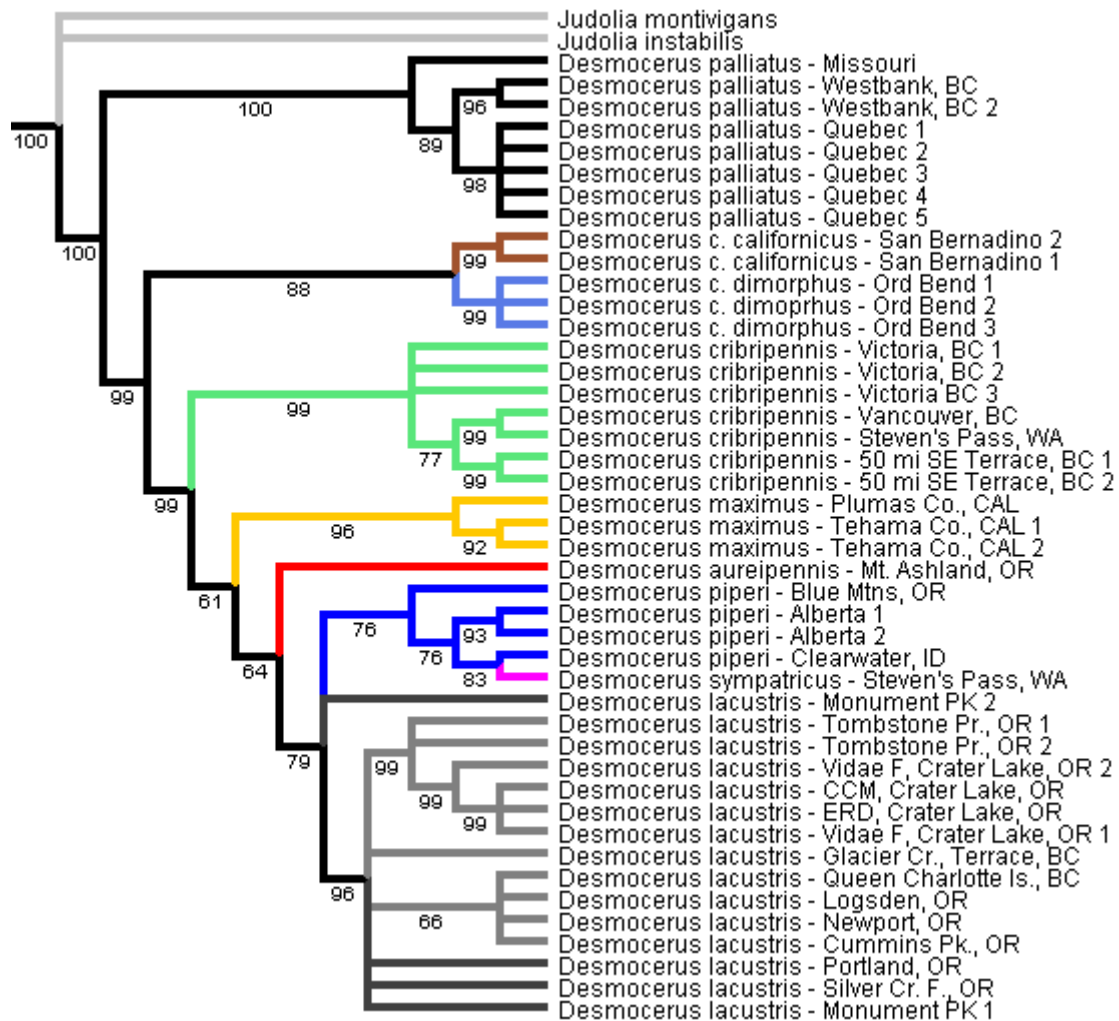
## Bayesian

The two majority-rule consensus trees produced using separate outgroups yielded nearly identical tree topologies that differed only in the placement of the two *D. californicus* subspecies (**Figs 3.17, 3.18**). Statistics derived from the analysis are given in figure captions. *Desmocerus* is recovered as a clade, with a basal split between *D. palliatus* and the western species (monophyly supported 89% outgroup set A, and 100% outgroup set B). The next divergences are those of *D. californicus* s.l., which under the limited outgroup (set B) form a clade (support: 88%) but alternatively appear as a paraphyletic grade (set A), with *D. c. dimorphus* allied more closely to more derived members of *Desmocerus* than to *D. c. californicus*. In both outgroup treatments, the *D. aureipennis* complex is monophyletic with high support: 100% in Outgroup A and 99% in Outgroup B.

*Desmocerus cribripennis* is sister to the rest of the *D. aureipennis* species complex, forming a distinct, well-supported clade (99%) in both outgroup sets. The next lineage to diverge is *D. maximus* which appears as the sister to the remaining species. As in the parsimony and ML analyses, relationships between the *D. lacustris* populations are poorly resolved, and the two haplotypes from the *D. lacustris* population at Monument Peak appear separately in the tree. One clade within *D. lacustris* (77% support) consists of four coastal populations, three around Newport, Oregon, and a disjunct population from the Haida Gwaii of British Columbia.



**Figure 3.17. Mitochondrial CO1 - BAYESIAN Analysis. Outgroup A - Four genera.** 50% Majority-rules consensus tree of 15002 trees. Node values represent proportion of trees having that clade. Branches not drawn proportional to lengths. Model: GTR+I+Gamma. MrBayes reported the following summary statistics for partitions with frequency  $\geq 0.10$  in at least one run: Average standard deviation of split frequencies = 0.003562; Max. SD split frequencies = 0.0013386; Avg. PSRF for parameter values (excluding NA and  $>10.0$ ) = 1.000; Max. PSRF for parameter values = 1.002.



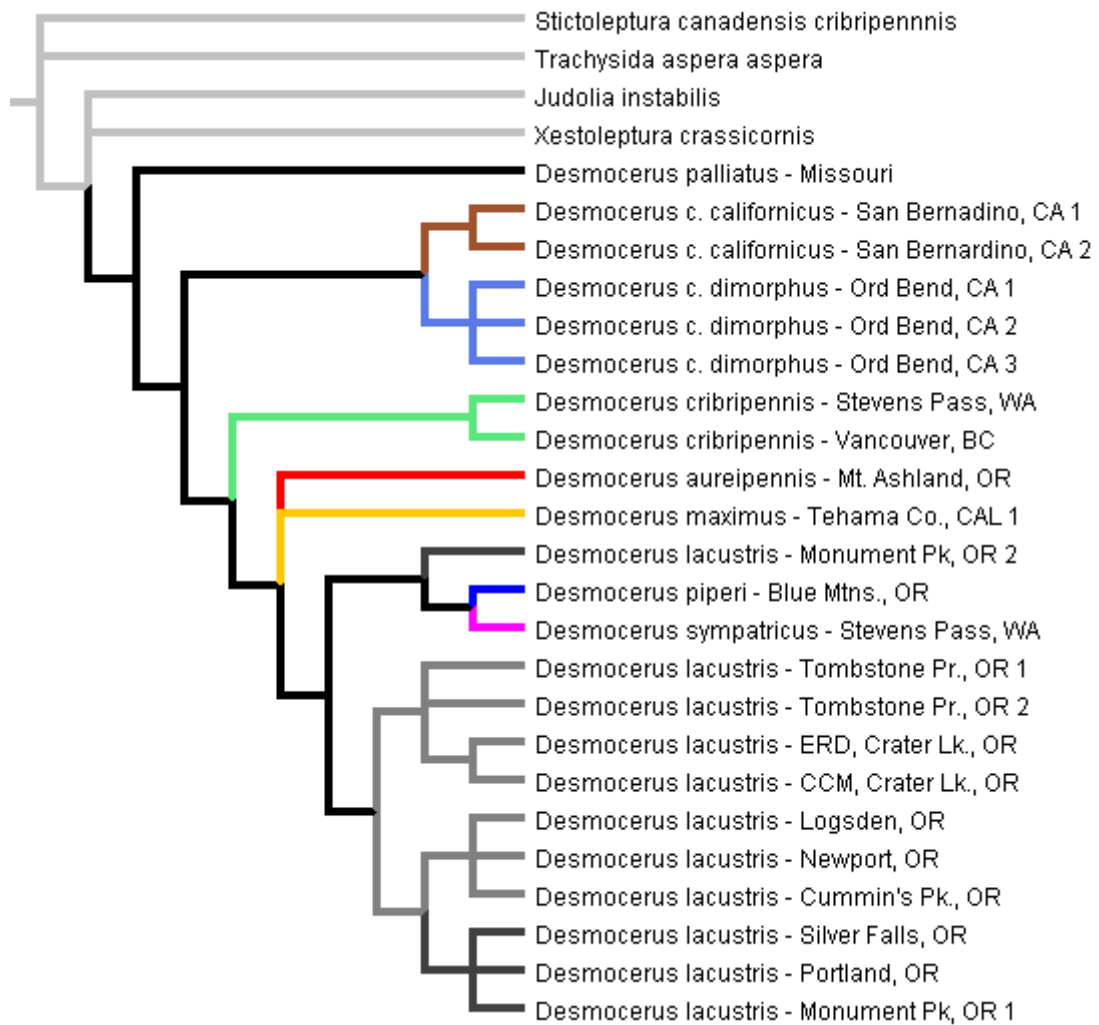
**Figure 3.18. Mitochondrial CO1 - BAYESIAN Analysis, Outgroup B – *Judolia*.** 50% Majority-rules consensus tree of 15002 trees. Node values represent proportion of trees having that clade. Branches not drawn proportional to lengths. Model: HKY + Gamma. MrBayes reported the following summary statistics for partitions with frequency  $\geq 0.10$  in at least one run: Average standard deviation of split frequencies = 0.005198; Max. SD split frequencies = 0.029883; Avg. PSRF for parameter values (excluding NA and  $>10.0$ ) = 1.000; Max. PSRF for parameter values = 1.002.

### *Combined-gene Analysis*

The results of Parsimony, Maximum Likelihood, and Bayesian analyses conducted on a matrix with the two genes CO1 mtDNA and 28S rDNA combined are given below. In each analysis, *Desmocerus* is recovered as monophyletic relative to the four lepturine outgroups, and is part of a larger clade that includes *Judolia instabilis* and *Xestoleptura crassicornis*. 28S rDNA sequence data was not available from several populations of *D. palliatus*, *D. cribripennis*, and *D. lacustris* that were represented in the CO1 analyses. These populations were removed from the combined-gene matrix.

### **Parsimony**

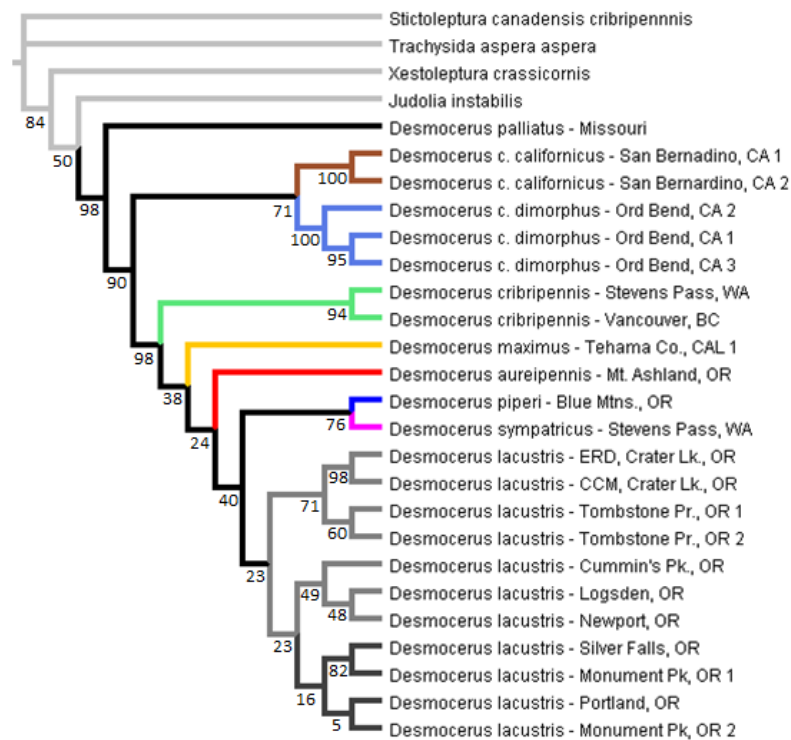
Of 1688 characters in the combined-gene matrix, 181 characters were parsimony-informative, 1390 were constant, and 117 variable characters were parsimony-uninformative. A heuristic search yielded 8 shortest trees of length 562. The strict consensus tree for the combined-gene parsimony analysis (**Figure 3.19**) is largely resolved. *Desmocerus* is recovered as a clade relative to the 4 lepturine outgroups, and the western species of *Desmocerus* form a clade that is sister to *D. palliatus* of the Eastern USA. The *D. californicus* and *D. aureipennis* species complexes are reciprocally monophyletic sisters. Within the *aureipennis* complex, *D. aureipennis* and *D. maximus* form an unresolved polytomy basal to *D. piperi-lacustris* group. The populations of *D. lacustris* from the Oregon Coast Range form a clade sister to 3 of the 4 individuals from the Northern Oregon Group of *D. lacustris*. One haplotype from that latter group arises at the base of the *D. piperi* clade.



**Figure 3.19. Combined gene matrix – Parsimony Analysis.** Strict consensus of 8 best trees of length 562 resulting from a heuristic search in PAUP\*. Branches are not shown proportional to length.

### Maximum Likelihood

A single ML tree (log likelihood score of -4854.214009 (**Figure 3.20**) was obtained that is fully resolved. *Desmocerus* is recovered as monophyletic with 100% bootstrap support. The two western species groups formed a clade sister to *D. palliatus* with 90% bootstrap support. All of the supposed *Desmocerus* species and subspecies included in the analysis are recovered as clades with bootstrap support percentages ranging from 23% (*D. lacustris*) and 16% (*D. lacustris* – NOG (dark grey)) to 100% (*D. c. californicus* and *D. c. dimorphus*, respectively). The two subspecies of *D. californicus* formed a clade with 71% bootstrap support, while the *D. aureipennis* species complex was recovered in 98% of the analyses.

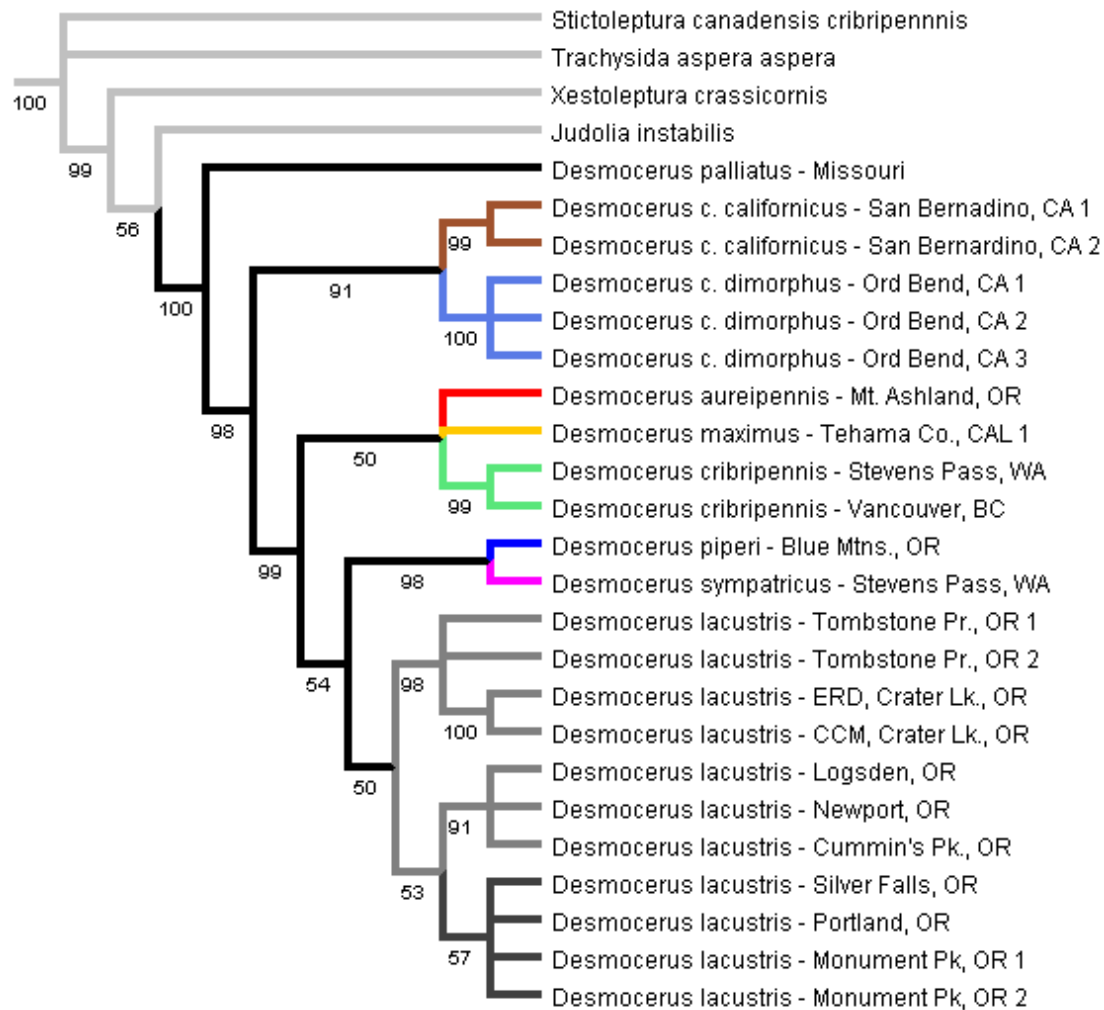


**Figure 3.20. Combined gene matrix – Maximum Likelihood Analysis.** Best log likelihood tree is shown with node values representing bootstrap percentages from 100 non-parametric bootstrap pseudoreplicates performed in RAxML Blackbox version 7.2.6. Final ML Optimization Likelihood: -4854.214009. Branches are not drawn proportional to length.

## Bayesian

The Bayesian analysis was terminated after 10 million search replicates, when the two independent runs had an average standard deviation of split frequencies of 0.003811. 15002 trees remained after the initial 25% of trees were discarded (burn in) and summarized by a 50% majority-rules consensus tree (**Figure 3.21**).

*Desmocerus* is monophyletic in 100% of the sampled trees. A clade consisting of *Desmocerus*, *Xestoleptura crassicornis*, and *Judolia instabilis* is supported at 99%. The eastern North American species *D. palliatus* is sister to a clade containing the two western North American species groups. The latter clade was found in 98% of trees sampled. The subspecies *D. c. californicus* and *D. c. dimorphus* each formed distinct clades with 99% and 100% support, respectively, while the two were grouped in the same clade in 91% of tree samples. The *D. aureipennis* species complex was recovered as a clade with 98% support, with internal nodes generally well-resolved but with low support. *Desmocerus aureipennis*, *D. maximus*, and *D. cribripennis* form a clade (50%). *Desmocerus lacustris* forms a clade (50%) with internal nodes corresponding to geographic provinces: the Crater Lake/Tombstone Prairie group (98% support), the Coast Range group (Logsdon, Newport, and Cummin's Peak, Oregon (91%)), and the Northern Oregon Group (Silver Falls, Portland, and both haplotypes from Monument Peak (57)). Finally, *Desmocerus piperi* and *D. sympatricus* n.sp., form a clade with 98% support.



**Figure 3.21. Combined gene matrix— BAYESIAN Analysis.** 50% Majority-rules consensus tree of 15002 trees. Node values represent proportion of trees having that clade. Branches not drawn proportional to length. Model: GTR +  $\Gamma$ . Summary statistics for partitions with frequency  $\geq 0.10$  in at least one run: Avg. SD of split frequencies = 0.007391; Max. SD split frequencies = 0.023906; Avg. PSRF for parameter values (excluding NA and  $>10.0$ ) = 1.000; Max. PSRF for parameter values = 1.003.



