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A Review of *Araeopidius monachus* (LeConte, 1874) (Coleoptera: Dryopoidea: Ptilodactylidae), with Main Emphasis on Its Biology and Ecology

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Abstract: *Araeopidius monachus* (LeConte, 1874) is the only species in the subfamily Araeopidiinae within the beetle family Ptilodactylidae. Its geographic distribution is mainly along the western coast of North America, where adults are uncommon. A diagnosis is provided along with detailed collection records highlighting its seasonality, elevational range, plant associations, and collection methods. Collection records from larvae and adults indicate a three-year life cycle. Digestive tract dissections show that the larvae consume woody material while the adults probably do not feed. Additionally, we briefly discuss the problems and prospects for research of this enigmatic species.

Keywords: beetle; collections; distribution; elevation range; larva; morphology; Nearctic realm; plant associations; seasonality

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1. Introduction

The family Ptilodactylidae is a small group of beetles, with most representatives living near water, often with larvae that have special adaptations for survival in aquatic habitats [1,2]. Ptilodactylidae belong to the superfamily Dryopoidea [3], but the detailed relationships of the family remain unclear [4–6]. The subfamilial and generic classification of Ptilodactylidae is in urgent need of revision [1,7–9]. Currently, approximately 500 described extant species of Ptilodactylidae are classified into 29 genera and 5 subfamilies [7,10]. The family is known primarily from the tropical and subtropical parts of the world, and only several species exist in the Nearctic and Palearctic realms [1,7,10]. Subfamilies Ptilodactylinae (ca. 400 spp.), Anchytarsinae (ca. 60 spp.), and Cladotominae (ca. 30 spp.) are distributed in all major zoogeographical realms; Aploglossinae (14 spp.) are known only from South and Central America, and monotypic Araeopidiinae occupy western parts of North America [10].

Whereas the first four subfamilies were erected (at various levels) more than a century ago [11–13], Araeopidiinae were created by Lawrence in 1991 [1]. This subfamily includes only a single genus, *Araeopidius* Cockerell, 1906 [14], with a single species, *A. monachus* (LeConte, 1874). The species was originally described as *Araeopus monachus* LeConte, 1874 [15], but the generic name was later changed to *Araeopidius*, since *Araeopus* LeConte, 1874 was preoccupied with the hemipteran genus *Araeopus* Spinola, 1839 [14].

Araeopidius monachus was initially considered to be a member of the family Dascillidae [14,15] and this was followed by subsequent authors [16–19]. Arnett [16] even placed the species in the tribe Cneoglossini within Dascillidae, a tribe that is currently considered its own monogeneric family (but in fact may be just a group within Ptilodactylidae, see e.g., [20,21]). In his unpublished PhD thesis, Stribling [7] revised the family Ptilodactylidae and placed *Araeopidius* along with *Anchycteis* Horn, 1880, *Epilichas* White, 1859, and *Byrrocryptus* Broun, 1893 in his Epilichinae (sic!). It should be noted that the subfamily name was later corrected to Epilichadinae by Lawrence and Stribling [22], and although the name was treated as available by Ivie [8], it was considered unavailable by Lawrence and Newton [23] and

Bouchard et al. [24]. Lawrence [1] placed *A. monachus* as the sole member in the newly proposed ptilodactylid subfamily Araeopidiinae, and this placement has nowadays been accepted by the community [8–10,20,23,25]. However, Lawrence and Newton [26] and Lawrence [1] have already pointed out that *Araeopidius* probably should be placed in a separate family, partly based on the findings by Forbes [27], and its phylogenetic placement is still uncertain [20,28,29].

Araeopidius monachus (Figures 1–3) is of particular interest to coleopterists, not only because of its enigmatic phylogenetic position within Dryopoidea. It is one of the more challenging and interesting North American beetles in many more ways: uncommon, geographically restricted, highly seasonal as adults, and with larvae at the interface of aquatic and terrestrial habitats. The species is known from a limited number of specimens scattered across many museums and collections. It has been collected mainly along the western continental margin of North America, from southern Alaska to central California [2,25] (Appendix A), although it has been recorded as far eastward as Montana [8,30,31] (Figure 4). This species has been associated with old growth forests and clearcut forests [32], sphagnum bogs [33], shore pine forests, ponderosa pine forests [18], and Douglas-fir forests [17]. Adults have been collected during the summer months of May through August. The adults have been found on streamside flowering plants. LaBonte [33] questioned whether or not adults feed, although they are often found on flowers. Larvae of *A. monachus* have been reported in and adjacent to streams [1,2,22,25,34], in seeps [35] (Appendix A), and in duff and leaves in creeks [34]. The larvae have been described as potentially detritivorous [25,33] or feeding on the roots of emergent vegetation [31]. Ivie [8] noted that the larvae only enter the water by accident. The larval lateral plastron plates have been described as helping survive flooding [1,22,23,25,31]. Probably because of the questions about the larval habitat, *A. monachus* has not been included in the taxa described in any North American aquatic entomology text. The life cycle of *A. monachus* has not yet been described, and particularly the egg, different larval instars, and pupa need more investigation.

In this study, we summarize the available information on *Araeopidius monachus*. We provide a brief diagnosis based on a study of almost 300 specimens from 21 collections. Further, we collate detailed collection records with an emphasis on the seasonality, elevational range, and plant associations of *A. monachus*. We also dissected the digestive tract of several larval and adult specimens to obtain information on what they fed upon. Additionally, we discuss the current problems and prospects for research on this species.

2. Materials and Methods

2.1. Morphological and Museum Work

Measurements were taken using a dissecting microscope fitted with a calibrated ocular grid. Adult measurements included total body length, pronotal length, pronotal width at the base, and elytral length. Total body length was measured directly (where no gap was present between prothorax and elytra) or calculated as pronotal length plus elytral length, i.e., without head. Due to specimen conditions, not all measurements could be made on all adults that were measured. Larval measurements included total body length, pronotal length, pronotal width at the base, and width of the base of abdominal segment IX.

Six adult males and three adult females that had been preserved in alcohol had the abdomen removed to expose the digestive tract to determine what adults were consuming. Three larvae had sagittal sections made along the length of the abdomen, exposing the digestive tract to determine what they fed upon. One of the larvae was just post-molt.

Collection data are from specimens deposited in the below-listed collections, databases, or online sources such as BugGuide [36] and iNaturalist [37] (Appendix A). Label data are reported as on the labels, although the order may be changed. Where elevations were not given but coordinates were given, Google Earth Pro® was used to find approximate elevations. These elevations are presented in brackets in Appendix A, as are occasional explanatory notes in the text. The approximate distribution map for *A. monachus* was created using the SimpleMappr online tool [38] and Adobe Photoshop CC (version 2019-20.0.5;

Adobe Systems, San Jose, CA, USA). Not all adults could be measured for total body length due to separation of the pronotum or the elytra. Not all individuals had dates of collection on the labels. Where possible, adult specimens had the sex determined. In most cases, this was done by examining extruded genitalia. However, in some cases, dissection of genitalia was required. For dissections, specimens were submerged in hot water for approximately one minute, then removed, and then the genitalia were dissected with fine-tipped forceps. In Appendix A, the different sexes are indicated by sex symbols. However, where the sex could not be determined externally and no dissection was done, an "A" was used to indicate an adult of unknown sex.

One large larva collected in March 2022 was retained in a plastic dish with a tight lid containing wet sand, fine gravel, moss, and wood shavings, in an attempt to have the larva pupate.

We list all relevant references known to us for *A. monachus*, particularly those that include information on systematics, phylogeny, biology, and ecology. The page given is usually the page where the taxon name is mentioned for the first time (not including abstracts); in some cases, we add the additional page on which the important information is printed.

Photographs of adults (other than the type specimen and some images from online sources) and larvae were done using a Syncroscopy Auto-Montage system. Images were manipulated using Adobe Photoshop CC (version14).

Abbreviations used in the text include the following: A—adult; L—larva; M1—elytral pattern morph 1, with golden setae scattered over elytra; M2—elytral pattern morph 2, with golden setae in W-shaped patch on anterior third of elytra, a second patch in a form of a wide band just behind middle, and a third apical patch.

Specimens, data and/or images have been obtained from the following collections and museums:

AAC Albert Allen Collection, Boise, ID, USA
ABRC Austin Brady Richards collection, Chico, CA, USA
ANIC Australian National Insect Collection, Canberra, Australia
CASC California Academy of Sciences Collection, San Francisco, CA, USA
CDFA California Department of Food and Agriculture, Sacramento, CA, USA
CNC Canadian National Collection of Insects, Ottawa, ON, Canada
EMEC Essig Museum of Entomology, University of California, Berkeley, CA, USA
FMNH Field Museum of Natural History, Chicago, IL, USA
GWCC Gregory W. Courtney collection, Ames, IA, USA
INHS Illinois Natural History Survey, Champaign, IL, USA
MCZ Museum of Comparative Zoology, Harvard University, Boston, MA, USA
MFNB Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions-und Biodiversitätsforschung, Berlin, Germany
NHMUK The Natural History Museum, London, UK
NMNH National Museum of Natural History, Washington, DC, USA
SBNHM Santa Barbara Natural History Museum, Santa Barbara, CA, USA
SEM-UBC Spencer Entomological Collection, University of British Colombia, Vancouver, BC, Canada
UAM University of Alaska Museum, Fairbanks, AK, USA
UCDC Bohart Museum of Entomology, University of California, Davis, Davis, CA, USA
UCEC Entomological collection, University of California, Riverside, Riverside, CA, USA
UWIM University of Wyoming Insect Museum, Laramie, WY, USA
WSUC Washington State University, Pullman, WA, USA
WFBM William F. Barr Entomological Museum, University of Idaho, Moscow, ID, USA