## DISCUSSION

### *Implications for the Classification of Desmocerus Species*

The standard treatment of the western North American populations related to *D. aureipennis* Chevrolat as subspecies (*sensu* Linsley and Chemsak, 1972) is no longer valid. Multiple instances of sympatry among the supposed subspecies are demonstrated by museum specimens (Halstead and Oldham, 1990), and by the author's observations at Steven's Pass Summit confirming that adults of *D. cribripennis* Horn and *D. sympatricus* Schapker (formerly considered a population of *D. piperi* Webb) occur at the same time of day within 100 meters. These populations apparently do not interbreed, as evidenced by the sequences sampled falling in distinctly separate CO1 clades (see *Results*, Figs. 3.13-3.17). Halstead and Oldham's (1990) revised taxonomy for *Desmocerus* (Fig. 3.2 of this chapter) follows from this classical argument for species delimitation. Those authors recognized three distinct species in the Pacific Northwest: *D. aureipennis*, *D. cribripennis*, and *D. piperi* that in most cases (particularly where they occur in sympatry) are distinctly dissimilar in their external appearance, and use exclusively different elderberry species as host plants.

The purpose of this study was to search for more subtle evidence of lineage separation among allopatric populations where sympatry did not provide a "smoking gun" for the existence of species. The morphological examinations, which included evidence from the adult hindwings and male genitalia, led to two discoveries. First, after careful review of many specimens it was discovered that among the populations in western North America that have historically been called "*D. aureipennis*," two geographically-cohesive sets can be identified that are marked by a suite of discrete differences in both external and internal anatomy. Taken together, these observations suggests the existence of two separately-evolving lineages, or species. Careful examination of the *D. aureipennis* holotype specimen places the holotype among the forms known primarily from northwest California, Oregon and Washington. The forms

that occur primarily in the Sierra Nevada Range of California are described and provided a new name, *D. maximus* Schapker, in the review of *Desmocerus* species at the end of this section. Interestingly, review of historical documentation corroborates the notion that the holotype of *D. aureipennis* was collected either in the Rocky Mountains of Canada, or in one of several smaller adjacent ranges (see Appendix A).

Evidence for the existence of a second, even more cryptic species, was discovered while examining patterns of variation in the structure of the male genitalia throughout the range of *D. piperi*. Among the populations of presumptive *D. piperi* from nine widely disjunct localities investigated, a single population was found with parameres that differed by a degree not seen within the normal variation of this structure within other species. That population, the same just mentioned existing in sympatry with *D. cribripennis* at the summit of Stevens Pass, Washington, is here considered a separate species, *D. sympatricus* Schapker. The very minor CO1 divergence between the two species implies that the unique paramere structure in *D. sympatricus* may have developed fairly rapidly, perhaps as a mating-isolation mechanism caused by its interactions with *D. cribripennis* at Steven's Pass. Given the general interest in the role of genitalia in mating isolation between species (see Eberhard, 2004; Eberhard, 2010) and the open debate about the role of the paramere in cerambycid copulation (Hubweber & Schmitt, 2010), the population at Stevens Pass would be an interesting subject for further study.

Patterns of morphological and geographic variation were especially complex, and difficult to interpret, among the populations that bore into red elderberry (*Sambucus racemosa* subsp.) in west and central Oregon, where a number of forms superficially resemble intermediates between *D. cribripennis*, *D. lacustris*, and *D. piperi*. Analysis of the CO1 mtDNA revealed three distinct clades that corresponded to three geographically- and phenotypically-related units: males of *D. cribripennis* (coast range from British Columbia to California) are narrow-bodied and have a dark patch covering

the entire extent of the elytra (corresponding phenotypes south of the Columbia River basin not sampled in the molecular analysis); males of *D. piperi* (Cascades of central WA, and Rocky Mtns. from Alberta to eastern OR and MT) are more robust in form, and have the dark patch faint or lacking; and in *D. lacustris* (central and western Oregon, to coastal British Columbia) the male elytral patch varies in its extent within populations. The author considers the morphological differences between *D. piperi* (type locality: Blue Mountains, Wash.) and *D. lacustris* (type locality: Crater Lake, Oregon), associated with separate biogeographical provinces and mtDNA lineages, sufficient to reject Halstead and Oldham's (1990) argument that *D. lacustris* should be considered a junior synonym of *D. piperi*.

#### *Molecular analysis*

Overall, the trees produced from the combined matrix were consistent with results from the single-gene analyses, and statistical support for major nodes enhanced, either by the combination of concordant phylogenetic signal or removal of certain conflicting groups. The trees inferred by the parsimony, ML, and Bayesian approaches on were not identical however, and offer three different views on the *Desmocerus* sequence data which are instructive in forming a final hypothesis for the phylogeny of the genus. In particular, the differences in resolution of the *D. aureipennis* complex inferred by the three approaches indicate the degree to which parameterization of the nucleotide substitution model might affect a final hypothesis.

The combined-gene maximum parsimony tree (**Fig. 3.19**) provides a simple, honest assessment of the data as a whole: the model is agnostic to particular nucleotide substitution rates—base pairs are either shared or not, and taxa are grouped accordingly. Clades are reduced to polytomies in a strict consensus of 8 equally-parsimonious hypotheses. Although relationships within the *D. aureipennis* complex are well-resolved, nothing can be said of the relationship between *D. maximus* and *D. aureipennis* sensu strictu. Also notable in the parsimony analysis is that the two *D.*

*lacustris* specimens taken from the same bush at Monument Peak in the Cascades still appear separately on the tree, despite the additional information provided by a shared 28S nucleotide. The unweighted parsimony analysis does not have the ability to favor a single shared nucleotide from one gene over the significance of multiple shared nucleotides from another gene. The full set of molecular data is however able to resolve *Desmocerus* as monophyletic (compare to CO1 Outgroup A, **Fig. 3.15**).

Unlike the parsimony consensus tree given in **Fig. 3.19**, the best Maximum Likelihood tree (**Fig. 3.20**) represents the single best hypothesis given the data and assumptions of the ML model. The ML tree has incorporated separate estimates of nucleotide evolution for each gene partition on the matrix, an approach that is warranted in theory given our prior knowledge indicating that these two particular genes should have evolved differently. It is fully resolved, and has the distinction of being the only tree in all of the analyses in which the **Northern Oregon group** of *D. lacustris* appears as a single clade. The information from the 28S rDNA thus appears to be affectively incorporated—the single shared 28S nucleotide was enough to overrule the polyphyly caused by the two CO1 alleles from Monument Peak. The 28S rDNA also appears to have stabilized the monophyly of *Desmocerus* (100% support), and *D. californicus* (66%), which was paraphyletic in the CO1 analysis with Outgroup A (**Fig. 3.15**), and monophyletic with 46% support in Outgroup B (**Fig. 3.16**). In the combined analysis, the *D. aureipennis* complex is monophyletic with 99% support, compared to 92% in CO1 Outgroup A and 62% in Outgroup B.

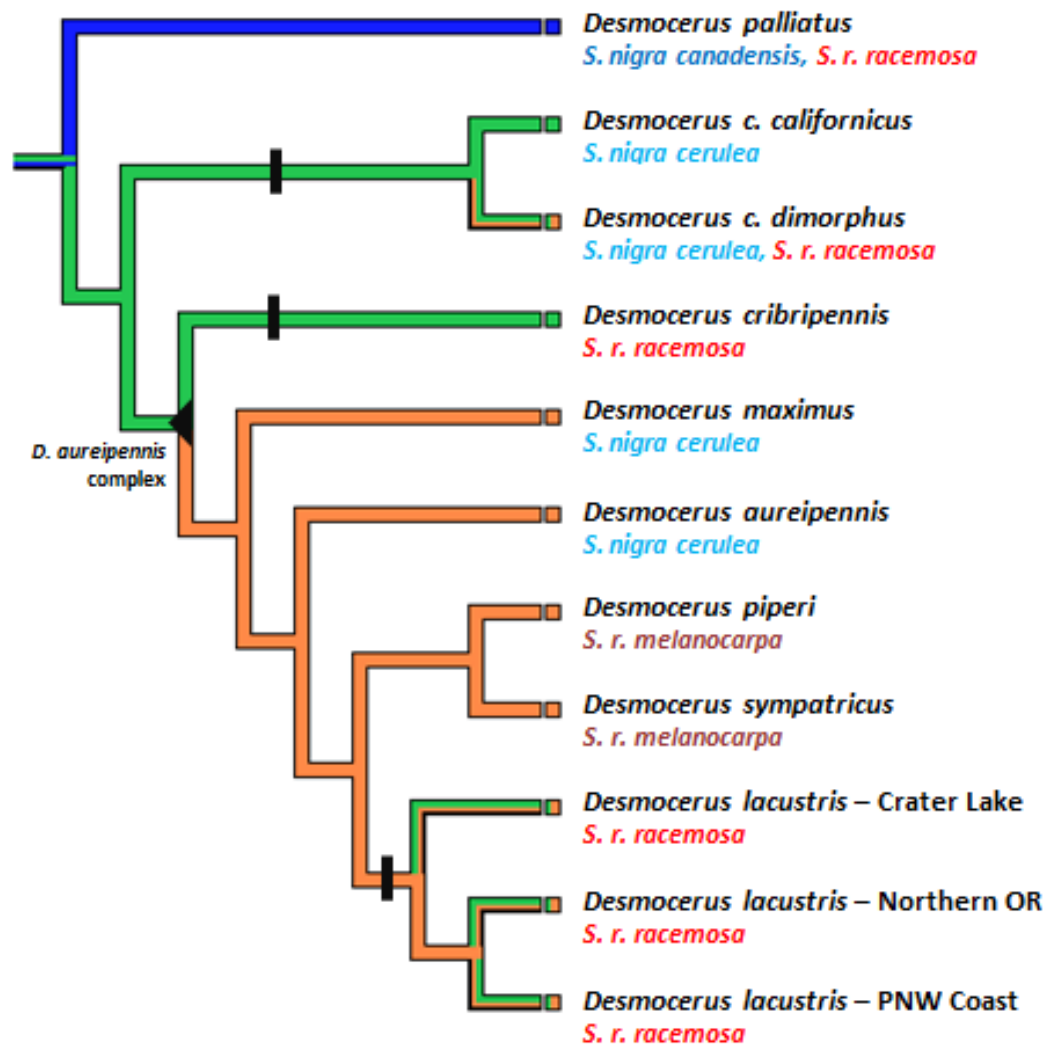
The least-resolved tree is the majority-rules consensus tree resulting from the Bayesian analysis (**Figure 3.21**). Since it is formed from a cloud of possible evolutionary parameters, the Bayesian tree indicates the degree to which particular estimates of nucleotide substitution rates—such as those estimated for the best ML tree—can affect the inferred phylogeny. In *Desmocerus*, this effect may be expected to be particularly pronounced within the *D. aureipennis* species complex where differences

between sequences are small. Still, the Bayesian analysis recovered the higher-order *Desmocerus* clades with very high support and is in congruence with the other two methods.

### *Preferred phylogeny*

Considering the preceding analyses, **Figure 3.22** represents the preferred hypothesis for the species delimitations and evolutionary relationships within *Desmocerus*. The topology is largely consistent with the combined-gene ML tree using all four outgroups (**Fig. 3.20**). The three types of the male elytral patterns (Lycid-mimic, red/aposematic, and dark green/cryptic) and host plant associations (the two most easily observable characteristics among *Desmocerus* species) are also mapped onto this phylogeny. Longer pubescence on the dorsal pronotum (Fig. 3.22, black bars) appears to be associated with the development of dark green elytral coloration in males.

The relative positions of *D. maximus* and *D. aureipennis*, which are weakly supported by the molecular data, were established in the preferred topology based on consideration of geographical and morphological data. The species *D. maximus* is presumed to be of older origin given its relatively extreme anatomical characteristics, which are constant across a relatively large geographical distribution, including an unusual disjunction: populations in Vancouver Island, Canada and the Sierra Nevadas. *Desmocerus aureipennis* occurs along a narrower range in the Pacific Northwest, and overlaps partially with that of its presumptive sister taxa, *D. piperi*, *D. lacustris*, and *D. sympatricus*. The smaller specimens of *D. aureipennis* are very similar in external appearance to those species, and share subtle similarities suggestive of a fairly recent divergence. The distal dark areas on the transparent hindwings of *D. piperi* are a putative synapomorphy with *D. aureipennis* (see character matrix, Table 3.4).



**Figure 3.22. Preferred Phylogeny for *Desmocerus*, with *Sambucus* host species, and morphological characters mapped onto tree.** Branch colors represent ancestral state reconstruction of male elytral patterns. **Orange:** ♂ elytra fully covered in orange pigment that fades to yellow in pinned specimens; **Green:** ♂ elytra with orange pigment restricted to narrow strip on elytral margin; **Orange/Green:** extent of orange area variable; **Blue:** ♂ elytral pattern Lycid-like, fading orange pigment absent. **Black Bars:** ♂ pronotum with dorsal pubescence long.

### *Phylogenetic and Biogeographic Implications*

The *Desmocerus* phylogeny provides two essential functions. Not only is it a framework for understanding the development of adaptive traits among the species, but it also bares implications for reconstructing the actual physical pathways the various lineages followed through the shifting environments and geographies of North America's deep past. The oldest, and most clouded history to be told is that between the three major species groups. On the other hand, the low 28S sequence divergence among members of the *D. aureipennis* complex suggest that those forms are of relatively recent origin. Despite lacking discrete differences in external anatomy, the species nevertheless vary dramatically in size, color, and ecological niches, enabling the fast-evolving CO1 gene to reveal six recently-diverged mitochondrial clades that, for the most part, unambiguously correspond to morphologically, ecologically, and geographically cohesive units. Given that *Desmocerus* species tend to occupy relatively specific types of habitats, the observation of widely disjunct populations with identical, or nearly-identical mitochondrial sequences allows for inferences to be made about the habitat conditions that must have connected those localities in fairly recent history, for example, between the *D. lacustris* populations on Haida Gwaii and the central Oregon coast. The phylogeny also suggests that several of the species pairs with similar habits and appearances, such as the small red elderberry boring species *D. cribripennis* and *D. lacustris*, and the large blue elderberry-boring species *D. aureipennis* and *D. maximus*, may have developed these physical features and host plants independently, perhaps in response to similar selective pressures. These topics and others are discussed in detail below, starting from the base of the *Desmocerus* phylogeny (Fig. 3.22) and following it outward to its most derived branches.

The first split on the *Desmocerus* tree is that between *D. palliatus*, from eastern North America, and the remaining *Desmocerus* species in the west. This particular distribution pattern, combined with substantial morphological and genetic dissimilarity

between *D. palliatus* and the western species is suggestive of an early divergence. We know from fossils present at the Oligocene fossil beds at Florissant, Colorado, that modern genera of Lepturinae, such as *Pidonia* and *Leptura* were present in North America as early as 25 mya (Linsley, 1959), and probably much earlier. From about 35-30 mya, the early Rocky Mountain system, which had served as a barrier to dispersal across North America since the receding of the intercontinental seaway, was diminished by erosion, apparently allowing for a period of biotic exchange across the continent that lasted until the second round of Rocky Mountain formation, beginning in the late Oligocene. The rise of the modern Rockies cast a rain shadow over the central plains of North America that has remained an effective barrier to dispersal ever since (Tiffney, 1985). The period of east-west exchange, and the particular routes that may have been followed by dispersing plants and animals is not well understood. A future study employing additional genes, and a molecular clock analysis may be able to pinpoint the most likely time of the basal *Desmocerus* split, potentially lending valuable evidence to the more general discussion on that particular problem in historical geography. (See discussion and references in Sanmartin, Enghoff, and Ronquist, 2010, pp. 349-350, 371-372.)

The second major division, that between *D. californicus* and the *D. aureipennis* complex, is also marked by a set of discrete—albeit less dramatic—differences in the external adult anatomy, the most obvious being the size and densities of elytral punctuation observable between the two clades. The distributions of the two species groups are similar to the “Californian” and “Vancouverian” faunal classes Linsley (1959) identified in a number of western Cerambycid species, however the origins of these faunas are not well understood. Linsley (p.315) remarks that the southern Californian species groups usually appear to be of earlier origin, and are often associated with fauna in the semi-arid southwest coast of South America.



The two subspecies of *D. californicus*, which occur in the Coast Range and Sacramento Valley of California, respectively, are nearly indistinguishable morphologically, and specimens sampled had identical nuclear 28S sequence data. Despite this, the monophyly of *D. californicus* was dependent on outgroup choice in the CO1 analyses (**Figs. 3.15 & 3.16**); the two subspecies failed to form a clade when four outgroup genera were included, which could simply be the result of incomplete lineage sorting in the gene tree. Another possibility are the presence of non-homologous base pairs between distant outgroups and the *D. californicus* CO1 sequences, since each subspecies appears to have a relatively high number of autapomorphic base pairs (as demonstrated by the long branch lengths in **Fig. 3.14**). The two *D. californicus* subspecies were represented in the molecular analysis by only one population each, and these were quite distant from one another geographically. Further molecular work should include populations where the two subspecies come into closer proximity, or where the sub-specific identity of a population is ambiguous.

Within the *D. aureipennis* group, the first two species to diverge are also the most different, both in their physical structure and life history. *Desmocerus cribripennis* is a small, red-elderberry borer, the males having their elytra entirely covered in greenish-black pigmentation. *Desmocerus maximus* males are more than two times as large as *D. cribripennis* males, bore in blue elderberry, and have bright red elytra. Both of these species also have the largest geographic ranges, with disjunct localities from British Columbia to California.

The particular distribution of *D. cribripennis* in British Columbia, Vancouver Island, and Washington is nearly identical to the distribution of *Peromyscus* deer mice studied by Zheng et al. (2003), who found evidence for southward dispersal of *P. keeni* and *P. maniculatus* into Washington from a Vancouver Island refugium during the mid- to late Pleistocene glacial fluctuations. Not concordant with the range of *Peromyscus* species were the populations we identified as *D. cribripennis* in Oregon and coastal North

California. Perhaps this reflects the older age of *D. cribripennis*. Maybe the difference is simply due to alternative pathways of dispersal for two species with non-identical niche requirements. (Although the Californian populations were assumed to be the same species as *D. cribripennis* based on morphological similarity, it is also possible that these populations represent a separate lineage that have developed similar traits in parallel with *D. cribripennis*.) *D. maximus*, which primarily occurs in the Sierra Nevadas, also has a disjunct population at Vancouver Island, indicating that the species was present at northern latitudes, perhaps once existing in Washington and Oregon, later replaced by the other large, blue elderberry-boring species, *D. aureipennis*.

As has already been discussed, the relative position of *D. maximus* and *D. aureipennis* is tentative given the weak molecular data and limited sampling within each lineage. Both of these species, as well as the species in their sister clade, *D. piperi*, *D. lacustris*, and *D. sympatricus*, tend to occur in association with high-elevation springs that develop below melting snow lines. These cold-adapted species are likely to have tracked these ice-lines through periodic glacial cycles in the Pleistocene as they fluctuated from high in the mountains during glacial minima, then down into valleys during glacial maxima, allowing isolated populations to come into contact. The resolution of phylogenetic relationships of animals and plants with closely-related species in the Sierra Nevadas, Cascades, and Northern Rocky mountains has been an ongoing problem for Pleistocene-age biogeographers, and many of the studies have turned up inconclusive due to incongruency between gene trees (Galbreath et al, 2010; Schoville et al., 2011; *see also*: Richardson et al., 2002; Bain & Golden, 2005; Jarvis & Whiting, 2006; Spellman et al., 2007; Schoville & Roderick, 2010). The alpine pika populations studied by Galbreath et al. (2010) had phylogenetic relationships and distribution patterns similar to those of *D. maximus* (Sierra Nevada, with northern range limit at Mt. Shasta), *D. aureipennis* (Oregon Cascades), and *D. piperi* (Blue Mountains and Northern Rockies), with molecular clock models estimating the divergence of the Sierra Nevadan lineage from the latter two at around 1.3 million

years before present. Schoville et al. (2011) estimated the divergence between the Sierra Nevadan endemic alpine butterfly *Colias behrii* and the northern Rocky Mountain *C. meadii* at 144,775-651,249 years BP. Certainly, *Desmocerus* holds potential to be a valuable addition to this particular field of research, however, more genes, and a much wider range of populations, especially the Cascadian and Rocky Mountain populations *D. aureipennis* will first need to be obtained and sequenced.

Another phylogeographic/biogeographic problem is presented by the populations here considered *D. lacustris*, which form a ring of apparently transitional forms around the Willamette Valley of central Oregon, and which may ultimately turn out to represent several distinct species. In the 28S analyses, four sequences of *D. lacustris* (highlighted in dark grey, **Figs. 3.10-3.11**) fell outside the rest of the *D. aureipennis* complex due to a single nucleotide—a thymine at position 414 in the trimmed sequences—shared with *D. californicus* s.l., *D. palliatus*, and all the rest of the lepturine outgroups. These particular sequences are from three phenotypically-similar populations that occur in relatively close proximity (Portland, and the foothills of the Cascades east of Salem, Oregon) outside the typical range of *D. lacustris* (type locality = Crater Lake, Oregon; see **Fig. 3.1**). Nevertheless, the sequences fall in the same CO1 clade with *D. lacustris* (**Figs. 3.13-3.18**) and share important morphological similarities with the populations of that species from Crater Lake, namely, the long pubescence on the head and pronotum, and the tendency for the dark pattern on the male elytra to vary among individuals within a population. The populations in the Oregon Coast range and Haida Gwaii, though genetically very similar, also bear subtle morphological distinctions, and may also turn out to represent species. (see Miller, 2006, for a detailed population genetic study on a species of red tree vole with a similar distribution to *D. lacustris*.)

An open question is whether, and to what degree, the populations in western Oregon here considered *D. lacustris* may have historically hybridized with *D.*

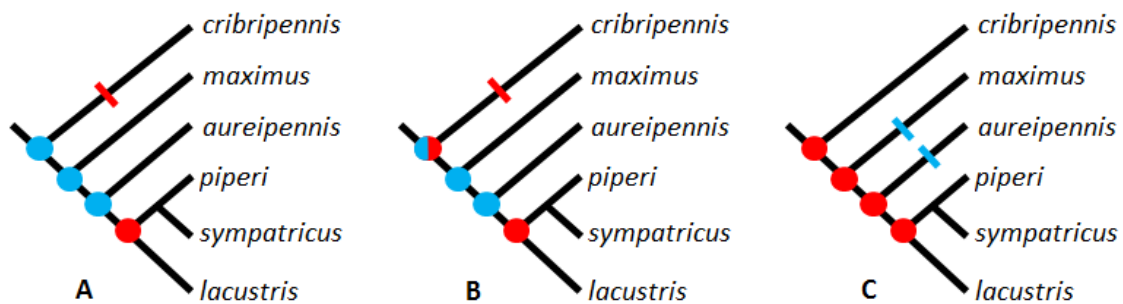
*cribripennis*, to which they are nearly identical except for the extent of elytral patterning and separate mtCO1 clades. The phylogeny suggests that the two species may look alike due to atavism or parallel evolution, perhaps due to similar selective pressures from coastal habitats. Unfortunately, although specimens of putative *D. cribripennis* were sought from populations in Oregon that overlapped with the range of the *D. lacustris* mtCO1 clade, none were obtained. Thus, there is potential at least that the conception of these two species as here presented is flawed.

### Host plants

As far as is known, all the *Desmocerus* species except *D. palliatus* and *D. c. dimorphus* are restricted to using only one type of *Sambucus* species for their larval hosts, even when multiple types of elderberry co-occur along that species' range (see discussion on *D. piperi* in the species review section of this chapter). Prior to the molecular analysis, the assumption had been that in the *D. aureipennis* complex, there would be only two phylogenetically-related groups: those associated with red elderberry and those associated with blue elder. Depending on the condition of the common ancestor, this would require only one host-plant switch in the *D. aureipennis* complex (or perhaps two separate developments of specificity in the case of an ancestor that could use either host plant). The preferred phylogeny however, in addition to implying the independent or parallel development of several anatomical characters among different *Desmocerus* lineages, also suggests that multiple independent host plant switches were made as well in a similar fashion.

**Figure 3.23** outlines several different host-plant switching scenarios within the *D. aureipennis* complex, given the preferred phylogeny, that differ depending on the specific host plant (or plants) used by the ancestor to the *D. aureipennis* clade. In the first scenario (**Fig. 3.23—A**), the ancestor uses blue elderberry, *Sambucus nigra* ssp. In this case the phylogeny requires that two separate transitions were made to red elderberry, first by *D. cribripennis*, and then by the ancestor to *D. piperi-sympatricus-*

*lacustris*. In the second scenario, **B**, an ancestor that could utilize either elderberry species as a larval host requires at least two transitions to host plant specificity, followed by a host plant switch. In scenario **C** a set of lineages derived from a red elderberry-boring ancestor undergoes two independent transitions to blue elderberry, first by *D. maximus* and then by *D. aureipennis*. The first and third scenarios (A & B) require only two evolutionary steps while the second scenario (B) requires three.



**Figure 3.23.** Several possible scenarios for the evolution of host-plant specificity observed in present-day *Desmocerus* populations, given the preferred phylogeny (Fig. 3.21). Ancestral-state conditions are either blue elderberry (*Sambucus nigra* subsp.) or red elderberry (*Sambucus racemosa* subsp.).

#### *Outgroup Selection and the Phylogenetic Placement of Desmocerus within Lepturinae*

A robust analysis of the relationships within *Desmocerus* requires the inclusion of an *outgroup* — a set of taxa outside of the genus — as a reference point for rooting the tree topology. By rooting the topology, a reader may then assess the order in which character states evolved with respect to the root. This practice, referred to as the *polarization* of character states, is achieved according to what Wiley and Lieberman (2011:191) describe as *The Outgroup Rule*: “given two (or more) homologous character states within a group studied, the state found outside this group in close relatives is the plesiomorphic state and the character found only within the group is the apomorphic state.” Maddison et al. (1984) demonstrated that a minimum of two outgroup taxa,

(ideally) the sister group and one additional outgroup are required for ancestral character states to be unambiguously resolved.

The use of outgroup taxa as closely related as possible to the ingroup is generally thought to maximize the odds that character states observed in the outgroup taxa are homologous to those of the ingroup. Rosenfeld et al. (2012), working with seven genome-level data sets, demonstrated a linear correlation between the use of outgroups successively more genetically distant from the ingroup taxon and the degree of incongruence in tree topology. Surprisingly, those authors found the consequences of the “random rooting effect” (a special case of long-branch attraction) on phylogenetic inaccuracy in their data set to be substantially greater than that posed by incomplete lineage sorting (see also: Wheeler, 1990; Smith, 1994; Sanderson and Shaffer, 2002; Luo et al., 2010).

No single genus, group of genera, nor any particular tribe within the Lepturinae, stands out as a sure candidate for a sister group to *Desmocerus*. This is evidenced by *Desmocerus* having the long-time status as occupying the sole position in the tribe Desmocerini Blanchard, 1845. Members of *Desmocerus* are characterized by a pronotum with the posterior angles strongly produced over the elytral humeri; a trait that is also characteristic of the members of number of genera in the tribe Lepturini Latreille, including *Leptura*, *Judolia*, *Pygoleptura*, *Typocerus*, *Dorcasina*, and others. If this is a derived character state, it may represent a synapomorphy indicative that any of these genera might be reasonably close to *Desmocerus* phylogenetically, and thus represent a suitable outgroup. By contrast, *Desmocerus* also has distinct pronotal tubercles and convergent tempora, not the sharp ridges behind the eyes and distinct neck characteristic of the preceding genera. These characters instead suggest an affinity with a quite different set of genera, such as *Rhagium* and *Pseudogaurotina* of the tribe Rhagiini Kirby. A number of other characters that occasionally provide clues to phylogenetic relationships among beetles are completely anomalous in *Desmocerus*.

According to Gardiner (1970:288), the “brown, scaly, longitudinally striated eggs [of *Desmocerus*] are distinct from all other known lepturine eggs.”

Švácha and Danilevsky (1989, p.15) argued that *Desmocerus* was more closely related to the *Gaurotes* - *Pseudogaurotina* group based on a unique larval character *D. palliatus* shares with *Pseudogaurotina excellens* (Brancsik, 1874)<sup>39</sup>. In support of this putative synapomorphy, *Pseudogaurotina* species, like *Desmocerus*, have metallic purplish integument, and blue or green metallic elytra. But perhaps more intriguingly, the European and Asian species of *Pseudogaurotina*<sup>40</sup> utilize living host plants in the family Caprifoleaceae, with which *Sambucus*, the host plant of *Desmocerus*, is thought to be closely related. The use of living hosts in the Lepturinae as a whole is relatively uncommon.

The limited molecular evidence available appears to support the first hypothesis, that *Desmocerus* is related to the Lepturini (Sýkorová, 2008, bachelor thesis in Czech). That study employed Bayesian, Likelihood, and Parsimony approaches using a single mitochondrial gene 16S rDNA, with 132 species in 8 cerambycid subfamilies. *Desmocerus palliatus* and *Pseudogaurotina excellens* were both represented among the 81 lepturine species in the analysis. In every analysis, *D. palliatus* grouped with the Lepturini, though the clades were not consistent and all trees in the study had relatively low nodal support values. *Pseudogaurotina* never appeared in the same clade as *Desmocerus*, often placing distantly with other Rhagiini genera, such as *Rhagium*, *Acmaeops*, and *Gaurotes*.

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<sup>39</sup> The character referred to by the authors: “Proth coxae relatively well defined (also in some other forms with long legs, e.g. *Dinoptera*, *Acmaeops* sg. *Gnathacmaeops*, *Grammoptera ustulata*, *Judolia* etc.), but in this genus followed by +/- complete fusion of sternal (bst) portion of exst with stlf (i.e. also with medial portion of bst; see Part 1, p.56, and “all Lepturinae” on line 14 should be replaced by “almost all Lepturinae”).” (Švácha and Danilevsky (1989, p.80, Fig. 15B)

<sup>40</sup> The type of *Pseudogaurotina* is the Siberian species *P. splendens* Jakovlev, 1893. Švácha and Danilevsky (1989) expressed doubt as to whether the North American forms of *Pseudogaurotina* truly belong to the genus. The North American *P. cressoni cressoni* apparently uses decaying wood as a host, but *P. cressoni lecontei* may use living *Lonicera* (see more extensive remarks in *Pseudogaurotina* section of this thesis).

In order to further inform our search for an appropriate outgroup for the mt CO1 analysis, in the present study the more slowly-evolving gene, 28S rDNA, was used to compare our full set of 28S rDNA sequences of *Desmocerus* to as many lepturine taxa as were available. Preliminary trials using different subsets of the lepturine taxa in the 28S analysis did not affect the phylogeny within *Desmocerus*, and are not shown in the results. Although the taxon sampling was limited in scope, and trees were generally poorly resolved, the two genera *Judolia* and *Judolidia* (tribe Lepturini), and the genus *Stenocorus* (tribe Rhagiini) both grouped consistently with *Desmocerus*. Furthermore, in a visual comparison of the entire set of lepturine 28S sequence data available, it was discovered that the species *Desmocerus palliatus*, *D. c. californicus*, and *D. c. dimorphus* have a 3 base pair insertion sequence (TAC) at the same position at which *Judolia sexmaculata*, *J. instabilis*, and *Judolidia bangi* also have an insertion (TTA). None of the other *Desmocerus* species, or other lepturines available had an insertion sequence at this position. It is thus conceivable that the insertion is a shared, derived character for the three genera.

For the reasons discussed above, *Judolia instabilis* (Haldeman, 1847), was included among the outgroups in the CO1 and combined-gene analyses. An additional three taxa, *Stictoleptura canadensis cribripennis* (LeConte, 1859), *Trachysida aspera aspera* (LeConte, 1873), and *Xestoleptura crassicornis* (LeConte, 1873) were also included, primarily because these were the only taxa in the Lepturini for which both 28S rDNA and CO1 mtDNA were available. *Stenocorus* (Tribe Rhagiini) is relatively dissimilar to *Desmocerus* morphologically and never grouped with *Desmocerus* in the 16S rDNA analysis by Sýkorová (2008). Although *S. amurensis* fell in a clade with *Desmocerus* in this 28S rDNA analyses, it appears on a much longer branch than *Judolia/Judolidia*, indicating the possibility that it may be placed as a result of long-branch attraction (See *Results*, **Fig. 3.8**). That taxon was thus considered a sub-optimal candidate for an outgroup to *Desmocerus*.



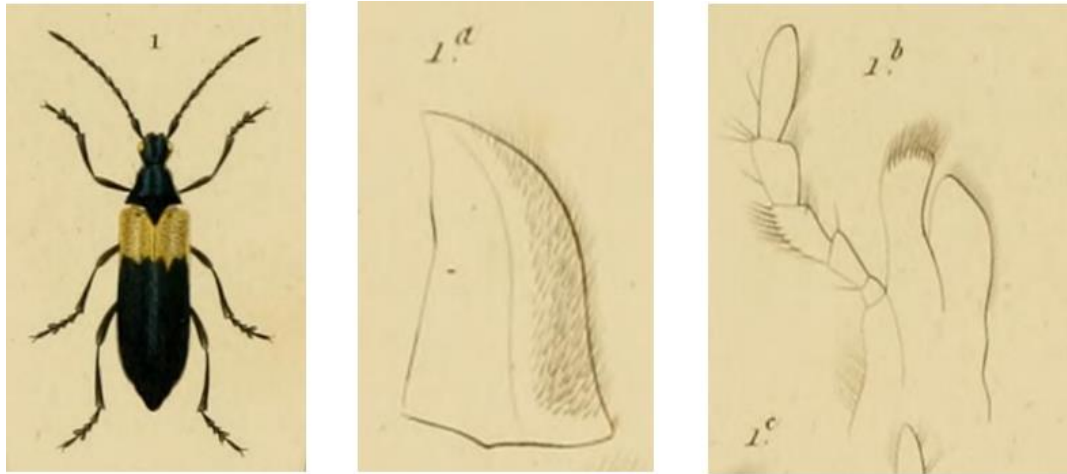
Ultimately, what will be needed is a more thorough understanding of the natural groups in the Lepturinae, and their evolutionary relatedness to one another before a set of the most optimal outgroups for *Desmocerus* can be defined.

### *Review of Desmocerus Species*

A new classification for *Desmocerus* is given below that includes two newly-described species and a revised interpretation of specific limits within the *D. aureipennis* species complex. The species names now considered valid in *Desmocerus* are listed in bold italics. For each species, a bibliography of selected references is given to indicate where previous authors had referred to the same species by a different name, or under a different genus (a more comprehensive bibliography for earlier works was produced by Linsley and Chemsak, 1972.) Further notes on each species' biology, distribution, and taxonomic history are also included.

### DISCLAIMER

This thesis is not to be regarded as a publication issued for public and permanent scientific record, or for purposes of zoological nomenclature as required for the availability of new species names in Article 8 of the International Code of Zoological Nomenclature. The species descriptions below are preliminary drafts intended for publication at a later date.

***Desmocerus palliatus* (Forster, 1771) (Fig. 3.24)**

**Fig. 3.24.** *Desmocerus palliatus* (Forster, 1771). Plate from Cuvier (1836) showing maxilla and mandible lacking internal pubescent fringe.

Referenced as:

*Cerambyx palliatus* Forster, 1771:40

*Desmocerus palliatus*; Harris, 1841:92 (habits); Fitch, 1845:250 (habits); Horn, 1881:vii; Townsend, 1884:221 (habits); Townsend, 1885:70 (habits); <sup>41</sup>Stevenson, 1905:90 (habits); Morris, 1915:22 (habits); <sup>42</sup>Hess, 1917:63; Burke, 1921:451 (habits); Boppe, 1921:30, pl. 2, fig. 6, 6a, 6b.; Herrick, 1923:546, pl. 7 (habits and figs); Craighead, 1923:87, pls. 17, 31. (habits, larva, pupa); Goldman, 1933:93, pl. 5, figs. 40-44); etc.

*Colopus blandus* Fabricius, 1775:182

*Stenocorus cyaneus* Fabricius, 1775:823; Fabricius, 1781:226; etc.

*Desmocerus cyaneus*; Dejean, 1821:111; Audinet-Serville, 1835:202; Cuvier, 1836, pl. 69. (figs.); <sup>43</sup>Croft, 1872:120.

*Desmocerus elongatus* Bland, 1862; Bland, 1863 (synonymy)

*Desmocerus palliatus* occurs throughout eastern North America, from Northeastern Canada and Maine, to Louisiana, Nebraska, Kansas, and Oklahoma. So far, the species is

<sup>41</sup> *D. palliatus* is said to be "swarming" at *Sambucus canadensis* Linn., at Cote St. Paul, Quebec, during the second week of July, 1904.

<sup>42</sup> *The chordotonal organs and pleural discs of cerambycid larvae.*

<sup>43</sup> "*Desmocerus cyaneus*.—About 25 years ago, I took a colony of about 30 specimens off some elder bushes in rear of Trinity College. I have never met with another specimen near Toronto, one I found in fall of 1870 at the Sault St. Marie."

not known to occur in Florida or Texas (maps in Linsley & Chemsak, 1972, and Halstead and Oldham, 1990). It is easily recognized by the blue and gold coloration of the elytra.

In the United States, *D. palliatus* is typically collected on American elderberry, *Sambucus canadensis*, but the northern populations apparently also use the red berried elder, *S. racemosa*. Morris (1915:22) reported collecting “nearly fifty specimens” on *S. racemosa* in an alder swamp in the Port Hope District of Ontario, in late June and July when the berries were ripe, while the flowers of “the late elder,” *S. canadensis*, were just beginning to open. “The beetles love to rest on the underside of the foliage, and more frequently were found in small thickets of Elder within the borders and under the shadow of hardwoods. Very few were found on the Late Elder and none on the blossom.” In Ithaca, New York, Herrick (1923:546) reported finding *D. palliatus* on wild *S. canadensis*, as well as a variety of ornamental elderberry he calls Golden elder.

The origin of the *D. palliatus* holotype is unclear. The type locality, “*Habitat in America septentrionali*” is a Latin phrase often used to denote the unexplored northern boreal regions of North America. Forster indicates in his preface (Appendix B) that the specimens described are from the collection of Linnaeus, which that author did not include in his *Systema Natura*, as well as additional specimens from his friends. In July 1771, Joseph Banks and Daniel Solander had returned from Captain Cook’s first voyage on the *Endeavour*, bringing with them a massive quantity of biological specimens. *Novae Species Insectorum* is dedicated to Banks, who was planning a second journey (see Appendix B and Hoare, 1976: 69). However, Whitehead (1978) does not trace any first voyage insects to Linnaeus or to Forster. Many of the first voyage insects collected by Banks were examined and described by Fabricius, and this was probably the origin of *Stenocorus cyaneus* Fabricius, 1775.

***Desmocerus californicus californicus* Horn, 1881 (Fig. 3.25, left)**

Referenced as:

*Desmocerus californicus* Horn, 1881:vii; Blaisdell, 1903:276 (habits); Webb, 1905:105; Garnett, 1918:211; Burke, 1921:45 (habits); Davis and Comstock, 1924:179 (larva, pupa, and habits); Davis, 1931:187 (habits); etc.

*Desmocerus californicus californicus*; Linsley and Chemsak, 1972:, fig. 2 (map, habits, bibliography); Monné & Giesbert, 1995:157; Ray et al., 2012:157; etc.

*Desmocerus californicus* Horn is distinguished from the species in the *D. aureipennis* complex by their larger size, relatively stout antennae, and the punctures on the elytra, which are minute and densely-clustered. There are two recognized subspecies in California, separated by the coloration of the male elytra. The nominative subspecies, *D. c. californicus*, ranges along coastal California, from the Trinity Mountains of northern California, to the San Diego River at the very southern end of California. The males of *D. c. californicus* always have the elytra entirely dark green, bordered by a thin red margin.



**Fig. 3.25.** *Desmocerus californicus* Horn, 1881. Left: male specimen of *D. c. californicus*. Right: male specimen of *D. c. dimorphus* Fisher, 1921

***Desmocerus californicus dimorphus*** Fisher, 1921 (Fig. 3.25, right)

Referenced as:

*Desmocerus dimorphus* Fisher, 1921:207

*Desmocerus californicus dimorphus*; Doane et al., 1936:178; Linsley & Chemsak, 1972:69:7, fig. 2 (map, habits, bibliography); USFWS, 1980:52803-52807; USFWS, 1984; Arnold, 1984; Barr, 1991; Monné & Giesbert, 1995:157; USFWS, 1999; Huxel, 2000:81-85; Collinge et al., 2001; Talley, 2005; Talley et al., 2007; Ray et al., 2012; USFWS, 2012:60238-60276; etc.

*Desmocerus californicus*; Halstead and Oldham, 1990 (map, habits, bibliography, synonymy); Halstead and Oldham, 2000 (distribution map, synonymy).