2.2. Field Work

Samples were taken in seeps where a larval *A. monachus* had been collected by W.D.S. in 1987 (Colusa Co.: Mendocino N Forest, Rd M10, 5.4 mi W Fouts Spring turn off, unnamed spring and seep, 1056 m, 39°19.988′ N 122°43.065′ E) (Figure 5). An aquatic net was held open so that wood from the seep could be broken up and fall into the net bag. On the second and fourth sampling trips, some of the wood from the seep was brought back to the lab, where it could be processed through a Berlese funnel. On the third sampling trip, one larva was collected using an aquatic net while disturbing the substrate and emergent macrophytes.

Adults were collected from a spring run in CA: Tehama Co. (Highway 32 mile marker 269, 31 mi N of Chico, 1096 m, 40°04.632′ N 121°35.760′ W) (Figure 6) to obtain females for gut content analysis and eggs. Both sweep net and beating sheet were used.

3. Results

Order Coleoptera Linnaeus, 1758.
Suborder Polyphaga Emery, 1886.
Series Elateriformia Crowson, 1960.
Superfamily Dryopoidea Billberg, 1820.
Family Ptilodactylidae Laporte, 1838.
Subfamily Araeopidiinae Lawrence, 1991.

Araeopidiinae Lawrence, 1991: 250 [1]. Type genus, *Araeopidius* Cockerell, 1906. See also, Bouchard et al. (2011: 297) [24].

Areopidiinae: Ivie, 2002: 135 [8] (unavailable name, incorrect subsequent spelling not in prevailing use; ICZN 1999, Art. 33.3 [39]).

3.1. Genus Araeopidius Cockerell, 1906

Araeopus LeConte, 1874: 56 [15]. Gender: masculine. Type species, *Araeopus monachus* LeConte, 1874; by monotypy. Preoccupied by *Araeopus* Spinola, 1839: 204/336 [40] (Insecta: Hemiptera: Fulgoromorpha: Delphacidae; currently as a synonym of *Delphax* Fabricius, 1798).

Araeopidius Cockerell, 1906: 241 [14]. Gender: masculine. Replacement name for *Araeopus* LeConte, 1874.

Areopus: Harvey, 1906: 3 [41] (unavailable name, incorrect subsequent spelling not in prevailing use; ICZN 1999, Art. 33.3 [39]).

Areopidius: White et al., 1984: 405 [42] (unavailable name, incorrect subsequent spelling not in prevailing use; ICZN 1999, Art. 33.3 [39]).

Composition and distribution. Only *A. monachus* from the western USA and Canada.

3.2. Araeopidius monachus (LeConte, 1874)

(Figures 1–3)

Araeopus monachus LeConte, 1874: 57 [15].

Araeopidius monachus: Cockerell, 1906: 241 [14].

Araeopidius monochus: Shepard, 1993: 8 [35] (unavailable name, incorrect subsequent spelling not in prevailing use; ICZN 1999, Art. 33.3 [39]).

Type material. Described based on an unknown number of specimens from Oregon, collected by Lord Walsingham [15]. Syntype, sex unknown, "*Araeopus monachus* Lec., Or., Type 2331" (MCZ) (Figure 1a–c).

Type locality. USA: Oregon (without any further data).

Material examined. In this study, we examined 284 adults and 12 larvae. Additionally, we examined 17 photographs of adults on BugGuide [36] and iNaturalist [37], and 1 photograph of a larva provided by Gregory W. Courtney (Ames, IA, USA) (see Appendix A for all materials and more information).

Diagnosis. *Adults* (Figures 1 and 2). Body length, 8.3–12.2 mm (n = 43); pronotal length 1.6–2.5 mm (n = 69); pronotal width 2.3–3.4 mm (n = 69); elytral length, 6.7–9.7 mm (n = 69). Head hypognathous. Antennae serrate in both sexes. Pronotum with lateral margins obsolete, sometimes faintly carinate in posterior half; posterior margin granulate to crenulate.