In the subspecies *D. c. dimorphus*, which ranges primarily throughout the Sacramento Valley of California, the male elytra is usually red with four dark spots. According to a recent report by the U.S. Fish and Wildlife Service (2012), the ranges of the two subspecies may abut, or overlap in several places, along the foothills of the eastern Coast Range and the southern San Joaquin Valley, and possibly also in Placer and Yolo Counties, and in the Sierra Nevada foothills as far north as Mariposa County (p. 60240).

Halstead and Oldham (1990) recorded a number of new observations on the life history and behavior of *D. c. dimorphus* based on extensive observations both in the field and caged experiments, and Talley et al. (2007) performed a detailed study on the habitat choice of *D. c. dimorphus*. Ray et al. (2012) recently synthesized a pheromone, or sex attractant for *D. c. dimorphus*, that is now known to be used by several other species in the genus (see Ray et al., *in prep*). The US Fish and Wildlife Service recently proposed delisting *D. c. dimorphus* as a threatened species, due to the revelation that the subspecies is much more widespread than initially thought when it was proposed for listing in 1980. That report (USFWS, 2012) reviews the history of conservation efforts for that species in California, and includes a thorough review on the life history and biology of *D. c. dimorphus*, as well as a table of localities where *D. c. dimorphus* is known to occur.

There has been some controversy in the literature regarding the specific status of the federally-threatened subspecies *D. californicus dimorphus*. Halstead and Oldham (1990) first proposed synonymizing *D. dimorphus* under *D. californicus*, but this report was never published in a journal, and it was vocally condemned by John Chemsak, then the authority on North American cerambycids (see Barr, 1991:3). Later, Halstead and Oldham (2000) published a new distribution map for *D. californicus* (including *D. dimorphus* as a junior synonym) in which a huge number of new localities were reported based on museum specimens. Again the authors recommended synonymizing *D. dimorphus* under *D. californicus*, but this appears to have been ignored by the taxonomic community.

The present study was primarily focused on assessing relationships among species in the *D. aureipennis* complex, and I was only able to borrow or view a small number of specimens of *D. c. dimorphus*. In the phylogenetic analysis, the distance between the two mitochondrial CO1 clades (**Fig. 3.14**) might appear to suggest that the two populations are easily separable as distinct species. However, each subspecies is only represented by one population each, and these are widely separated geographically. Ideally, a much larger number of populations, especially from areas where both forms co-occur, should be sequenced before making any inferences based on molecular data. Given the surprising cryptic diversity that I have realized within the *D. aureipennis* complex, among species that are superficially only barely separable, I prefer to maintain the two subspecies of *D. californicus* as valid until a more thorough investigation can be performed.

***Desmocerus aureipennis* Chevrolat, 1855 (Fig. 3.26)**



**Figure 3.26. *Desmocerus aureipennis* Chevrolat, 1855.** Female on leaf of blue elderberry, *Sambucus nigra cerulea* at Mt. Ashland summit, Oregon. ~7000 ft., July, 2012.

Referenced as:

*Desmocerus aureipennis* Chevrolat, 1855:187; Chevrolat, 1858:325, pl. 8, fig. 6.

*Desmocerus auripennis*; LeConte, 1857:23; Chevrolat, 1858:325; Halstead & Oldham, 1990.

*Desmocerus auripennis auripennis*; Hatch, 1971:145; Linsley & Chemsak, 1972.

*Desmocerus aureipennis aureipennis*; Monné and Giesbert, 1994: 157

The earliest *Desmocerus* species described from western North America was *D. aureipennis*, a large, magnificently-colored species that bores exclusively into blue-berried elder, *Sambucus nigra cerulea*. It is distinguished from *D. californicus* by its narrower form and elytra with large, irregularly-spaced punctures. (The elytral punctures are small and densely-clustered in both subspecies of *D. californicus*.) The remaining *Desmocerus* species also share these same anatomical characteristics with *D. aureipennis*, and although they vary widely from one another in their sizes, colors,

relative amounts of pubescence, and life history strategies, they are still so similar in their external structure that Hatch (1971) and Linsley and Chemsak (1972) considered them subspecies of *D. aureipennis*. Following more recent evidence that the supposed subspecies are apparently largely reproductively isolated and occur sympatrically in several localities (Halstead and Oldham, 1990, and personal observations by present author), those populations are here elevated to full species, and are referred to, for convenience, as the *D. aureipennis* species complex. This complex includes *D. aureipennis* Chevrolat, *D. cribripennis* Horn, *D. piperi* Webb, *D. lacustris* Linsley & Chemsak, and two new species described presently *D. maximus* Schapker and *D. sympatricus* Schapker.

#### Notes on life history of *D. aureipennis*

Larvae bore into the roots and trunk of *Sambucus nigra cerulea*. Specimens have been taken both at extremely high elevation (near 7000 ft. at the summit of Mt. Ashland, in Siskiyou Co., Oregon) and (presumably, based on specimen records) at low elevations, along the Klamath River, and at Camp Sherman, Oregon, along the Metolius River. (At the latter locality, the author found no evidence of *Desmocerus* infestation after two days of collecting in August, 2013, in a variety of habitats and elevations.) Although *S. nigra cerulea* grows abundantly at all elevations in the Siskiyou mountains of southern Oregon, the *D. aureipennis* population at Mt. Ashland is apparently restricted to the dwarfed elderberry plants that grow in full sunlight along springs and small streams in the meadows at the summit of the mountain.

Between July and August of 2013, the author collected 24 males from the Mt. Ashland summit population using (R)-Desmolactone pheromone lures, as part of a study to determine pheromone usage within the genus (see Ray et al., 2012, and Ray et al., *in prep*). Several copulating pairs were observed and a short digital video was taken. The video, available by request from the author, demonstrates a series of behaviors that appear to fall outside of the patterns of copulation behavior observed in other



lepturines (see Michelsen, 1963). The male mounting the female on a leaf, after which the female begins to move forward in an apparent effort to dislodge the male. At this point the male began to wave his large antennae with great fervor, rapidly tapping the female's head and antennae. The female then stops, and begins to feed on the edge of an elderberry leaf while copulation proceeds, and the male, with antennae at rest, begins bobbing his head, scraping his pronotum along the mesonotal stridulatory plate to make a slightly audible chirping noise. During this time another male was observed sitting on a leaf of the same plant about a half meter away. No further observations were made—copulation was interrupted and the specimens were placed into alcohol.

#### The known range of *D. aureipennis* substantially revised

Historically, the name *D. aureipennis* Chevrolat was applied to the numerous populations of blue-elderberry boring *Desmocerus* that occur throughout the Sierra Nevadas and related mountain ranges of California, and at the time of Linsley and Chemsak's (1972) revision, the northern range limit for *D. aureipennis* was thought to be the Siskiyou of southern Oregon. In the course of this study, however, it was discovered that two sets of populations superficially resembling *D. aureipennis* occur, which are distinguished by a series of discrete morphological differences. The first set ranges from the Marble and Klamath Mountains of Northern California to the Cascades of northern Washington. Specimens from those populations have long, white pubescence on the thorax and abdomen, relatively narrow, transparent hindwings with a distinctive dark spot distally, male parameres that are black and lack dorsal setation, and females with the red elytral pigmentation reduced to thin margins along the edge of the elytra. The second set, which primarily occurs from the Sierra Nevadas to Mt. Shasta and southeastern Oregon, has brown pubescence, broad orange hindwings, male parameres with prominent dorsal setation, and females with the red pigmentation usually covering a large portion of the elytra. (See Figs. 3.28-3.30)

Interestingly, examination of the holotype of *D. aureipennis* places it unambiguously with first set of populations that range from northwestern California to Oregon and central Washington, and this is substantiated by further historical evidence related to the itinerary of its likely collector, John Jeffrey (of *Pinus jeffreyi*). Notes on the original description, holotype, and type locality of *D. aureipennis* are given in Appendix A at the end of this chapter. The second set of populations are thus described as a new species, *D. maximus* Schapker.

***Desmocerus maximus* Schapker, new species (Fig. 3.27)**



**Figure 3.27.** *Desmocerus maximus*, Schapker sp.n. - dorsal habitus of adult male.  
(SM0348204 KUNHM-ENT)

Referenced as:

*Desmocerus auripennis*; Horn, 1879:xxx; Blaisdell, 1892:35 (habits); Fall, 1901:147; Webb, 1905:105; Garnette, 1918:211; Burke, 1921:452 (habits); Essig, 1926:355 (habits and fig.).

*Desmocerus auripennis auripennis*; Hatch, 1971:145; Linsley & Chemsak, 1972, Figs. 1, 3 (map, fig., habits, bibliography)

*Desmocerus aureipennis aureipennis*; Monné & Giesbert, 1995:157; Ray et al., 2012:166.

*Desmocerus piperi*; Hardy, 1926:c30.

*Description.*— Body elongate, integument lustrous blue/black. Elytral punctures large, separate. Head and hypomeron sparsely covered in thin, long pubescence. Pronotum rugose, lacking hairs dorsally. Underside of abdomen and thorax mostly lacking pubescence. Antennal segments thick, sub-serrate; segments 1-5 bearing short, sub-erect setae; segments 6-11 velvety, often bearing multiple distinct pits on lateral apices. Hind wing broad, entirely orange-brown in color (as in **Fig. 3.29a**). Male paramere brown to dark brown, 4-5mm long, bearing several long setae on posterior apex, often with 1-3 thick dorsal setae emerging from an impression on the dorsal surface of the paramere (as in **Fig. 3.30a**).

♂ - *Body* 18-27 mm. long but typically greater than 22mm. Elytron tapering towards apex, entirely bright red, semi-metallic (pale yellow in pinned specimens). Antenna extending  $\frac{3}{4}$  length of body.

♀ - *Body* 22-30 mm long. Elytron broad, sub-parallel, with medial green/black discal area that varies in its extent, often taking the form of a keystone; elytron bordered by bright red (yellow in pinned specimens). Antenna extends  $\frac{1}{2}$  length of body.

Holotype (OSAC\_0000556507) – Adult male. USA: California: Tehama CO., CA Hwy 36 nr. mile 93.17, ~1.4km East of Child's Meadow. 40.34888°N 121.48386°W, 10-VIII-2012, el.~1505 m. (A. B. Richards). Body 22.5mm long from the front of the head to the posterior apex of the elytra. Hind wings (slide mounted with euparal on glass slide) 20.5mm long. Genitalia dissected, in vial on pin. Parameres dark brown, 1.0 mm long. DNA genomic extract OSAC: PAS1212001.

Paratypes. – 7 paratypes as follows: (1) allotype: label data same as holotype, DNA genomic extract: PAS1212003 [OSAC, 1 female, OSAC\_0000556505]; (2) same label data as holotype, DNA: PAS1212002 [OSAC, 1 male, OSAC\_0000556508]; (3) USA: CA: Tehama Co., elderberry plants along M2, 39.9370°N 122.74984°W, 12-VIII-

2012, elev.~1733 m. (A. B. Richards) [OSAC, 1 female: OSAC\_0000556506]; (4) same locality as in (3), 13 VIII 2011 [CAS, 1 female]; (5) same locality as in (3), 20 VIII 2011 [BMNH: 1 male]; (6) same locality as in (3), 30 VII 2011 [2 females, one each in the personal collections of Philip Schapker and Austin Brady Richards].

Geographic Distribution.— *Desmocerus maximus* occurs at high elevations in the Mt. Shasta, Modoc, and Sierra Nevada mountain ranges in California and Nevada. A disjunct population occurs at Vancouver Island, British Columbia.

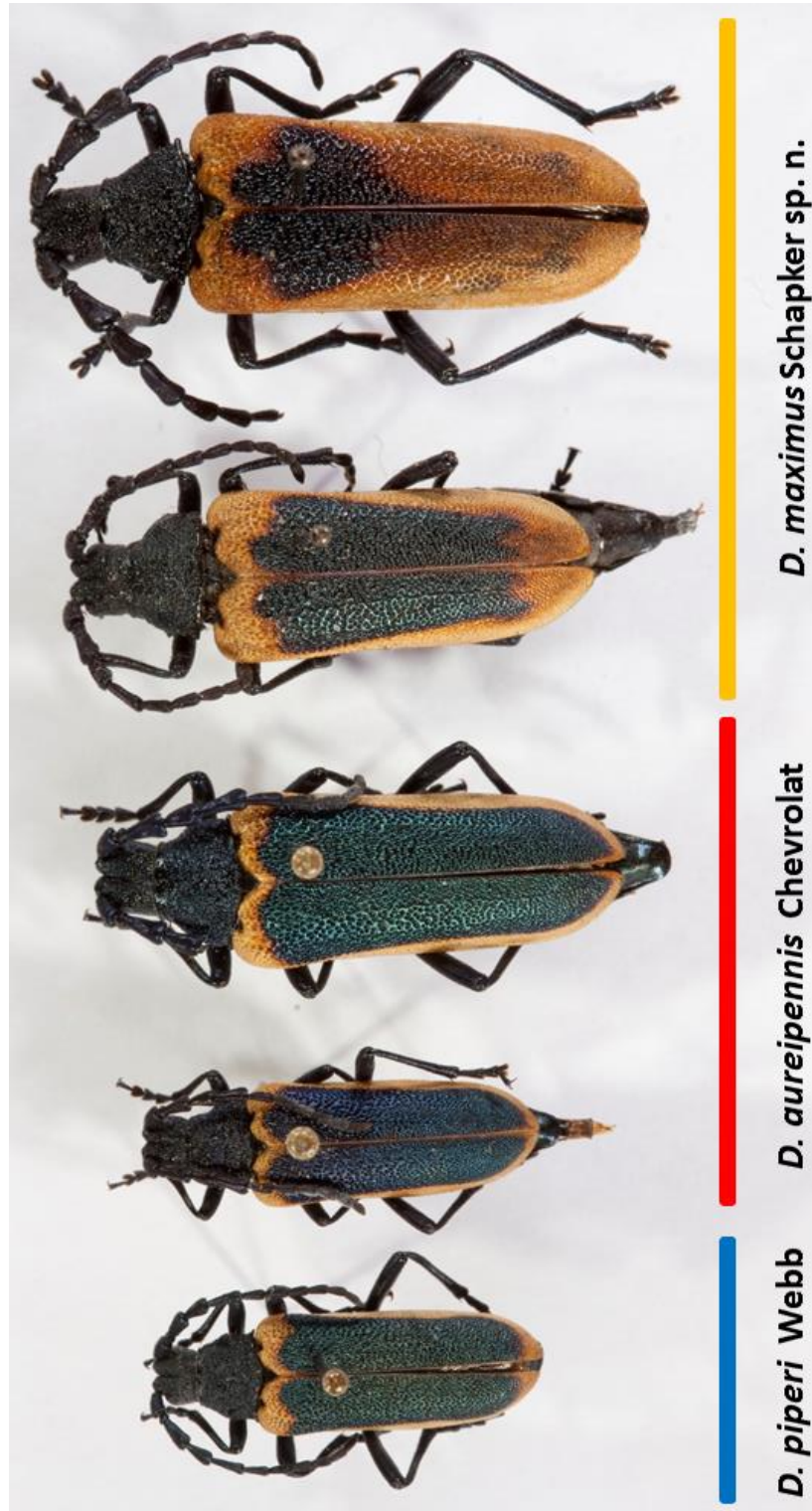
Host plant. – *Sambucus nigra* subsp. *cerulea*

As its name suggests, *D. maximus* is the largest *Desmocerus* species known, with some females measuring up to 3cm in length. Aside from its original and subsequent description by Chevrolat (1855, 1858), and the plate of a fully-colored female *D. aureipennis* depicted in the Peterson's Field Guide to Beetles (White, 1985), the literature references to *D. aureipennis* (or *D. aureipennis aureipennis*) refer primarily to the abundant populations in the Sierra Nevada and other mountains in the southwestern United States herein considered *D. maximus*. This includes all but a few observational records represented by dots on the range map produced by Linsley and Chemsak (1972, fig. 1)), and a few additional localities provided by Halstead and Oldham (1990). A forthcoming report on the use of pheromones in several *Desmocerus* species by Ray et al. (*in prep*) refers to a population of *D. aureipennis* (*sensu strictu*) from the Oregon Siskiyou Mtns., and not to *D. maximus*.

*Desmocerus maximus* is separated from *D. aureipennis* by the following characteristics: (1) abdomen sparsely covered in short black or brown hairs (white and usually long in *D. aureipennis*); (2) female elytron with dark pigmented area variable in extent (fully covering elytron in *D. aureipennis*) (fig. 3.28); (3) hindwing broad, and orangish-brown, compared to narrower, and mostly transparent in *D. aureipennis* (figs. 3.29a,b); and (4), male parameres brown, often bearing short, thickened setae on the dorsal surface. The male parameres of *D. aureipennis* are typically dark black with setae confined to the posterior apices (see figs. 3.30a,b).

Based on the specimens available, the ranges of the two species do not appear to overlap in Northern California, nor have I observed “intermediate” populations between the two allopatric ranges. The sharp morphological discontinuity between the *D. maximus* populations found around Mt. Shasta (California), and the *D. aureipennis* populations found in the Klamath and northern Coast Ranges of California appears to be concordant with biogeographical patterns found in other western animal taxa (see Galbreath et al., 2010:356; Brunsfeld et al., 2001). At the Canadian National Collection there is a large specimen (CNC COLEOPT #05-309)—resembling *D. maximus* in every respect, collected by W. H. A. Preece at Bear Hill, Vancouver Island, B.C., on May 6, 1930 (“*Pupa dug from cell in Sambucus.*”). The latter is an uncommon disjunction that (unless somehow a result of anthropogenic dispersal) indicates that at one time *D. maximus* may have spanned the entire range between British Columbia and the Sierra Nevadas.

A note by Hardy (1926) in which *D. piperi* Webb was reported as occurring on Vancouver Island, British Columbia, is probably also another record for *D. maximus*: “... Male with elytra entirely orange. April to June. Rare. Breeds in base and stems of elder (*Sambucus*), forming galls at base, often killing the host-plant. Duncan (A. W. H.); Departure Bay (G. W. T.). British Columbia to California. Collection of A. W. Hanham.” As far as is known to the author, the gall-forming behavior has never since been verified for either species and could refer to scarification of the plant tissue as a result of the larval tunneling rather than true gall formation involving secreted plant growth hormones.



**Figure 3.28.** Dorsal habitus of females from *D. piperi*, *D. aureipennis*, and *D. maximus* Schapker, sp. n.. The two female *D. aureipennis* were taken from the same population at Mt. Ashland Summit (el. ~7000 ft.), and represent the range of female sizes in that species.



**Figure 3.29a. *Desmocerus maximus* Schapker sp. n.** – Hindwing from male.  
OSAC\_0000267958. Pyramid Ranger Station, Cal. (Hindwing venation varies.)



**Figure 3.29b. *Desmocerus aureipennis* Chevrolat** – Hindwing from male.  
OSAC\_0000556839. Mt. Ashland, Oregon. (Hindwing venation varies.)



**Figure 3.30a. *Desmocerus maximus* Schapker sp. n.**  
Parameres of the male genitalia. Dorsal view.  
OSAC 0000267958. Pyramid Ranger Station, CA.



**Figure 3.30b. *Desmocerus aureipennis* Chevrolat**  
Parameres of the male genitalia. Dorsal view.  
OSAC 0000556839. Mt. Ashland, Oregon.



***Desmocerus piperi* Webb, 1905 (Fig. 3.31)**



**Figure 3.31.** *Desmocerus piperi* Webb. *Left:* adult male. *Right:* adult female, potential paratype specimen (OSAC\_000824761).

Referenced as:

*Desmocerus piperi* Webb, 1905:104; Burke, 1921:452 (habits); Craighead, 1923:87 (larva and habits)

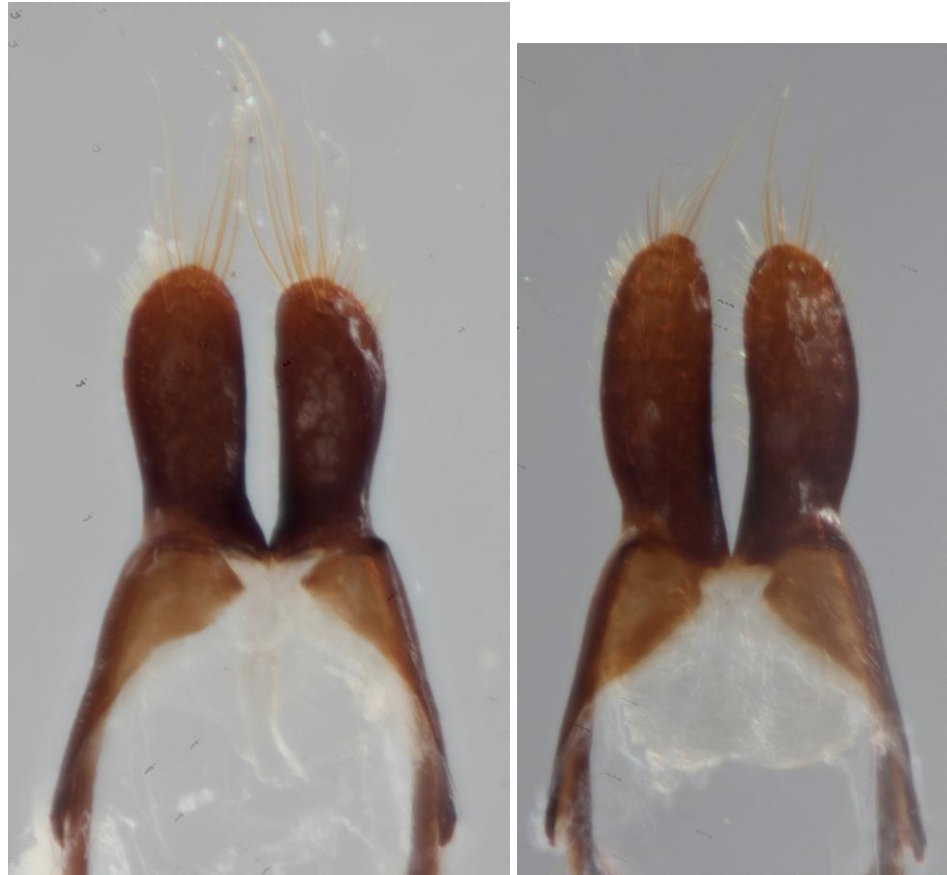
*Desmocerus cribripennis piperi*; Doane et al., 1936:178.

*Desmocerus auripennis piperi*; Hatch, 1971:145; Linsley & Chemsak, 1972:11, Fig. 1

*Desmocerus aureipennis piperi*; Monné & Giesbert, 1995:157

*Desmocerus piperi* occurs at higher elevations in the Wallowa and Blue mountains of northeastern Oregon and Washington (type locality= “Blue Mountains, Wash.”), and the Rockies of Idaho and Montana, and Alberta, Canada. A few disjunct populations are known in the Washington Cascades. *Desmocerus piperi* is easily recognizable in the field by its robust form and males with bright red elytra, which fades to yellow in pinned specimens. The species is distinguished from *D. lacustris* by the lack of long pubescence on the pronotum, and from *D. maximus* and *D. aureipennis* by its smaller size and uniquely-shaped male genitalia (**Fig. 3.32**).





**Fig. 3.32. *Desmocerus piperi* Webb** - parameres of male genitalia, dorsal view. Showing variation in shape and setation. *Left*: Mt. Adams, Washington (OSAC\_0000519853). *Right*: Alberta (CNCCOLEOPT#05-337) .

In *D. piperi*, the parameres are typically light brown, and smoothly rounded with a moderate amount of long setae clustered around the posterior apex, and occasionally shorter ones on the posterior dorsal-lateral portion. The shape of the male genitalia is fairly constant throughout the range of *D. piperi*, with the most extreme divergence in shape and size demonstrated by the two specimens in Fig. 3.32.<sup>44</sup>

<sup>44</sup> In total, genitalia from 11 *D. piperi* were inspected from 10 localities as follows: **USA**: Washington: Blue Mountains, Godman Springs (OSAC\_0000496856); Skamania Co., Mt. Adams, Takhlakh Pond (OSAC\_0000519853); Kettle R. Mountains (OSAC\_0000496846). Oregon: Wallowa Lake, Aneroid Lk. trail (OSAC\_0000491878); Wallow Co: Wallowa Mtns, Lustine Can., Lower Maxwell L. (2 specimens: OSAC\_0000617296 and OSAC\_0000617297). Montana: Glacier National Park, Many Glaciers (OSAC\_000302495); Lookout Pass (OSAC\_0000540790). Idaho: Lowell, Clearwater NF (CNCCOLEO00123621); Coeur d'Alene (CNC-PAS\_61.23). **Canada**: Alberta (CNCCOLEOPT#05-337).

The host plant used by *D. piperi* is the black elderberry, *Sambucus racemosa* var. *melanocarpa* (A. Gray) McMinn. The author made collections of the larvae (Fig. 3.33) of this species in mid August, 2012, at Mt. Emily, Oregon in the Wallowa Mountains. The host plant was numerous in a high elevation meadow that had developed in an area that appeared to have been burned at one point. Almost every black elderberry plant inspected by the author in that area was infested with *D. piperi*. At that locality, blue elderberry, *S. nigra cerulea*, also grew in abundance, often with its leaves overlapping those of the black elder. Over 20 blue elderberry plants were checked and none appeared to be infected with *Desmocerus*.



**Fig. 3.33.** *Desmocerus piperi* Webb, 1905 – larva, dorsal view. Extracted from *Sambucus racemosa melanocarpa*, in August, 2012 at Mt. Emily, Oregon (OSAC\_0000556475).

***Desmocerus sympatricus* Schapker, new species. (Fig. 3.34)**



**Figure 3.34.** *Desmocerus sympatricus* Schapker sp. n. *Left:* dorsal view of holotype male, OSAC\_0000556468. *Right:* dorsal view of female paratype, OSAC\_000777024.

Referenced as:

*Desmocerus auripennis piperi*; Hatch, 1971:145; Linsley & Chemsak, 1972:11, Fig. 1  
*Desmocerus piperi*; Halstead & Oldham, 1990.

*Description.*— Body elongate, integument lustrous blue/black. Elytral punctures large, separate. Head and hypomeron sparsely covered in thin, long pubescence. Pronotum rugose, usually lacking long hairs dorsally. Underside of abdomen and thorax moderately covered in short white pubescence. Male paramere elongate, bearing several thick dorsal setae widely spaced in a row along the midline (**Fig. 3.35**).

♂ - *Body* 18-21 mm. long. Elytron, entirely bright red, semi-metallic. Antenna extend  $\frac{3}{4}$  length of body.

♀ - *Body* 18-22 mm long. Elytron broad, sub-parallel, with green/black discal bordered by thin red margin. Antennae extend ½ length of body.

Holotype (OSAC\_0000556468) – Adult male. USA: WA: Steven's Pass Summit on *Sambucus racemosa* under power lines. 47.747550°N -121.090136°W, 8-VIII-2012, el. ~1261m. (About 130 m. uphill from *D. cribripennis* locality: 47.746325°N, -121.090136°W, el. 1244, caught on same day) (P. Schapker). Body 19.5mm long from the front of the head to the posterior apex of the elytra. Hind wings (slide mounted with euparal on glass slide) 16mm long. Genitalia dissected, in vial on pin. Paramere jet black, 0.85 mm long. DNA genomic extract OSAC: PAS1212018

Paratypes. – 9 paratypes as follows: (1) label data same as holotype, [OSAC, 1 male, OSAC\_0000554388]; (2) Wash., Steven's Pass Summit, Aug., 9, 1961. (D. V. McCorkle) [OSAC, 5 males, OSAC\_0000777019 – OSAC\_0000777023, and 3 females, OSAC\_0000777024 – OSAC\_0000777026]. Specimens 777021 and 777023 each have one hindwing removed and slide-mounted.

Geographic Distribution. – Cascades of central Washington (Steven's Pass).

Host plant. – Uncertain. Probably *Sambucus racemosa melanocarpa*.

In the course of studying geographic variation in the paramere structure of *D. piperi*, a population at the summit of Stevens Pass, in the central Washington Cascades, resembling *D. piperi* in every external aspect, was discovered to have genitalia that differed dramatically from those of the rest of the *D. piperi* specimens examined (11 *D. piperi* specimens from 10 disjunct localities; see Fig. 3.32 and discussion in previous section). A limited number of specimens of this population were available for study, however, the parameres of the two male specimens inspected were similar in being distinctly elongate and larger than those of *D. piperi*, almost jet black, and with a line of very prominent, thick setae set along the midline of the dorsal surface of the paramere. The typical paramere of the latter species are shorter, paler in color, and have relatively less robust dorsal setae that are restricted to the apical and dorso-lateral sides of the paramere. The relative length, color, and presence/absence of dorsal setae are all

characters that tend to be stable throughout the ranges of other species in *Desmocerus*.

It was further discovered that this same population existed within just 130 meters of a patch of red elderberry plants inhabited by another *Desmocerus* species, *D. cribripennis*. The author collected adult specimens of both species at Stevens Pass on the same day, August 8, 2012, just north of the highway along the Skyline Lake Trail. Mitochondrial CO1 was extracted and sequenced from individuals of both species, and fell into two distinct clades corresponding to *D. cribripennis* and *D. piperi*. Given the very minor CO1 sequence divergence, it seems reasonable to speculate that the genitalia of this *D. piperi*-like population have diverged fairly recently since becoming isolated at the summit of Stevens Pass, perhaps due to its interactions with *D. cribripennis*. Given its unique anatomical characteristics and ecological situation, the population at Stevens Pass is presumed now to be a separately-evolving lineage, worthy of specific status, and further study.

It seems worthy of note that after an entire day of searching, *D. sympatricus* was discovered on a lone elderberry plant growing in very close proximity to a residential facility at the ski lodge at Stevens Pass. The *D. cribripennis* population was in a weedy patch of a yard next to a cabin. That lone elderberry, and the weedy patch may well both have been mowed over before this thesis is printed.



**Fig. 3.35.** *Desmocerus sympatricus* Schapker sp. n. Parameres of male genitalia. Dorsal view. Holotype specimen: OSAC\_0000556468. Steven's Pass, Washington.



***Desmocerus lacustris* Linsley and Chemsak, 1972. (Fig. 3.36) new combination**



**Fig. 3.36.** *Desmocerus lacustris* Linsley and Chemsak, 1972. *Left:* male from Haida Gwaii, British Columbia. *Middle and Right:* males from Monument Peak, in the Cascade Range of central Oregon, showing within-population variation in elytral pattern.

Referenced as:

*Desmocerus auripennis lacustris*; Linsley & Chemsak, 1972:11, Figs. 1, 4.

*Desmocerus auripennis* "subsp. nov."; Hatch, 1971:145.

*Desmocerus aureipennis lacustris*; Monné & Giesbert, 1995:157

*Desmocerus piperi*; Halstead & Oldham, 1990.

The species *D. lacustris* Linsley & Chemsak, as presently construed, now comprises a number of populations ranging from Crater Lake, Oregon, north along the Cascades to northern Oregon, and along the coast ranges from around Newport, Oregon to several widely disjunct populations in coastal British Columbia and on Haida Gwaii. These are primarily defined by the presence of long hairs on the dorsal pronotum, and the tendency for the dark spot on the male elytra to vary in its extent within a population. Within *D. lacustris*, several clades are evident that were also predicted based on morphology. These are likely to be described as species, or at least subspecies of *D. lacustris* in the future.

***Desmocerus cribripennis* Horn, 1881 (Fig. 3.37)**



**Fig. 3.37.** *Desmocerus cribripennis* Horn, 1881. *Left:* male lectotype, MCZ Type 34546. *Right:* female, “Allotype 3739.” Both labeled “W.T” [Washington Territory].

Referenced as:

*Desmocerus cribripennis* Horn, 1881:viii; Burke, 1921:451 (habits); Craighead, 1923:87 (larva); Essig, 1926:454 (habits); Hardy and Preece, 1927:63 (habits).

*Desmocerus auripennis cribripennis*; Hatch, 1971; Linsley and Chemsak, 1972:9, *Fig. 1*.  
*Desmocerus aureipennis cribripennis*; Monné & Giesbert, 1995:157.

*Desmocerus cribripennis* bores into red elderberry, *S. racemosa*, along the coastal mountain range from British Columbia to the areas surrounding San Francisco, California. It is recognized by its small, narrow form, long pubescence around the head and pronotum, and the male elytra being entirely dark green, bordered by a thin red margin. A detailed account of the life history of *D. cribripennis* on Vancouver Island is given by Hardy and Preece (1927), and the larvae are described by Craighead (1923).



South of the Columbia River Gorge, in Oregon, populations of *D. cribripennis* are isolated by large distances, and overlap with the range of *D. lacustris*. The latter species is superficially similar in appearance to *D. cribripennis*, but may usually be separated by the male elytra being more extensively covered with red pigmentation. Presently, there is no way to reliably separate females of the latter species, or the males of *D. lacustris* with full elytral coloration, without DNA. The male genitalia of both species are similar, but relatively variable across their geographic ranges compared to other *Desmocerus* species, and difficult to characterize. In this phylogenetic analysis, the two species appear to be easily distinguished by the mitochondrial gene CO1. However, I was unable to obtain DNA from any of the suspected *D. cribripennis* populations south of the Columbia River gorge. More sampling is needed before the specific limits of these populations are fully resolved.

Remarks on the *D. cribripennis* lectotype, and type locality

The *D. cribripennis* lectotype bears only a small label printed “W.T.,” and Horn’s original description (1881: viii) states only that his specimen was “collected by Mr. Morrison in Washington Territory.” The author has had the opportunity to compare the lectotype to the ample *cribripennis* material available for study. Although the male genitalia were not examined, the particular shape and elytral coloration of the lectotype appears to bear the closest resemblance to a series taken from Olympia, Washington. The idea seems plausible, at least, in light of the limited historical evidence known regarding the activities of the collector.

“Mr. Morrison” is H. K. Morrison (1854-1885), a professional insect collector who traveled to the Pacific Northwest between the years of 1879 and 1881, and sold specimens to Dr. Horn (see Essig, 1931: 709 and Anonymous, 1885; cited in Hatch, 1949:4). No field journal, or any other account of the collecting event by Mr. Morrison is known to the present author, and the brief account by Melville Hatch indicates that little is known about Morrison’s collecting itineraries in general. The only apparent

evidence indicating a specific destination of Morrison within Washington is the description of *Choleva decipiens* Horn (1880: 259), in which Horn states that the type was collected at “Olympia, Washington Territory.”

Where are the *D. cribripennis* at Salem, Oregon?

There is a large series in the OSAC, presumably belonging to *D. cribripennis*, taken by Vince Roth in “Salem, Oregon,” from May 8-17, 1954. The males of this population are noticeably smaller than those of the Washington populations, and more closely resemble a few series of *D. cribripennis* from northern California, making it a desirable population to include in the phylogenetic analysis. I made multiple attempts in the spring of 2013 to locate *D. cribripennis* at Salem, where red elderberry is common and abundant both in, and around the city. I inspected plants, and hung pheromone traps at various localities in the Salem Hills, both along creeks and streams and at higher elevation springs (Vitae Spring Rd.). Plants were also inspected at Minto-Brown Island Park, but signs of boring activity were never discovered. Pheromone traps were hung in huge, dense thickets of flowering elderberry, and left for multiple weeks, but turned up empty.

Dr. Roth’s field notes, which are in the possession of his wife, Ms. Barbara Roth, contain no entries between May 2 and June 25, 1954. Ms. Roth notes that he tended to only make entries for collecting trips. It is possible that Roth collected the series near his home. An unpublished autobiography written by Roth in the 60’s, also in the possession of his wife, indicates that on April 15, 1954, Roth lived at Courts Run by a Mrs. Earle. In July, 1954, Roth moved to Rt. 1 Box 587, Salem, Ore. Ms. Roth does not recall the exact locality of the Courts Run house, noting she had only seen it once in 1977, “it was still outside of Salem, with a duck pond and a small house.” Dr. Roth’s life and work has been chronicled by Ubick (1999) and Ubick and Arnaud (2001).

## CONCLUSIONS

An examination of adult anatomy and molecular data from two genes, CO1 mtDNA and 28S rDNA, were used to assess species limits in *Desmocerus* and to generate a phylogenetic hypothesis for the genus. The available evidence suggests that the populations of *Desmocerus* in western North America formerly thought to comprise a single species, *D. aureipennis*, with multiple subspecies, are actually a complex of at least six distinct species. Two of the species in that complex are newly described, and cryptically resemble *D. aureipennis*, and *D. piperi*, respectively. Examinations of the *D. aureipennis* holotype, and the historical evidence related to its origin, indicate that the type locality is likely in, or near the Rocky Mountains of British Columbia, leaving the abundant populations in California historically called *D. aureipennis* without a name.

In the phylogenetic analysis, clades were recovered consistently, and with high support across multiple genes and analytical approaches, leading to a final phylogenetic hypothesis for *Desmocerus* that has some interesting implications. The following is concluded: (1) *Desmocerus* is monophyletic relative to the lepturine outgroups in the study; (2) the two western species groups, *D. californicus* spp. and the *D. aureipennis* complex, form sister clades; (3) a mitochondrial clade representing apparently recently-diverged populations from Haida Gwaii, and the coastal and Cascade ranges of Oregon, is interpreted to comprise the species *D. lacustris* Linsley & Chemsak; (4) *Desmocerus cribripennis* and *D. sympatricus* sp. n. occur in close sympatry in the central Washington Cascades, but apparently do not interbreed, as indicated by distinct mtCO1 lineages. The limited CO1 divergence between *D. sympatricus* and its sister species, *D. piperi*, suggests that the unusual male genitalia present in the former species developed fairly recently, following allopatric isolation, possibly in response to interactions with *D. cribripennis*; and (5) the inferred phylogeny (with *D. aureipennis* and *D. maximus* non-monophyletic) requires more than one instance of host-plant switching between red and blue elderberry.

The final proposed taxonomy is the best hypothesis for species limits in *Desmocerus*, given all the data currently available, and reflects a new layer of complexity to the story of that genus in North America. Some of the inferences, however, may be determined invalid with the addition of more genes or sampling from a wider range of specimens and localities. More research is needed, for example, to decide whether *D. lacustris*, as presently construed, actually represents one species, or is itself a complex of several cryptically-related species. In addition, the relationship between host plant specialization and species limits observed in the Pacific Northwestern *Desmocerus* may have implications for the eastern *D. palliatus*. In that species, some populations are apparently exclusive to either *S. racemosa* or *S. canadensis*, but a full morphological investigation of those populations was outside the scope of this study.

Much remains to be learned of the basic life history of *Desmocerus* species. For example, how does a long-range, generic pheromone work in the closely sympatric populations at Steven's Pass, and what is the role of the male paramere in mating isolation between species? And what about the roles of auditory stridulation and other seemingly anomalous courtship behaviors observed in *D. aureipennis*? Another interesting observation that should be worthy of further study is that the correlation between the use of a healthy, living host plant in *Desmocerus*, and the production of a long-range sexual pheromone appears to be inverse to the patterns observed by Hanks (1999) among species in the cerambycid subfamily Lamiinae.

Finally, several conservation concerns are noted for *Desmocerus* species in the Pacific Northwest. First, the population at the Steven's Pass ski resort in Washington is the only known population of *D. sympatricus*, and lives in close proximity to humans in areas that may easily be slated for construction in the future. A number of unique or important populations known from museum specimens cannot be found, and are potentially extirpated. These include a unique population of *D. cribripennis* in Salem,

Oregon, and two unique populations of *D. aureipennis* in Portland, Oregon, and Camp Sherman, at the head of the Metolius River. The species *D. aureipennis*, as here defined, is now among the rarest species in *Desmocerus*, with only a handful of populations known from specimen data. The only population recently confirmed to be extant is at the peak of Mt. Ashland, where the species occurs along a very narrow elevation range associated with snow-fed springs. The habitat occurs in an area protected for conservation, but it now seems likely that climate change poses a significant risk to the existence of this population. Effort is needed both at institutional and amateur level, to identify any other populations of *D. aureipennis* and assess the risk of this species' extinction.