Prosternum anterior to procoxae divided into two sections: an anterior more-or-less vertical section and a posterior horizontal section, sections divided by a bisinuate carina. Procoxae open laterally, with visible protrochantin. Scutellar shield cordate, with anterior median notch and impressed median longitudinal groove; disc covered with setae. Elytra covered with golden setae and brown setae; two color patterns: one (M1) (Figure 2a) with golden setae in scattered patches, some patches linear, with brown setae between golden setal patches; one (M2) (Figure 2b) with each elytron with golden setae in three large patches: anterior-most patch a V-shaped extending posteriorly from umbo diagonally across elytron to just before medially middle then anteriorly to scutellar shield; a wide transverse patch at middle; and a posterior-most patch along elytron lateral margin from near two-thirds to apex and then anteriorly along suture; brown setae between golden setal patches. Sutural stria wider anteriorly and more deeply impressed than other stria. Metathoracic wings well-developed, without a wedge cell. Tarsi simple, claws simple. The male reproductive tract with a sperm pump just proximal to aedeagus; sperm pump straight and swollen with heavy musculature.

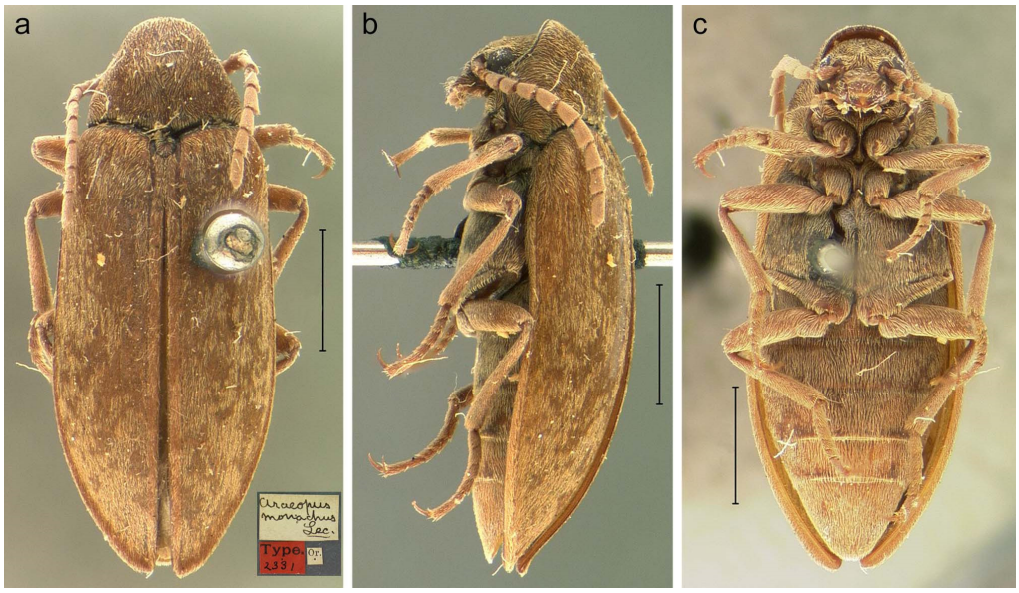

Figure 1. *Araeopidius monachus* (LeConte, 1874), syntype habitus. (**a**) Dorsal view (and original labels); (**b**) left lateral view; (**c**) ventral view. Photographs courtesy of Crystal Maier and Charles Farnum, Museum of Comparative Zoology, Harvard University, MA, USA. Scale bars = 2.0 mm.

For more details, see detailed descriptions in several previous works [2,7,8,15,20,25,43]. The aedeagus, an important character in modern descriptions and classifications, has been described and/or illustrated by Stribling [7], Costa et al. [20], and Lawrence et al. [25], and the ovipositor has been described and illustrated by Stribling [7], Costa et al. [20], and Lawrence [2,43]. The hind wing folding was illustrated and discussed by Forbes [27], and hind wing venation was described and illustrated by Lawrence et al. [44]. There is an abundance of photographs of adults available on the websites BugGuide [36] and iNaturalist [37].