### REFERENCES – Chapter 3

- Alcaide, M., Scordato, E. S. C., Price, T. D., and D. E. Irwin. 2014. Genomic divergence in a ring species complex. *Nature* 511(7507):83-85. doi:10.1038/nature13285.
- Anonymous. 1878. The Entomologist's Monthly Magazine 14: 215-216. <Full text from [Biodiversity Heritage Library](#)>
- Anonymous. 1885. Obituary notice [H. K. Morrison]. *Entomologica Americana*. 1:100. [<http://www.biodiversitylibrary.org/pdf4/022191300038099.pdf>]
- Arnold, R., 1984. The Endangered Valley Elderberry Longhorn Beetle in the north Sacramento area. Report to North Sacramento Land Company, 400 Slobe Avenue, Sacramento, CA 95815, 10pp.
- Audinet-Serville, J. G. 1835. Nouvelle classification de la famille des longicornes (suite). *Ann. Soc. Entomol. France*, (1)4:5-100.
- Avisé JC, Arnold J, Ball RM Jr, Bermingham E, Lamb T, et al. (1987) Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics* 18: 489–522. doi: 10.1146/annurev.es.18.110187.002421
- Bain, J.F. & J.L. Golden. 2005. Chloroplast haplotype diversity patterns in *Packera pauciflora* (Asteraceae) are affected by geographic isolation, hybridization, and breeding system. *Canadian Journal of Botany-Revue Canadienne De Botanique*, 83:1039-1045.
- Barr, C.B. 1991. The distribution, habitat and status of the Valley Elderberry Longhorn Beetle, *Desmocerus californicus dimorphus*. U.S. Fish and Wildlife Service, Sacramento, 133.
- Barrett, M., M. Donoghue, and E. Sober. 1991. Against consensus. *Syst. Zool.* 40: 486–493.
- Bevan, R., Bryant, D., and B. F. Lang. 2007. Accounting for gene rate heterogeneity in phylogenetic inference. *Systematic Biology* 56(2): 194-205.
- Bezark, L. 2014. A Photographic Catalogue of the Cerambycidae of the World. Accessed October 10, 2014. <https://apps2.cdfa.ca.gov/publicApps/plant/bycidDB/wdefault.asp?w=n>
- Blaisdell, M. D. 1903. Annual field day of the Pacific Coast Entomological Society at Leona Heights, Alameda Co. *Entomol. News*, 14:276. <[Biodiversity Heritage Library](#)>

- Blanchard, C.E. 1845. Histoire des insectes, traitant de leurs moeurs et de leurs métamorphoses en général, et comprenant une nouvelle classification fondée sur leurs rapports naturels. 2:163. <http://archive.org/details/histoirenaturell02blan>
- Bland, J. H. B. 1862. Descriptions of several supposed new species of Cerambycidae in the collection of the Entomological Society of Philadelphia, with observations of some already described. Proceedings of the Entomological Society of Philadelphia, 1:267-276.
- Bland, J. H. B. 1863. Descriptions of a few supposed new species of North American Coleoptera. Proceedings of the Entomological Society of Philadelphia, 2:319-323.
- Boppe, P. L. 1921. Genera insectorum, fam. Cerambycidae: subfam. Disteniinae, Lepturinae, fasc. 178, 119 pp., 8pls.
- Boppe, P. L. 1921. Genera insectorum, fam. Cerambycidae: subfam. Disteniinae, Lepturinae, fasc. 178, 119 pp., 8pls.
- Burke, H. E. 1921. Biological notes on *Desmocerus*; a genus of roundhead borers, the species of which infest various elders. Journal of Economic Entomology 14: 450-452. <[Biodiversity Heritage Library](#)>
- Brunsfeld, S.J., Sullivan, J., Soltis, D.E. & P.S. Soltis. 2001. Comparative phylogeography of northwestern North America. Integrating ecological and evolutionary processes in a spatial context (ed. by J. Silvertown and J. Antonovics), pp. 319–339. Blackwell Science, Oxford.
- Candeze, M. E. 1859. Monographie des Elaterides, Tome Second. Mémoires de la Société royale des sciences de Liège, Volume 14. 543 pp. + 7 pl. <[Google Books](#)>.
- Chevrolat, L. A. A. 1855. Description de vingt et une espèces nouvelles de coléoptères longicornes. Revue et Mag. Zool., (2)7:178-187. <[Biodiversity Heritage Library](#)>
- Chevrolat, L. A. A. 1858. Description de nouvelles espèces de coléoptères. Annales de la Société entomologique de France. ser. 3, t. 6. <[Biodiversity Heritage Library](#)>
- Collinge, S. K., Holyoak, M., Barr, C. B., Marty, J. T., 2001. Riparian habitat fragmentation and population persistence of the threatened valley elderberry longhorn beetle in central California. Biological Conservation 100, 103-113.
- Coville, F. V. 1897. The itinerary of John Jeffrey, an early botanical explorer of western North America. Proceedings of the Biological Society of Washington 11: 57-60. March 23, 1897.
- Craighead, F. C. 1923. North American Cerambycid Larvae. Canadian Department of Agriculture Technical Bulletin 27 (n.s.), 239 pp.

- Croft, H. H. 1872. Miscellaneous Notes. "Notes and queries—*Desmocerus cyaneus*". The Canadian Entomologist, 4:119-120.
- Cuvier, G., 1836. Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux, et d'introduction à l'anatomie compare. v. 6-7. Pt. 1. Atlas. Paris :Fortin, Masson et cie, [1836-49].  
<http://www.biodiversitylibrary.org/item/79115#page/317/mode/1up>
- Davis, A. C. 1931. California Collecting Notes II. Bull. Brooklyn Entomological Society, 26: 187-188.
- Darriba, D., Taboada, G.L., Doallo, R., and D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. [Nature Methods 9\(8\), 772.](#)
- Davis, A. C. and J. A. Comstock. 1924. Larva and pupa of *Desmocerus californicus* (Horn). South. Calif. Acad. Sci., 23: 179-181.
- Dejean, P. F. M. A. 1821. Catalogue de la collection de coléoptères de M. le baron Dejean. Crevot Libr., Paris, France. viii + 136 pp. + 11 pp.
- de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. Pages 57–75 in *Endless forms: Species and speciation* (D. J. Howard, and S. H. Berlocher, eds.). Oxford University Press, New York.
- de Queiroz, Kevin. 2007. Species concepts and species delimitation. *Systematic Biology* 56(6): 879-886. ISSN: 1063-5157 print / 1076-836X online. DOI: 10.1080/10635150701701083.
- Doane, R. W., E. C. Van Dyke, W. J. Chamberlin and H. E. Burke. 1936. *Forest Insects*. 463 pp. McGraw-Hill, New York. <[Hathi Trust Digital Library](#)>
- Douady, C.J., Delsuc, F., Boucher, Y., Doolittle, W.F., Douzery, E.J.P., 2003. Comparison of Bayesian and maximum likelihood bootstrap measures of phylogenetic reliability. *Mol. Biol. Evol.* **20**, 248–254. DOI: 10.1093/molbev/msg042
- Eberhard, W. G. 2004. Rapid divergent evolution of sexual morphology: comparative tests of antagonistic coevolution and traditional female choice. *Evolution*, 58(9):1947-1970.
- Eberhard, W. G. 2010. Evolution of genitalia: theories, evidence, and new directions. *Genetica* 138:5–18. DOI 10.1007/s10709-009-9358-y
- Essig, E. O. 1931. *A history of entomology*. Macmillan, New York. vii + 1209 pp.; 263 figs.



- Fabricius, J. C. 1775. *Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus.* Flensburgi et Lipsiae, 832 pp.
- Fabricius, J. C. 1781. *Species insectorum exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin adiectis observationibus, descriptionibus.* Hamburgi et Kilonii, 1: viii + 552 pp.
- Fisher, W.S. 1921. A new cerambycid beetle from California. *Proceedings of the Entomological Society of Washington*, 23(9): 206-208.
- Fitch, A. 1845. Insects injurious to vegetation – No. 1. *Am. Q. J. Agric. And Sci.*, 1:250-254.
- Forster, J. R. 1771. *Novae species insectorum, centuria I.* London, 100 pp.
- Galbreath KE, Hafner DJ, Zamudio KR, Agnew K. 2010. Isolation and introgression in the Intermountain West: contrasting gene genealogies reveal the complex biogeographic history of the American pika (*Ochotona princeps*). *Journal of Biogeography* 37: 344–362. doi: 10.1111/j.1365-2699.2009.02201.x.
- Gardiner, L. M. 1970. Biological notes on some Nearctic Lepturinae (Coleoptera: Cerambycidae). *The Pan-Pacific Entomologist*, 46:284-288.
- Garnett, R. T. 1918. An annotated list of the Cerambycidae of California. *The Canadian Entomologist*, 50: 172-177. <[Biodiversity Heritage Library](#)>
- Goldman, E. H. 1933. Comparisons of the mouthparts of adult longhorn beetles with reference to their food (Coleoptera: Cerambycidae). *Trans. Amer. Entomol. Soc.*, 59: 85-102.
- Green, P. 2009. Phrap, version 1.090518. <http://phrap.org>.
- Green, P. and Ewing, B. 2002. Phred, version 0.020425.c . <http://phrap.org>.
- Guindon, S., and O. and Gascuel. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood". *Systematic Biology* 52: 696-704.
- Halstead, J. A., and J. A. Oldham. 1990. Revision of the Nearctic *Desmocerus* Audinet-Seville with emphasis on the federally threatened valley elderberry longhorn beetle (Coleoptera: Cerambycidae). Environmental Section Staff Report No. 90-002, Kings River Conservation District, Fresno, CA.
- Halstead, J. A., and J. A. Oldham. 2000. New distribution records for the elderberry longhorn beetle *Desmocerus californicus* Horn (Coleoptera: Cerambycidae). *The Pan-Pacific Entomologist* 76(1): 74-76.

- Hardy, G. A. 1926. Cerambycidae of Vancouver Island (Preliminary annotated list). B.C. Prov. Mus. Rep., 1925:24-33, pls. 4-5. <[Google Books](#)>
- Hardy, G. A. and W. H. A. Preece. 1927. Additional notes on some Cerambycidae (Col.) from Vancouver Island, B. C. *The Pan-Pacific Entomologist*, 4:61-67.
- Harris, T. W. 1841. A Report on the Insects of Massechussettes Injurious to Vegetation. Cambridge: Folsom, Wells, and Thurston. 459 pp. <[Biodiversity History Library](#)>
- Harvey, A. G., 1947. "John Jeffrey: Botanical Explorer", in The Siskiyou Pioneer in Folklore, Fact and Fiction and Yearbook, Siskiyou County Historical Society. pp. 17-19, 39.
- Hatch, M. H. 1949. A century of entomology in the Pacific Northwest. University of Washington Press. Seattle. 43 pp.
- Hatch, M. 1971. The beetles of the Pacific Northwest. Part V. Rhipiceroidea, Sternoxi, Phytophaga, Rhynchophora, and Lamellicornia. University of Washington Publications in Biology, 16. <http://hdl.handle.net/1957/14350>
- Hausdorf, Bernhard. 2011. Progress Toward a general species concept. *Evolution* 65(4): 923-931.
- Hennig, W. 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana.
- Herrick, G. W. 1923. Notes on the biology of *Desmocerus palliatus*. *Journal of Economic Entomology*, 16: 546-548, pl. 7.
- Hess, W. N. 1917. The chordotonal organs and pleural discs of cerambycid larvae. *Annals of the Entomological Society of America*, 10:63-74. <[Biodiversity Heritage Library](#)>
- Hildebrandt D. A., Maddison D. R. 2011. A new species of Bembidion Latrielle 1802 from the Ozarks, with a review of the North American species of subgenus Trichoplataphus Netolitzky 1914 (Coleoptera, Carabidae, Bembidiini). In: Erwin T (Ed) Proceedings of a symposium honoring the careers of Ross and Joyce Bell and their contributions to scientific work. Burlington, Vermont, 12–15 June 2010. *ZooKeys* 147: 261–275. doi: 10.3897/zookeys.147.1872
- Hoare, M. E. 1976. The Tactless Philosopher: Johann Reinhold Forster (1729-98). Melbourne, The Hawthorn Press. 417 pp.
- Horn, G.H. 1879, *In*: Proceedings of the American Entomological Society, 1879:xxx. <[Biodiversity Heritage Library](#)>

- Horn, G. H. 1881. *In Monthly Proceedings*. Two new species of *Desmocerus*. Transactions of the American Entomological Society, 9: vii-viii.
- Hubweber, L., & M. Schmitt. 2010. Differences in genitalia structure and function between subfamilies of longhorn beetles (Coleoptera: Cerambycidae). *Genetica*. 2010 Jan; 138(1):37-43. doi: 10.1007/s10709-009-9403-x.
- Huelsenbeck, J. P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17:754-755.
- Huelsenbeck, J. P., F. Ronquist, R. Nielsen, and J. P. Bollback. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294:2310–2314.
- Huelsenbeck, J. P., B. Larget, R. E. Miller, and F. Ronquist. 2002. Potential applications and pitfalls of bayesian inference of phylogeny. *Systematic Biology* 51:673–688.
- Huxel, G. R. 2000. The effect of the Argentine ant on the threatened valley elderberry longhorn beetle. *Biological invasions* 2, 81-85.
- ICZN (1999) International Code of Zoological Nomenclature, Fourth Edition, adopted by the International Union of Biological Sciences. International Trust for Zoological Nomenclature, London, xxix + 306 pp.
- Jarvis, K.J. & M.F. Whiting. 2006. Phylogeny and biogeography of ice crawlers (Insecta: Grylloblattodea) based on six molecular loci: designating conservation status for Grylloblattodea species. *Molecular Phylogenetics and Evolution*, 41:222-237.
- Johnstone, J. T. 1939. John Jeffrey and the Oregon Expedition. Notes from the Royal Botanical Garden of Edinburgh 20(96): 1-53. <[Full text online](#)>
- Joplin, L. 1995. Uncle Sam's Cabins: A visitor's guide to historic U.S. Forest Service Ranger Stations of the West. Bend, Oregon. Wilderness Associates. 257 pp. <[Partial Preview from Google Books](#)>.
- Kjer, K. 2004. Aligned 18S and insect phylogeny. *Systematic Biology* 53(3):506-514. <[Link to Full Text](#)>
- Lakner C, Van Der Mark P, Huelsenbeck JP, Larget B, Ronquist F. 2008. Efficiency of MCMC tree proposals in Bayesian phylogenetics. *Systematic Biology* 57:86–103
- Lang, Frank A. 2006. John Jeffrey in the Wild West: Speculations on his life and times (1828-1854?). *Kalmiopsis* 13: 1-12.  
<http://www.npsoregon.org/kalmiopsis/kalmiopsis13/lang.pdf>
- Lange, Erwin F. 1967. John Jeffrey and the Oregon Botanical Expedition. *Oregon Historical Quarterly* 68: 111-124.

- LeConte, J. L. 1857. Report upon Insects collected on the survey. In, Report of Explorations and Surveys to ascertain the most practicable and economical route for a railroad from the Mississippi river to the Pacific Ocean. Made under the Direction of the Secretary of War, in 1853-5, according to Acts of Congress of March 3, 1853, May 31, 1854 and August 5, 1854, 12:1-72, 2 pls. <[Making of America Books](#)>
- Linsley, E. G. 1959. Ecology of Cerambycidae. *Annual Review of Entomology* 4: 99-138. <[PDF](#)>
- Linsley, E.G. and J.A. Chemsak. 1972. Cerambycidae of North America. Part VI. No. 1. Taxonomy and Classification of the Subfamily Lepturinae. University of California Publications in Entomology 69, xiii+138 pp, 2 pl.
- Luo, A. R., Zhang, Y. Z., Qiao H. J., Shi, W. F., Murphy, R. W., and C. D. Zhu. 2010. Outgroup selection in tree reconstruction: a case study of the family Halictidae (Hymenoptera: Apoidea). *Acta Entomologica Sinica*, 53(2): 192-201.
- Maddison, D. R. 1991. Discovery and importance of multiple tree islands of most-parsimonious trees. *Systematic Zoology*, 40:315-332.
- Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. *Systematic Zoology*, 33: 83-103.
- Maddison, W. P. and D. R. Maddison. 2011a. Mesquite: a modular system for evolutionary analysis. Version 2.75 <http://mesquiteproject.org>
- Maddison, D. R. and W. P. Maddison. 2011b. Chromoseq: a Mesquite module for analyzing sequence chromatograms. Version 1.0. <http://mesquiteproject.org/packages/chromaseq>.
- Maddison, D. R. 2008. Systematics of the North American beetle subgenus *Pseudoperiphus* (Coleoptera: Carabidae: Bembidion) based upon morphological, chromosomal, and molecular data. *Annals of Carnegie Museum* 77: 147–193. doi: 10.2992/0097-4463-77.1.147
- Maddison, D. R. 2012. Phylogeny of Bembidion and related ground beetles (Coleoptera: Carabidae: Trechinae: Bembidiini: Bembidiina). *Molecular Phylogenetics and Evolution* 63: 533–576. doi: 10.1016/j.ympev.2012.01.015
- Michelsen, A. 1963. Observations on the sexual behavior of some longicorn beetles, subfamily Lepturinae. *Behavior* 22 (1/2): 152-166. <http://www.jstor.org/stable/4533068> .

- Miller, M. P., Bellinger, M. R., Forsman, E. D. & S. M. Haig. 2006, Effects of historical climate change, habitat connectivity, and vicariance on genetic structure and diversity across the range of the red tree vole (*Phenacomys Zongicaudus*) in the Pacific Northwestern United States. *Molecular Ecology* 15:145-159. doi: 10.1111/j.1365-294X.2005.02765.  
[http://www.fs.fed.us/pnw/pubs/journals/pnw\\_2006\\_miller001.pdf](http://www.fs.fed.us/pnw/pubs/journals/pnw_2006_miller001.pdf)
- Monné, M.A. & E. F. Giesbert. 1994. *Checklist of the Cerambycidae and Disteniidae (Coleoptera) of the Western Hemisphere*. Wolfsgarden Books, Burbank, 409 pp.
- Morris, F. J. A. 1915. Report on insects of the year. Division No. 5, Port Hope District. 45<sup>th</sup> Annual Report of the Entomological Society of Ontario, pp. 20-22. <[Biodiversity Heritage Library](#)>
- Murray, A. 1853. "On some Insects from the Rocky Mountains, received from the Botanical Expedition to Oregon under Mr. Jeffrey" in: *Proceedings of the Royal Physical Society of Edinburgh*. February 12, 1853. *The Zoologist* 11: 3893-3895. <[Google Books](#)>
- Ray, A.M., Swift, I.P., McElfresh, J.S., Alten, R.L., and J.G. Millar. 2012. (R)-desmolactone, A female-produced sex pheromone component of the cerambycid beetle *Desmocerus californicus californicus* (subfamily Lepturinae). *J. Chem. Ecol.* 38:157-167.
- Ray, A. M., Arnold, R. A., Swift, I., Schapker, P. A., McCann, S., Marshall, C., McElfresh, J. S., and J. G. Millar. 2014. (R)-Desmolactone is a sex pheromone or sex attractant for the endangered Valley Elderberry Longhorn Borer *Desmocerus californicus dimorphus* and several congeners (Cerambycidae: Lepturinae). *In prep.* Submitted for Publication.
- Richardson, B. A., Brunsfeld, J., & N. B. Klopfesnstein. 2002. DNA from bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). *Molecular ecology*, 11, 215-227.
- Rohwer, S. A. 1917. The North American wasps of the subgenus *Pemphredon* Latreille. *Bulletin of the Brooklyn Entomological Society* 12(5) 98-102. [Link to text](#)
- Ronquist, F. and A. R. Deans. 2010. Bayesian Phylogenetics and its influence on insect systematics. *Annu. Rev. Entomol.*, 55:189-206. DOI: 10.1146/annurev.ento.54.110807.090529

- Ronquist, F. and J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572-1574.
- Rosenfeld, J. A., Payne, A., & R. DeSalle. 2012. Random roots and lineage sorting. *Molecular Phylogenetics and Evolution*, 64: 12-20.
- Sanderson, M. J. and H. B. Shaffer. 2002. Troubleshooting molecular phylogenetic analyses. *Ann. Rev. Ecol. Syst.*, 33: 49-72.
- Sanmartin, I., Enghoff, H., and F. Ronquist. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society*, 73: 345–390. doi:10.1006/bijl.2001.0542, available online at <http://www.idealibrary.com>.
- Schoville, S.D. & G.K. Roderick. 2010. Evolutionary diversification of cryophilic *Grylloblatta* species (Grylloblattodea: Grylloblattidae) in alpine habitats in California. *BMC Evolutionary Biology*, 10, 163.
- Schoville, S.D., Stucky, M., & G.K. Roderick. 2011. Pleistocene origin and population history of a neoendemic alpine butterfly. *Molecular ecology* 20, 1233-1247. doi: 10.1111/j.1365-294X.2011.05003.x
- Silfverberg, H. 1984. The coleopteran genera of Dejean 1821. 3. Curculionoidea and Chrysomeloidea. *Annales Entomologici Fennici* 50: 61-63
- Smith, A. B. 1994. Rooting molecular trees: Problems and Strategies. *Biol. J. Linn. Soc.*, 51: 279-292.
- Spellman, G.M., Riddle, B., & J. Klicka. 2007. Phylogeography of the mountain chickadee (*Poecile gambeli*): diversification, introgression, and expansion in response to Quaternary climate change. *Molecular Ecology*, 16: 1055-1068.
- Stamatakis, A. 2006. RAxML-VI-HPC: Maximum Likelihood-based Phylogenetic Analyses with Thousands of Taxa and Mixed Models. *Bioinformatics* 22(21):2688-2690.
- Stamatakis, A., Hoover, P., and J. Rougemont. [A Rapid Bootstrap Algorithm for the RAxML Web-Servers, Systematic Biology](#), 75(5): 758-771, 2008
- Stevenson, C. 1905. Notes on the season of 1904 (Western Quebec). 35<sup>th</sup> Ann. Rep. Entomol. Soc. Ont., 1904, pp. 90-91. <[Google Books](#)>
- Švácha P., Danilevsky M. L., 1987. Cerambycoid larvae of Europe and Soviet Union. (Coleoptera, Cerambycoidea). Part I-II. *Acta Univ. Carol. (Biol.)* 30[1986]: 1–176.

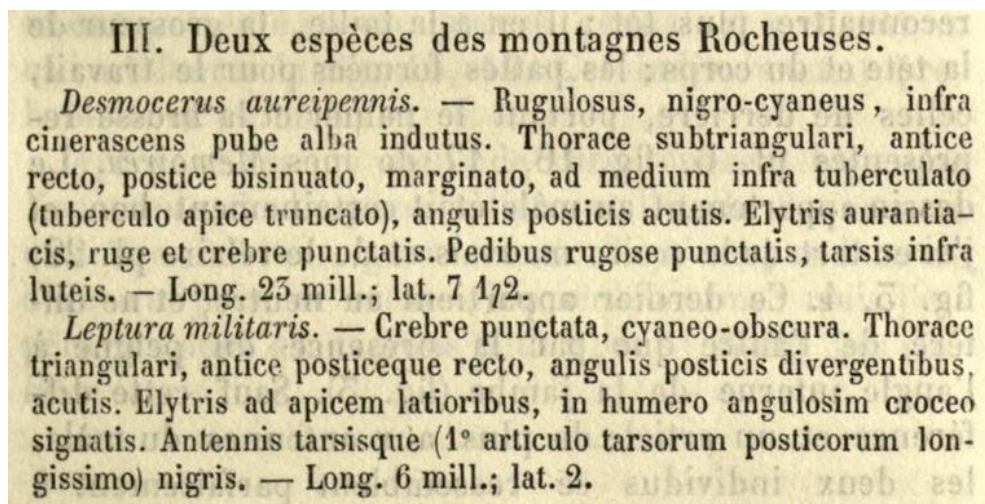
- Švácha P., Danilevsky M. L., 1989. Cerambycoid larvae of Europe and Soviet Union. (Coleoptera, Cerambycoidea). Part III. Acta Univ. Carol. (Biol.) 32[1988]: 1–205. [<PDF>](#)
- Swofford, D. L. 2002. PAUP\*. Phylogenetic Analysis Using Parsimony (\*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Sýkorová, M. 2008. Molecular phylogeny of the subfamilies Spondylidinae and Lepturinae (Coleoptera: Cerambycidae) based on mitochondrial 16S rDNA. Bachelor's thesis, Faculty of Natural Sciences, South Bohemian University, Ceske Budejovice. [<PDF>](#)
- Talley, T. S. 2005. Spatial ecology and conservation of the Valley elderberry longhorn beetle, Ph.D. Dissertation, University of California, Davis, CA.
- Talley, T. S., Fleishman, E., Holyoak, M., Murphy, D. D., and A. Ballard. 2007. Rethinking a rare-species conservation strategy in an urban landscape: The case of the valley elderberry longhorn beetle. *Biological conservation* 135: 21-32.
- Tiffney, B. H. 1985. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. *Journal of the Arnold Arboretum* 66:243-273.
- Townsend, C. H. T. 1884. Notes on some Coleoptera taken in South Louisiana. *Psyche*, 4:219-222. [<PDF>](#)
- Townsend, C. H. T. 1885. A list of Coleoptera collected in Louisiana, on or south of Parallel 30. *The Canadian Entomologist*, 17:66-73. [<Biodiversity Heritage Library>](#)
- Ubick, D. 1999. Obituary: Vincent D. Roth (1924--1997). *Pan-Pacific Entomologist*, 75(3):121-129.
- Ubick, D. & P.H. Arnaud. 2001. Vincent Daniel Roth (1924--1997): scientific publications, catalog of arachnid and plant taxa, and chronology. *Myia*, 6:169-185.
- USFWS, 1980. Listing the Valley elderberry longhorn beetle as a threatened species with critical habitat. Friday, August 8, 1980. Sacramento, CA. Federal Register 45, 52803-52807.
- USFWS, 1984. Recovery Plan for the Valley Elderberry Longhorn Beetle. U.S. Fish and Wildlife Service, Portland, OR.
- USFWS, 1999. Conservation Guidelines for the Valley Elderberry Longhorn Beetle. US. Fish and Wildlife Service, Sacramento, CA.

- USFWS, 2012. Endangered and Threatened Wildlife and Plants; Removal of the Valley Elderberry Longhorn Beetle From the Federal List of Endangered and Threatened Wildlife; Proposed Rule. Tuesday, October 2, 2012. Federal Register 77(191):60238-60276. <http://www.gpo.gov/fdsys/pkg/FR-2012-10-02/pdf/2012-23843.pdf>
- Webb, J. L. 1905. Description of a new species of *Desmocerus* with a synoptic table of the genus. *Proceedings of the Entomological Society of Washington* 7(2-3):104-105.
- Wheeler, W. C. 1990. Nucleic acid sequence phylogeny and random outgroups. *Cladistics*, 6: 363-367.
- Wheeler, W. C., and K. Pickett. 2008. Topology-Bayes versus Clade-Bayes in phylogenetic analysis. *Mol. Biol. Evol.* 25:447–453.
- White, R. E. 1985. A field guide to the beetles. The Peterson Field Guide Series. Limited Edition Bound in Leather. Houghton Mifflin Company, Boston, 368 pp.
- Whitehead, P. J. P. 1978. A guide to the dispersal of zoological material from Captain Cook's voyages. *Pacific Studies* 2:52–93
- Wiley, E. O. and Lieberman, B. S. (2011) Species and Speciation, in *Phylogenetics: Theory and Practice of Phylogenetic Systematics*, Second Edition, John Wiley & Sons, Inc., Hoboken, NJ, USA. doi: 10.1002/9781118017883.ch2
- Woods, P. and J. Woods, 1999. "The Oregon Expedition 1850-1854: John Jeffrey and his Conifers", *Acta Horticulturae* 615: IV International Conifer Conference.
- Zink, R. M. & G. F. Barrowclough. 2008. Mitochondrial DNA under siege in avian phylogeography. *Molecular Ecology*, 17:2107-2121.



## APPENDIX A –Discussion on the *D. aureipennis* holotype and type locality

The holotype of *D. aureipennis*, with its dense white abdominal pubescence, uniquely-shaped black parameres lacking dorsal setae, and transparent hindwings with a distal dark area, is easily assignable to those populations of large, blue elderberry-boring *Desmocerus* that occur throughout the Coast and Cascade Ranges of Northern California, Oregon and Washington. However, the specific type locality could become important, particularly if at some later date one or more of the several disjunct populations of *D. aureipennis* are discovered to actually represent distinct species. At present, the stated type locality of *D. aureipennis*, “montagnes Rocheuses” or “the Rocky Mountains, presents a dilemma. While the range of *D. aureipennis* is now known to extend into the Cascades of Northern Washington, and possibly into the Rockies of Idaho (Halstead and Oldham, 1990—unverified by author), the second of the “Deux espèces des montagnes Rocheuses” that Chevrolat (1855) described (**Fig. 3.38**), *Grammoptera militaris*, is still only known from the Great Valley of California. Since



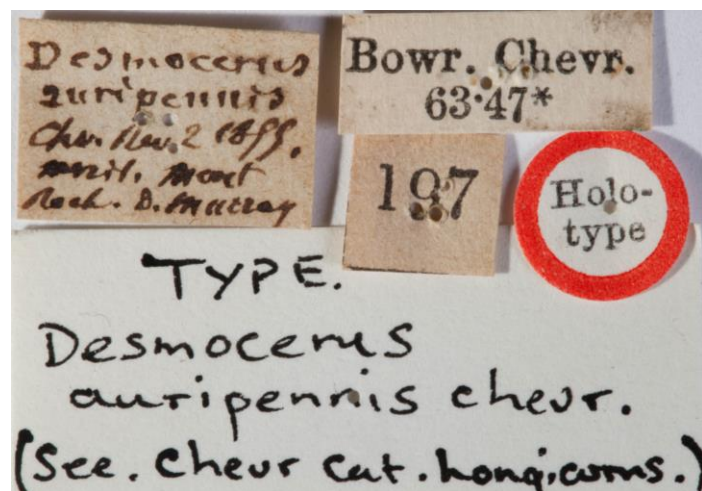
**Fig. 3.38.** Original description of *Desmocerus aureipennis* and *Leptura militaris*.

populations matching the holotype of *D. aureipennis* also occur in the northern California Coast Range, it would be reasonable to suspect that “the Rocky Mountains” is either a misnomer, or a mistake. Another intriguing possibility, however, is that *D.*

*aureipennis* was actually first collected in the Rockies (as defined in 1855), but in some obscure province where a disjunct population of *G. militaris* awaits rediscovery. In this section, I consider the historical evidence associated with the *D. aureipennis* holotype, and make the argument that the most likely origin of the holotype is from a range of mountains in British Columbia east of the Fraser River.

#### *Evidence from the Original Description and Holotype*

The original description of *D. aureipennis* is a very brief note in the *Revue et Magasin de Zoologie* (1855), appearing under a section “Deux espèces des montagnes Rocheuses” [Two species from the Rocky Mountains]. It records a male specimen 23 millimeters in length by 7.5 mm “infra cinerascens pube alba indutus” [clothed underneath with an ashy white pubescence]. I have verified that the holotype matches this description exactly. The holotype label data is given in **Figure 3.39**. The species name, misspelled on the label, is followed by a citation to the original description. The label reads: “*Desmocerus auripennis* Chv. Rev 2, 1855. Avril, Mont Roch. D. Murray.” (Reported incorrectly in Halstead and Oldham, 1990, as “Nov 2 1899,” (undecipherable word), ‘Mont Roch., B. Matlay.’”).



**Figure 3.39.** Labels associated with the *D. aureipennis* holotype specimen.

The holotype label indicates that the specimen was obtained by a collector named Murray. In pursuit of corroborative evidence, a fortuitous clue arises in Chevrolat's second, more detailed description of *D. aureipennis* (1858: 325, pl. 8 fig. 6). In that article, the author acknowledges that the specimen had been given to him by M. [Monsieur] Andrew Murray, referring to Chevrolat's friend, the mammologist and famed Darwin critic, Reverend Andrew Dickson Murray (1812-1878) of Edinburgh, Scotland (see Anonymous, 1878). From this starting point, though nothing may be proved definitely, there emerges a surprising story which appears to narrow considerably the range of localities from which the *D. aureipennis* holotype might have been collected. In the following three sections are presented: (1) a broad overview of relevant historical evidence from which are extracted, (2) a specific set of dates and localities that define the contours of the most likely type locality, followed by (3) some concluding memorabilia of general historical interest.

#### *Early Entomological Expeditions to the Pacific Northwest*

How might the Rev. Murray have come across his rocky mountain specimen? By 1855, only a small handful of expeditions to the Pacific Northwest are known which had produced any insects. Eschscholtze, Mannerheim, and Motschulsky had described 540 beetle species taken from present-day Alaska during the early Russian navy expeditions of 1823-1826, and a small number of species had also been described from specimens taken around the Columbia River by Peter Townsend in the 1830's (see LeConte, 1857 and Hatch, 1949). LeConte had acquired all of the beetles taken in the United States Exploring Expedition under Captain Charles Wilkes, as well as those taken by James G. Cooper, George Suckley, and James Gibbs during the "explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi river to the Pacific Ocean made under the Direction of the Secretary of War, in 1853-, according to Acts of Congress of March 3, 1853, May 31, 1854 and August 5, 1854." But none of those collectors had ventured as far north as the Rockies. In his report on the species

taken from that latter expedition, LeConte (1857) detailed these early entomological ventures from which presumably all, or nearly all species known to the Pacific Northwest had resulted. Both LeConte and Hatch, however, overlooked the story of one collector, from an unlikely province, who had already made his mark. That man, ultimately despised in his time by the few who knew of him, but later to become something of a mythological figure among botanists, was John Jeffrey, collector for the Oregon Botanical Association of Edinburgh, Scotland. Andrew Murray was the secretary for this Association, and chief promoter of Jeffrey's secondary mission while in the Oregon country, the collection of beetles.

*John Jeffrey and the Oregon Botanical Association*

The published proceedings of yet another organization, *The Royal Physical Society of Edinburgh*, describe a presentation by Andrew Murray, Esq., W.S., delivered February 12, 1853, titled *On some Insects from the Rocky Mountains, received from the Botanical Expedition to Oregon under Mr. Jeffrey* (Murray, 1853). In the presentation, Murray is said to have explained that, while the principal object of the expedition was to retrieve new conifer seeds for England, the collector had also been instructed to take beetles. There had been a general disappointment thus far in Jeffrey, who as a 21 year-old gardener's assistant at the Royal Botanical Gardens, had been hired for his enthusiasm, and skills as a tree-climber, but not as a naturalist. Still, Murray was able to showcase a number of beetle specimens that Jeffrey collected on his way from Hudson's Bay to Fort Vancouver. These were divided into three lots, those taken "near York Factory and on the way to the Rocky Mountains, a few taken at Jasper House on their east flank, and the rest on the west flank." Unfortunately, only a few of the more interesting specimens are described in detail in the proceedings:

"Among them were a few specimens of a representative of our blister-fly, and next to these, on coloured paper, was placed the common blister-fly of Europe. A considerable number of these beetles was received, in fact, a greater proportion of them than of any other species; from which it was inferred by Mr. M. that they are

found in large numbers, in the same way as they are in Europe, and that when a great empire shall have grown up on the west of the Rocky Mountains, the apothecaries of its cities would be supplied with this essential article from their own hills.” (p.3894)

However, no specific tally is given, nor mention of individual specimen records. While the actual presence of longhorn beetles at the table is not confirmed, the article nevertheless establishes a definite link between Chevrolat, Murray, and a beetle collector in the Pacific Northwestern Rockies.

Fortunately, we now have a surprising amount of information on Jeffrey and the Oregon Botanical Association that adds a far deeper resolution to the question of the *D. aureipennis* type locality. At the turn of the 20th century, Frederick Coville had come across an obscure reference to Jeffrey's early travels in the Rocky Mountains, in Hooker's original description of *Pinus jeffreyi*. While consulting Jeffrey's herbarium specimens at the Royal Botanical Gardens in Edinburgh, Coville discovered in the archives a detailed minute book of the Oregon Botanical Association, and many other letters and circulars related to the Expedition. Coville (1897) made a detailed sketch of Jeffrey's itinerary as he travelled for four years around western North America, from when he first landed at Hudson's Bay in 1850 and travelled by foot across Canada, to Fort Vancouver, and eventually to the Sierra Nevadas of California, and beyond.

“All this distance I walked on snow shoes, the snow being on average 2 feet deep. The distance from Cumberland to Jasper House is 1200 miles. During this journey I slept with no other covering than that found under the friendly Pine, for the space of 47 nights, on several occasions the thermometer standing from 30 to 40 below zero. I found no bad effects from exposure, the only thing that happened to me, was that once or twice I got slightly frost bit; that was nothing uncommon amongst us, and little cared for.” (Letter from Jeffrey to J. H. Balfour, dated April 7, 1851 – Page 60 of the OBA minute book)

Later, Johnstone (1939) substantially augmented our knowledge of Jeffrey's activities and itinerary, with a complete list of known herbarium samples, a summary of the contents of each shipment sent by Jeffrey to the Association, and other notes accompanied by a complete bibliography of known citations to Jeffrey. Additional

notes on Jeffrey's life and times have also been added by Harvey (1947), Lange (1967), Woods and Woods (1999), and Lang (2006). In all of the available sources, both primary and secondary, no specific localities or field notes pertaining to beetles are to be found. However, the intervals during which Jeffrey collected insect specimens are known, and his itinerary and field notes during these times may be used to establish a specific boundary for likely origin of the *D. aureipennis* type.

*The Most Likely Range of the D. aureipennis Type Locality*

John Jeffrey sent back to the Oregon Botanical Association a series of boxes containing herbarium specimens—with corresponding dates and localities—taken from various stages of his collecting excursions through western North America. Some boxes are known to have contained insects, and other boxes are known to have *not* contained insects. Lacking any other information or evidence to the contrary, the *D. aureipennis* holotype specimen is now hypothesized to have originated from a range that is defined by those parameters. We know from the OBA Minute Book that of the 10 boxes shipped by Jeffrey between the years 1851 and 1853, only two were received that are said to have contained insect specimens, and these were precisely the boxes pertaining to Jeffrey's travels through the Rocky Mountains and adjacent ranges of British Columbia and northern Washington. The evidence associated with these boxes are outlined below, and conclude with a list of localities (Table 3.5) that likely include or approximate the area of the *D. aureipennis* type locality.

The first shipment (**Box 1** of 10), received in November of 1851, contained “a pill bottle and small box” of the beetles taken from Jasper house, and the east flank of the Rocky Mountains of British Columbia (OBA Minute Book, p. 64). In a letter to Professor Balfour on April 7, 1851 (transcribed in full by Johnstone, pp. 8-10), Jeffrey states that he had collected “a good many Beetles,” since arriving at that place, before proceeding west to Fort Vancouver. **Box 2** never arrived, but **Box 3**, sent from San Francisco and opened at a meeting of the OBA on August 24, 1852, is also said to have contained a

small bottle and box of beetles. From the San Francisco shipping locality, it would seem that the beetles in Box 3 could have been derived from nearly anywhere. However, a letter sent to the subscribers of the Association, giving the full list of seeds and field notes received in that shipment, indicates that all of the contents of Box 3 were collected in the general vicinity of Vancouver, British Columbia, between there and Mt. Baker in northern Washington, and as far north as the 50<sup>th</sup> parallel in the Rocky Mountains east of the Fraser River (Minute Book, p. 76). That list, partially transcribed as **Table 3.5** (with some irrelevant botanical notes excluded), indicates the most likely range from which the *D. aureipennis* type was first collected. The collections made in late July, at high elevations in the mountains east of the Fraser River, correspond with the typical habitat and flight periods of *D. aureipennis*, and its congener *D. maximus*, throughout their known ranges. Further details on the specific routes used by Jeffrey as he travelled between the points indicated in the table are given by Coville (pp. 58-59) and Johnstone (pp. 11-12). Johnstone lists some additional herbarium specimens taken in the vicinity of Mt. Baker, in early September 1851, but these are not given in the contents of Box 3.

The specimens Jeffrey collected between Vancouver Island and northern California from 1851 -1852 were shipped in **boxes 4 - 6**, but these contained no insects. (**Box 4** was in the form of a letter containing just a small bag of seeds, and the full contents of boxes 5 and 6 are listed in Johnstone, p. 16-21) On April 15, 1853, Murray wrote a disparaging letter to Jeffrey in which he writes “you take no notice of beetles” (OBA minute book, p. 99), and in another entry in the minute book, for June 20, 1853 (p. 108) “the secretary stated that the Coleopterists were complaining that no beetles had come in the last 3 boxes” (referring to shipments 4-6). Later correspondences from Jeffrey to Balfour, in which Jeffrey describes the contents of **shipment 9**, indicate an attempt was made to send beetles collected from Northern California (p. 54 of transcribed letters), but **shipments 7, 8 and 9** never arrived in Scotland (see Woods and Woods, 1999:4), and the last box (**10**) consisted of a just a small packet of seeds.