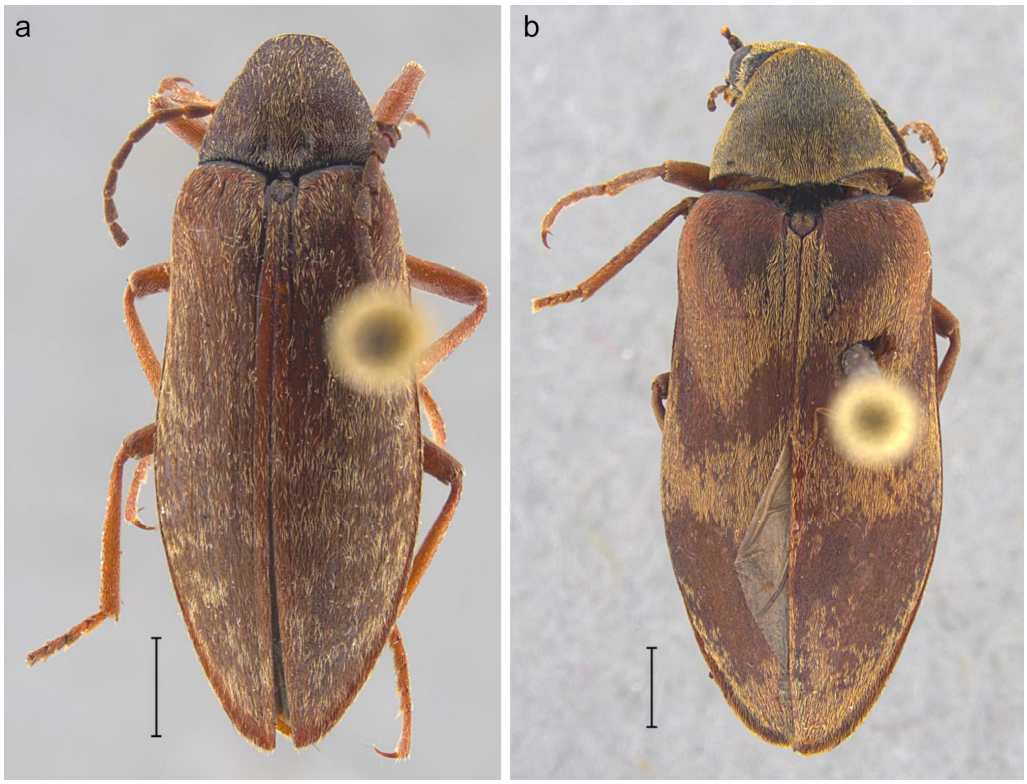

Figure 2. *Araeopidius monachus* (LeConte, 1874), dorsal habitus. (**a**) M1 color morph; (**b**) M2 color morph. Scale bars = 1.0 mm.

Larvae (Figure 3). Body length, 12.0–23.0 mm. Elongate fleshy body, semicircular in cross-section; body color black except with white longitudinal mid-dorsal triangular spots on meso- and metathorax and abdominal segments I–VIII, a white spot on sides of head around stemmata, paired white spots just lateral to ventral midline of abdominal segments I–VII, and larger, white ventral longitudinal lines on abdominal segments VI–VII; surface densely punctate, punctures large and shallow. Each thoracic segment and abdominal segments I–VII with two linear, wide depressions going from venter to near midline of dorsum, abdominal segments VIII–IX with one linear depression; sometimes anterior depression hidden under posterior border of previous segment. Abdominal segments I–V with narrow sternites, segments VI–IX ring-shaped; pleurites absent. Spiracles on mesothorax and abdominal segments I–VII non-functional, associated with large, round (mesothorax), or tri-lobed lateral plastron plates; spiracles on abdominal segment VIII placed dorsally near midline. Abdominal segment IX dorsally with two short apical spines and a ventral operculum; operculum apically with two ventrally pointed hook-like spines; no gills under operculum.

For more details on larval *A. monachus*, see detailed descriptions and illustrations in several previous works [1,20,22,28].

Eggs. Eggs dissected from three females were spherical, 0.6 mm wide, and with a small, raised, cylindrical micropyle.

Intraspecific variability. The two color morphs are present in about equal numbers across the range. The patchily colored morph (M1) (Figure 2a) is more common in more southern localities, while the banded color morph (M2) (Figure 2b) is more common in more northern localities. Some localities in British Columbia, Washington, and Oregon have a mix of both color morphs. In a few specimens there seemed to be a mixture of the two color patterns. The male genitalia are the same in both color morphs. The color morphs do not correlate with sex, years of collection, or elevation of collecting site.

The size measurements of the two sexes overlap, but the females are often larger than the males. Males (n = 14): body length 8.3–9.8 mm; pronotal length 1.6–2.0 mm; pronotal

width 2.3–2.7 mm; elytral length 6.7–7.8 mm. Females (n = 33): body length 8.5–12.2 mm; pronotal length 1.7–2.5 mm; pronotal width 2.6–3.4 mm; elytral length 6.8–9.7 mm.