**Table 3.5.** Localities visited by John Jeffery in the Rocky Mountains in 1851, based on a complete inventory of herbarium specimens in Box 3. These localities likely include or approximate the type locality of *D. aureipennis*. Taxon names, specimen numbers (#), and field notes are from list enclosed in the box by John Jeffrey. Transcribed (in part) by Schapker from a circular sent to the subscribers of the Oregon Botanical Association, dated September 4, 1852 (OBA Minute Book, p. 76).

1851	Locality	Lat., El.	Taxon	#	Notes
-----	Near the Kontani River	49° 20", 3400 ft.	Erythronum	49	Growing in the crevices of granite rocks.
May	Near Kontani River		Lupinus.	46	Growing on the margin of a lake on sandy soil. (Few seeds)
May 13	Columbia, near Colville		Scilla, Sp.	21	Found on dry sand-banks; height two feet; flowers in umbels; dark blue. (Not many seeds).  This pretty little plant is only found in dry arid places, growin on pure sand. The indians eat its roots, and consider it to be one of the Great Spirit's greatest gifts to them. The Indian name is Petlum asd Ilse-ne-mare. The roots have an agreeable flavour when boiled, rather bitter. I have no doubt that it will prove to be an excellent tonic. Flowers, rose, large; leaves about an inch long, narrow and awl-shaped. (Not many seeds).
June 16	Columbia		Lewisia rediviva	32	
July 9	Forks of Okinagon River	49°	Pedicularis	60	(few seeds)  This plant resembles a Sedum in its appearance. It is found growing on dry sandy soil; the flowers are large, white, and produced in lax umbels; the plant is perennial, with strong running roots. (Few seeds)
July 15	Seme-ke-mele River	49°		177	Flowers yellow; resembles <i>A. canadensis</i> , of which it may be a variety. (Few seeds)
July 15	Seme-ke-mele River		Aquilegia	178	[etc.]
July 19	Campment-des-Femmes	49° 51", 6000ft.	Claytonia	180	[etc.]
July	Near Campment-des-Femmes	49° 50", 6000 ft.	Pentstemon	183	[etc.]
July	Campment-des-Femmes		Pentstemon	184	Near the base of the mountain. Perennial. Along the bank of a small stream on clay soil. (Few seeds).
July 20	Summit of Manson's Mnt., E. of Fraser's R.		Penstemon	188	[etc.]
July	Summit of Manson's Mnt., E. of Fraser's R.	50° 23", 7000 ft.	Compositae	185	[etc.]



Table 3.5 *continued*

July 29	Mullachard, Vancouver's Is.		Malvaceae	280	Found growing in moist prairies; [etc.]
July	Vancouver's Island		Triteleia ?	374	[etc.]
July	Vancouver's Island		Allium, sp.	376	[etc.]
July	near Victoria, Vancouver's Island		Lupinus, sp.	375	[etc.]
August	Vancouver's Island			400	[etc.]
Aug. 11	Banks of Fraser's River, near Fort Hope		Gentiana	260	
Sept. 17	Fraser's River		Saxifraga	200	[etc.]
Sept. 20	Mountains east of Fraser's River	Lat. 50°, 6000 ft.	Rhododendron?	206	[etc.]
Sept. 20	Mountains east of Fraser's River	Lat. 50°, 8000 ft.	Rhododendron?	207	[etc.]
-----	Mountains east of Fraser's River		Spiraea?	193	Growing at the margin of perpetual snows; flowers white. Perennial. (Few seeds).
Sept.	Mountains east of Fraser's River		Saxifragaceae	201	By the margins of small streams; near the region of perpetual snow. Perennial. (Leptarrena pyrifolia, Br. ?)
Sept. 23	near Fort Hope, Fraser's River	Lat. 50°, 7000 ft.	Pinus, sp.	398	Found on the summit of a mountain near Fort Hope, Fraser's River.
Sept. 25	Base of mountains near Fraser's River		Rhododendron?	208	[etc.]
-----	Fraser's River		Picea, sp.	393	Found on the banks of Fraser's River, from the falls all the way down to the ocean.
Sept. 27	Mountains east of Fraser's River	Lat. 50°	Picea (P. lasiocarpa?)	409	Found on the sloping sides of the mountains; growing on gravelly soil, at an elevation of 4000 feet; [etc.]
Oct. 2	Mt. Baker			290	Found on the margin of a small stream, at the base of Mount Baker, growing on sandy soil. ...
-----	Mt. Baker range		Abies, Sp.	430	Found on the Mt. Baker range of Mountains. This species makes its appearance at the point where A. canadensis disappears, that is, at an elevation of about 5000 feet above the sea; from that point to the margin of perpetual snow it is found. [etc.]

*Additional Remarks on John Jeffrey*

While the few Coleopterists were expressing their frustration to the secretary, the botanists were downright thirsty for blood. Nearly four years after Jeffrey set forth for the New World, the committee had virtually nothing to show the 140 individuals and institutions<sup>45</sup> that had paid his salary for the promise of a copious bounty of new conifers. There is much more to the story (Lang, 2006, has composed a thorough account that is a joy to read), but in the end, the Association decided to fire Jeffrey for negligence. The collector may have never learned of his dismissal, however, for he is thought to have perished on a collecting trip somewhere in the deserts east of the Sierra Nevadas, either by starvation, or murder – it may never be known.

In a letter marked San Francisco, 19<sup>th</sup> May, 1854, W. Murray wrote to his brother in Scotland, informing him that he had completed the task of sending out a notice of Jeffrey's dismissal to a variety of journals, newspapers, consulates, and other individuals who were likely to encounter him, since his whereabouts had been for some time unknown. The closing of this letter captures the feelings of the Association towards Jeffrey at the end of his tenure. (Jeffrey correspondences<sup>46</sup>, p. 68-70):

"I spoke to Sam Price about it and he says the only satisfaction you can get out of a fellow of that kind is to come out here and shoot him through the navel with a Mississippi Yangur, nobody will say anything to you; or if there is an investigation it will brought in, justifiable homicide.

"There was an advertisement in one of the papers the other day, somewhat after this fashion: 'The publication of the Police Gazette will be postponed for a month in consequence of the assassination of the Editor.'

"Them's not the words, but them's the sentiments. Cool, isn't it?"

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<sup>45</sup> See Johnstone, p. 21, and Woods and Woods, 1999.

<sup>46</sup> Made available to me by Dr. Frank Lang. Soon available in digital format from the Royal Botanical Garden of Edinburgh.

**APPENDIX B – Dedication and Preface to Forster’s (1771) *Novae Species Insectorum*.**

The following translations of Forster’s Dedication and Preface to *Novae Species Insectorum* were graciously provided by Dr. Michael Cusick and the 2013 Rockhurst High School AP Latin Class (Kansas City, Missouri).

*Dedication to Banks*

“With this huge and laborious journey completed, on which circuit you have encircled the whole globe which we inhabit; this certainly has made it so that our England, in future consultations concerning nature, will be able to offer richer treasures for examining things relating to botanical and zoological pursuits, than all the rest of Europe. These great merits in the pursuit of natural science, later posterity with grateful spirit will declare yours. Allow, I ask, that I may inscribe chiefly with your name this century [“100”] of new insects. For even if in this little work, only a few and minute insects should be described, these same minute insects are nevertheless new, and on that account I trust that some small part of natural science will be illustrated in these little pages. And this brings me hope that, for the great love with which you have embraced natural history, you will deign to accept this century of insects with a serene countenance, and that it will be a monument by which I may declare publicly with how willing and inclined a spirit I profess my name among those who respect, honor and admire you; and with how great an honor for me I consider it to publicly congratulate you and the literary republic for your happy and auspicious return from the other world and how prepared I am in the whole strength of my mind and body for sustaining the labors of the new journey which you are contemplating; and not only to pray that all things turn out prosperous and happy and that your return is blessed and weighed down with new spoils of the sea and the new world, but also, if it pleases the divine will, to undergo the same dangers with you and to participate in the same delights derived from the study of nature under the new sky with you. VALE”

*Praefatio*

“For these two or three years, before I first saw with how many species of insects our England abounds and how great an abundance flows together annually from every region across the sea into the various collections of British naturalists; I adopted a plan on my own to describe all the new species seen by me and which the illustrious Linnaeus did not insert into the last edition of his system. This work grew beyond a century in a brief time and still such a great supply of new insects in the various collections of the best and my friends has been examined by me so that easily from there I was able to collect a second century of new insects. Therefore with this century of insects sent out into the public for the place and sake of testing it, I will determine whether this small work of mine pleases the public or not, and if it is pleasing to many, willingly and gladly and as much as I am able, I will make a second century for the public right, but if it turns out otherwise, my inclination is to stop in only this century. I decided it is redundant to add tables to this work now, since the descriptions have been dug up with such great care and diligence that tables would be less necessary: furthermore it is my intention to insert certain tables here pertaining to the work, in which I formerly decided to deal with entomological philosophy and the kinds of insects in the English language. Therefore with the Latin language, in particular I have written these things because through all of Europe there is use of this language for the educated community and because on these shores more of the most noble and most famous women finally understand it. The insects described by us are in part native to England and in part brought from foreign shores, certain ones carried from India and China, others belonging to North America, and others imported from the strait of Cadiz. If ever the authors made mention of these insects which have been described by us, wherever I was able I added them, lest any diligence seem to be lacking on our part. Furthermore, I believe that it is my obligation to thank publicly my friends who not only opened up their most ample collections to me so that I might describe from there many new insects; but also they gave to me many things as a gift so that I would be able to publish the things examined and described more carefully.”

## CHAPTER 4: General Conclusion

This thesis began with a review of the lepturine longhorn beetles of the Pacific Northwest, and ended with a detailed analysis of just one of 35 genera found in that region. The second study followed naturally from the first: once we were able to see across a whole landscape, one spot appeared particularly intriguing, so we began to explore. Returning now with a fruitful basket — two new species, and a phylogenetic hypothesis to boot — we consider the landscape again as a whole. What can be said, in summary, about the diversity of lepturines in the Pacific Northwest? What is the state of our knowledge, and what good is it? What do we still hope to find, and why? And finally, for whom is this information ultimately intended, and how best might it be conveyed?

### *A kaleidoscope of forms*

It turns out that the Pacific Northwest has a surprisingly high diversity of lepturines. That is to say, not only is there a fairly high number of species (90), genera (35), and tribes (7ish) relative to other regions around the globe, but there are also many different *sorts* of lepturines. In our fauna, there are examples of both the nocturnal and the diurnal, the bee mimic, the lycid mimic, the small and cryptic, and the large, red, and aposematic. From the desert to the sub-alpine prairie, there are flower-visitors, leaf-eaters, and species that may eat nothing at all. There are species whose larvae bore in soil, roots, stems, in bark, under bark, and in dead, decaying, or living herbs, shrubs, or trees. There are high-accuracy, long-distance sex attractors, and there are males that will never find a mate unless he literally runs into her by accident. In the end, when all of this diversity is surveyed, one, very simple fact becomes immediately apparent: there are a *lot* of different ways to be a lepturine! And really we have seen only less than 20% of the genus-level diversity worldwide. With such a broad suite of adaptive strategies and lifestyles existing among these often inconspicuous, and unsung creatures, it seems unfortunate (at least to this author) that the lepturines have

for so long been referred to in manuals simply as “*the flower-visiting longhorn beetles*.” Although largely accurate, it would be a bit like calling the birds, “*the tree-faring, downy vertebrates*,” to the exclusion of the penguins, ostriches, and all the rest who long ago discovered completely different, though equally noble ways of being a bird. So I now simply call them lepturines.

The myriad different morphological forms we observe hint at a deep and complex history for the lepturine clade. We know from the fossil record that the lepturines have occupied this planet for well over 30 million years (Linsley, 1959), and they have landed in nearly every sector of the globe, from Brazil to Alaska, to England and Japan, Madagascar and Borneo (only Australia, Greenland, and the Hawaiian islands appear to have evaded them). Starting from a single ancestor, as the various lepturine lineages descended through time, they diverged from one another again and again as populations split and became isolated, and then fell under different selective pressures in their separate environments. We understand that all along each branch of this ancient tree, isolated mutations and oddities developed that were passed down to all the ancestors of the branch, and preserved along each split thereafter. A signal of this history should remain in the present-day genera and species, in the form of a nested hierarchy of character states, allowing us to reconstruct the lepturine tree of life. In addition, as these lepturine lineages have floated above earth’s moving continents and rising mountains, and meandered along its shifting meadows and streams, they also bear traces of the deep geographical history of earth. In principal these lepturines, like many other diverse sets of plants and animals, hold the potential to reveal a truly immense amount of information about the otherwise unobservable past.

Much of this potential is only beginning to be within reach. Before we can use the lepturines as a tool to explore the deep complexities of earth’s history, we must know the properties and boundaries of this tool. On the global stage, we are still within a period of basic discovery and organization. There is a single, authoritative list for the

lepturines of the western Hemisphere, but not yet for the world (the majority are in the eastern hemisphere). Genera are still being revised, new species and new patterns are being discovered on an ongoing basis. The arrangement of the tribes, the larger sub-clades within Lepturinae, are still only conjectural at best. Conflicting character sets between the external or internal anatomy of adults and larvae, and now genes, must be resolved, and more data are needed from a broader sampling of species and genera. Aside from DNA, one potentially promising avenue is the study of the male genitalia: Hubweber and Schmidt (2010) found that all substructures of the parameres were preserved at the level of the tribe, rather than the subfamily in Cerambycidae (see also Fragoso, 1985). An initial study on the Lepturinae male genitalia was performed by Ehara (1954), but the ink line drawings are difficult to interpret. The technology exists for these structures to be explored and photographed with high-resolution cameras, and uploaded to the internet on places like MorphoBank, to be instantly accessible by the world taxonomic community. Finally, a great deal of basic information on the life histories and behavior of all the species, and their distribution through both through time and space, is also either lacking, or locked away in some practically inaccessible form.

#### *A role for naturalists and citizen scientists*

The fundamental basis for all our knowledge on the lepturines (or any other beetle for that matter) are specimens. Unlike a report of an observation, or a description, or a photo, the specimens are the *thing in themselves*—the hard evidence. But specimens are still only glimpses into a world which is really, ultimately unknowable in the fullest sense. Like respondents to a national poll—specimens are point samples, giving us the ability to make an informed estimate of the underlying “reality” of the situation. The more samples that are taken through time and space, the higher becomes our resolution on the full story.

We would not know anything at all about lepturines, were it not for the collective effort of hundreds of insect collectors that have explored the world over the centuries, taking back samples of their discoveries. Many of these explorers were ordinary people, not academic scientists. In fact, a significant portion of the beetle specimens residing in the stacks at the Oregon State Arthropod Collection currently bear the name of Kenneth Fender (1910-1987), who collected beetles while on his mail route in rural Oregon. Anyone who takes up the collection of beetles, and who takes the proper care to pin and label them appropriately, is potentially making a valuable contribution to science. And fortunately, there are a lot of proactive ways an individual can put a private collection to use before eventually turning it over to a research museum.

Aside from using a collection to bolster one's own natural history knowledge, and to impress friends and relatives, some collectors share their findings with the public, through online blogging for example. A few good examples are Dave Hubble's [Ecology Blog](#), in which he comments on pattern variation on a species of lepturine found in a local park, or Ted MacRae's [Beetles in the Bush](#) blog. Other hobby collectors also contribute to periodicals like the Oregon Entomology Bulletin. (A recent article by [Lyons](#) (2014) is an excellent example from an active amateur collector.) For those interested in lepturines, a great thing to do would be to go out to Crater Lake, and see if *Pseudogaurotina cressoni lecontei* is really using living honeysuckle as a host plant, or to find out if *Judolia instabilis* is really using the roots of living lupine as a host. Are there more specimens to be found of *Pseudoxylosteus ornatus* blacklight trapping in the Siskiyou in August? And what is going on with *Piodes coracia*? Even a simple note or a photo uploaded to [www.BugGuide.net](http://www.BugGuide.net) would be a valuable contribution. And of course, any of these would be suitable for the Bulletin, or a peer-reviewed journal such as the Pan-Pacific Entomologist, especially if voucher specimens were submitted to a museum for future study by experts. Another way for citizen scientists to make a meaningful contribution is to simply volunteer at a local insect collection, to photograph and database such voucher specimens.



### *Insects in the classroom*

The same reasons insect collections are great for amateur scientists make them ideal for classrooms. Beetles especially, which make up one in four known animal species, are indispensable for introducing biodiversity, not just for their incredible aesthetic forms and extremes in size, shape, and adaptive functions, but because they are found everywhere, and can actually be observed and studied first hand by students. Although it may not be proven definitively, it seems intuitive that students have the most to gain by the study of actual specimens in the classroom, which can be explored under a microscope, dissected, compared, illustrated, and identified with a dichotomous key. Students should have the opportunity to experience first hand a specimen collection, and the process of taxonomic organization and reference to physical data that has been the backbone of biodiversity knowledge for centuries. Historically, the lack of accessible identification guides made it difficult to study insects in much detail, but the continued development of guides such as this, that are publicly accessible on the internet will facilitate the study of beetles in the classroom.

### *Reflections on *Desmocerus**

In my own encounter with the specimens, I have had to wonder and conjecture at the true story of *Desmocerus*, based on the limited evidence that was available to me. I believe that I have arrived at a truer vision of what is the story to *Desmocerus*—but I am also certain that my vision is not perfect. I present my evolutionary hypothesis, and its implications for the species and the biogeographical history of western North America, with the expectation and hope that this hypothesis will be re-examined in the future, with new tools and evidence that will either refine and elaborate upon it, or overturn it completely.

What I do know, and what I can tell the world with confidence, is that there is more diversity in *Desmocerus* than can be represented by names at this time. There are

not just seven species or eight species—there is a kaleidoscope of forms that have resulted from a deeply complex history of populations and their evolutionary trajectories through time and space in the Pacific Northwest. What remains to be done is more sampling, especially in Oregon, Washington, and British Columbia, with a greater attention to detail to the specific locations, and properties of the habitats, the host plants, etc. *Desmocerus lacustris* now presents the same problem to future researchers as the “subspecies” of *D. aureipennis* did for me. The story of the elderberry hostplant also remains unclear. How many different species of this plant are there really? Do these play a role in the subtle variety we see among *Desmocerus* species? And how about the behavior of the *Desmocerus*? How do the sympatric populations differentiate one another if they use the same long-range sex attractant? Is there a preference in females for shinier males, as once suggested by Townsend (1884)? Is the answer to that question even worth knowing? And if it is answered, what new questions will then need to be asked? And in this thesis I have not even had time to comment on the bizarre microscopic landscapes I have observed with an SEM on even a single antennal segment of *D. maximus*. The true story of this genus, like all genera in the Lepturinae, remains, almost entirely, a mystery. If I have succeeded in communicating that much, then I believe my work is done.

#### REFERENCES – Chapter 4

- Ehara, S. 1954. Comparative Anatomy of Male Genitalia in Some Cerambycid Beetles (With 199 Text-figures). Journal of the faculty of science Hokkaido University Series 6/Zoology, 12(1-2): 61-115.
- Hubweber, L. and M. Schmitt. 2010. Differences in genitalia structure and function between subfamilies of longhorn beetles (Coleoptera: Cerambycidae). Genetica. 2010 Jan; 138(1):37-43. doi: 10.1007/s10709-009-9403-x.
- Linsley, E. G. 1959. Ecology of Cerambycidae. Annual Review of Entomology 4: 99-138. [<PDF>](#)
- Lyons, R. 2014. *Cicindela bellissima* Leng (Pacific Coast Tiger Beetle) in Southern Oregon (Coleoptera: Carabidae). Bulletin of the Oregon Entomology Society. Spring, 2014. Available online: [http://odonata.bogfoot.net/oes/OES\\_Bulletin\\_2014\\_Spring.pdf](http://odonata.bogfoot.net/oes/OES_Bulletin_2014_Spring.pdf)
- Townsend, C. H. T. 1884. Notes on some Coleoptera taken in South Louisiana. Psyche, 4:219-222. [<PDF>](#)