Figure 3. *Araeopidius monachus* (LeConte, 1874), larva. (**a**) Dorsal view; (**b**) ventral view; (**c**) right lateral view. Scale bar = 1.0 mm.

Geographic distribution. *Araeopidius monachus* is known from western Canada and western United States. It has been collected from far southern Alaska, on Annette, Etolin, Mitkof, Prince of Wales, and Revillagigedo Islands, south to British Columbia, Washington, Oregon, and north-central California (north of the San Francisco Bay area, although it also occurs in the Sierra Nevada) and east to Idaho and Montana (Figure 4). Specific locality data for specimens examined are in Appendix A.

Biology and ecology. *Seasonality of adults*. Adults of *A. monachus* have been collected from March to August, with a peak in May (n = 262; March: 2 exemplars, April: 16 exemplars, May: 112 exemplars, June: 95 exemplars, July: 35 exemplars, August: 2 exemplars). Earlier collections are from more southern localities while later collections are from more northern localities (see Appendix A). Adult emergence occurs across a few months at any one locality, with the males emerging before the females. The 284 adults that were examined, plus the 18 reported from the ABRC collection, had been collected over 118 years (1904–2022), so the collection of adults averaged 2.6 per year.

Figure 4. Approximate distribution of *Araeopidius monachus* (LeConte, 1874). State abbreviations: AK, Alaska; BC, British Columbia; CA, California; ID, Idaho; MT, Montana; OR, Oregon; WA, Washington.

Elevational range of adults. Adults have been collected at elevations of 1.2–2013.0 m, with most collections below 1000 m. Collections from the lowest and highest elevations are both from British Columbia (Appendix A).

Plant associations of adults. Specimens have been collected from a diversity of forest types (see Introduction). They are found around streams, bogs, springs, and seeps that occur in a variety of vegetation types. They have been found on stream-side plants such as spearmint (*Mentha spicata* L.), cow parsnip (*Heracleum maximum* W. Bartram), goat's beard (*Aruncus dioicus* (Walter) Fernald), California lilac (*Ceanothus* L.), dogwood (*Cornus sanguinea* L.), dwarf mountain ash (*Sorbus reducta* Diels), and Western mountain ash (*Sorbus sitchensis* M. Roem.) (Appendix A; BugGuide [36]).

Adult digestive tract. Dissection of the abdomen of six adult males and three adult females found the digestive tract to be empty, although the fat bodies were large. Lack of food in the digestive tract indicates that the adults are using the plants on which they are found for "bush-topping", a method of mate location. Both adult males and females had well-developed fat bodies.

Larval habitat and microhabitat. The larvae can be found in very shallow (1–3 mm) seeps in forests (Figures 5 and 6). They were found on grooved, water-logged, rotting wood that projects above the water's surface, hence they are semiaquatic at best. Perhaps a better term for their microhabitat is quasi-aquatic, i.e., seemingly aquatic but not actually; or, in a certain sense or to some degree aquatic. One larval *Lara avara* LeConte, 1852 (Coleoptera: Elmidae) was collected in association with the two September larvae of *A. monachus*, 10 *L. avara* were collected with the two October *A. monachus* larvae, and 66 larval *L. avara* were collected with the two March *A. monachus* larvae. The two September *Araeopidius* larvae were collected by hand-netting, the two October larvae were collected from wet wood processed in a Berlese funnel, and in March, one larva each was collected by hand-netting and by Berlesing wet wood. Larval *L. avara* and *A. monachus* are both wood gougers. The large larva of *A. monachus* collected in March 2022 died before pupation. At the larval collecting site, other aquatic insects collected co-incident with the *A. monachus* larvae included the following: two genera of nemourid stoneflies (Plecoptera), many larval *Lara avara* (Coleoptera: Elmidae) and Scirtidae, many larval Tipulidae, Psychodidae, and Stratiomyidae (Diptera), and a few larval Trichoptera. All of these are classed as shredders/gatherers/collectors [45]. The few predators found included one chloroperlid stonefly (Plecoptera), several corydalid larvae (Megaloptera), several adult dytiscid beetles, and a few adult terrestrial staphylinid beetles. This aquatic insect community is predominately detritivorous.

Figure 5. Larval habitat of *Araeopidius monachus* (LeConte, 1874). USA: California, Colusa Co.: Mendocino N Forest, Rd M10, unnamed spring and seep, 1056 m, 39°19.988′ N 122°43.065′ W.

Larval digestive tract. Three larvae were dissected to expose the digestive tract. Two larvae were well-sclerotized, and one was weakly sclerotized (post-molt). The two well-sclerotized larvae had the digestive tract full of chewed up woody material. The post-molt larva had the digestive tract empty.

Life cycle. The three largest larvae (total length 21.2–23.0 mm) likely represent latter instars (third-year larvae). The smaller larvae represent middle instars (second-year larvae). All our 2020 larvae were collected 2–3 months after adults were normally gone, and the other seven larvae were too large to have just hatched, so larval *A. monachus* have a stadium that exceeds one year. Measurements of the body length of the larvae (Table 1) and examinations of the months of adult collection (see above) indicate the potential of a three-year life cycle, with oviposition in summer of year 1, larva growth through years 1 and 2 with larval overwintering, and final larval growth in year 3 (Table 1), with pupation in April and May of year 3 followed by most adult emergence after then. No larvae small

enough to be early instars (first-year larvae) have been collected. What is not obvious is how many larval instars there are in the life cycle of *A. monachus*.

Table 1. Collection of larval *A. monachus* arranged by months (n = 12). Measurements are in millimeters. AbdT IX-abdominal tergite IX; *—taken from [1].

Month of Collection	Body Length	Pronotal Length	Pronotal Width	AbdT IX Width
March	13.5	1.4	1.9	1.2
March	22.3	2.3	2.6	1.6
April	23.0	1.9	2.6	2.5
June	13.0	1.4	1.6	1.2
July	15.3 *	-	-	-
September	12.0	1.7	1.5	1.3
September	14.0	2.0	2.1	1.4
September	15.7	2.2	2.2	1.6
October	13.3	2.0	2.0	1.5
October	14.0	1.5	1.4	0.8
October	21.2	2.7	2.7	2.0
December	18.0	2.1	2.1	1.4

Literature. LeConte (1874: 56, 57): original descriptions of *Araeopus* and *A. monachus* (in Dascyllidae; sic!) [15]; Horn (1880: 88): redescription, morphology, drawings of dorsal habitus, frontal head and thorax, and tarsus (as *Araeopus*; in Dascyllidae: Dascyllini; sic!) [46]; LeConte and Horn (1883: 170): catalog, identification key (as *Araeopus*; in Dascyllidae; sic!) [47]; Cockerell (1906: 241): nomenclatural act, *Araeopidius* as a replacement name for *Araeopus* LeConte, 1874 (in Dascyllidae; sic!) [14]; Harvey (1906a: 3): remark (as *Areopus*; sic!) [41]; Bush (1914: 59): checklist (as *Araeopus*) [48]; Forbes (1926: 107, 134): hind wing folding, illustration of hind wing (as *Araeopus*; in Ptilodactylidae or "? family") [27]; Clark (1949: 23): checklist (in Dascillidae) [49]; Hatch (1961: 97, 408): identification key, morphology, drawing of adult habitus (in Dascillidae: Cneoglossinae) [50]; Arnett (1963: 443): catalog, identification key (in Dascillidae: Cneoglossini) [16]; Hlavac (1975: 172): morphology of adult prothorax, drawing of adult lateral prothorax (in Ptilodactylidae: Anchytarsinae) [51]; Mispagel and Rose (1978: 42): ecology, association with Douglas-fir forests (in Dascillidae) [17]; Lawrence and Newton (1982: 278): discussion on a systematic placement, diagnosis, larval morphology (only the genus name mentioned) [26]; Evans (1983: 22): checklist, ecology, occurrence in shore pine and pondereosa pine forests (in Dascillidae) [18]; White et al. (1984: 363, 405): remarks (also as *Areopidius*; sic!) [42]; Stribling (1986: 72, 154): diagnosis, redescription, revision, drawings of head and prothorax, anterior half of dorsal habitus, tarsus, and ovipositor [7]; Stribling (1986: 231): identification key to New World genera of Ptilodactylidae, distribution [30]; Lawrence (1988: 14): morphology, phylogeny (only the genus name mentioned) [52]; Stribling and Seymour (1988: 152): larval biology and ecology [34]; Lawrence (1991: 391): larval biology, ecology, and morphology, figures of habitus, plastron plate, and abdominal apex [1]; Parsons et al. (1991: 48): checklist, biology, and ecology [19]; Lawrence and Stribling (1992: 25): larval morphology and ecology [22]; Shepard (1993: 8): checklist, ecology (as *A. monochus*; sic!) [35]; Beutel (1995: 147, 158): phylogeny, morphology, illustration of larval head [28]; Lawrence and Newton (1995: 847): catalog, diagnosis, and nomenclature (only the genus name mentioned) [23]; Lawrence et al. (1995: 393): morphology-based phylogeny (only the genus name mentioned) [29]; LaBonte (1998: 16, 74): biology and ecology of larvae and adults [33]; Costa et al. (1999: 233, 241): morphology of adults and larvae, phylogenetic analysis, detailed illustrations of adult and larval body parts [20]; Lawrence et al. (2000: 1): morphology, photograph of habitus [25]; Funk and Fenstermacher (2002: 344):

remark on larval ecology (only the genus name mentioned) [53]; Ivie (2002: 135): morphology, ecology, and classification (also as *Areopidius*; sic!; also in Areopidiinae; sic!) [8]; Lawrence (2005: 536): larval morphology and ecology, classification, and illustrations of larval morphology [43]; Lee et al. (2005: 383): morphology and ecology of larvae, morphology-based phylogeny [54]; Lawrence et al. (2011: 99): photograph of ventral prothorax [55]; Chatzimanolis et al. (2012: 570): classification [9]; Lawrence and Ślipiński (2013: 72): comparison with another genus, discussion on phylogeny [56]; Stockbridge (2014: 86): checklist and ecology (unpublished master thesis) [32]; Lawrence (2016: 632): larval morphology and ecology, classification, and illustrations of larval morphology [2]; Evans (2021: 245): diagnosis, morphology, and ecology [31]; Kundrata et al. (2021: 11): classification (only the genus name mentioned) [10]; Lawrence et al. (2021: 436/556): hind wing venation description, photograph of hind wing [44].

Figure 6. Habitat of *Araeopidius monachus* (LeConte, 1874). (**a–d**) USA: California: Tehama Co.; Highway 32 mile marker 269, 31 mi N of Chico, unnamed seep/spring, 1096 m, 40°04.632′ N 121°35.760′ W.

4. Discussion

Araeopidius monachus is definitely one of the most interesting lineages in Ptilodactylidae, due to its remarkable larval morphology and ecology and uncertain phylogenetic position [2,43]. This species is relatively rarely found in collections, especially as a larva,

as its biology and ecology are generally not well-known, and the available information is scattered through isolated papers.

Adults are often collected by picking them off stream-side vegetation, especially flowering bushes, and by sweeping such vegetation. Pitfall traps have been successful in collecting some female adults [32,33]. An automatic, rotary-net device employed 1.83 m above the ground and running for two hours has also caught adults [17]. Two adults have been caught with Lindgren funnels baited with A-pinene and EtOH lures (Appendix A-Idaho: Boundary Co., Moyie Springs). One adult was collected in a Frick trap (Appendix A-CA: Siskiyou Co.). Larvae have been caught mainly by hand-netting in seeps and streams. One larva was collected by processing flood debris from along a stream in a Berlese funnel (Appendix A-CA: Trinity Co.: 4 mi W Forest Glenn), similar to our October and March larvae.

A multi-year larval stadium of *A. monachus* is characteristic of aquatic insects that feed on wood, such as the elmid beetle *Lara avara* [57] and the fly *Axymyia furcata* McAtee, 1921 [58,59]. The ptilodactylid *Anchytarsus bicolor* (Melsheimer, 1846), which also feeds on wood and leaves, has a three-year life cycle [2,43,60].

Water-logged, rotting wood supports larvae and adults of several specialist xylophagous beetles, including the ptilodactylids *A. monachus* and *Anchytarsus bicolor* [60] and the elmids *Lara avara* [57], *Macronychus glabratus* Say, 1825, *Ancyronyx variegatus* (Germar, 1824) [61], *Kingolus* Carter and Zeck, 1929, *Notriolus* Carter and Zeck, 1929, and *Simsonia* Carter and Zeck, 1929 [62]. In western North America, it may be that *A. monachus* is complementary to *L. avara* in decomposing woody debris in seeps, with the former gouging wood above the water line while the latter gouges wood below the water line. Thus, both may be considered "keystone coleopterans" [62]. The geographic distributions of *A. monachus* and *L. avara* greatly overlap, with the main difference being that *L. avara* can be found much further eastward from the Pacific Coast states and provinces, with its distribution extending into Utah and Colorado. Larvae of *A. monachus* have been reported at the edges of streams [1,2,22,25,34,43], which may be when they migrate to the shore for pupation or it may be found where water-logged wood is located. Larvae of some aquatic ptilodactylids consume wood along with other plant debris, such as leaf packs, e.g., *Anchytarsus palpalis* Champion, 1897 [63,64] and *Anchycteis brunneicornis* (Lewis, 1895) [65], while the larvae of *Paralichas trivittis* (Germar, 1824) feed on amorphous detritus [53]. The life cycle and microhabitat requirements of *A. monachus* are remarkably similar to the dipteran *Axymyia furcata* [58,59]. Both are considered to be rare; both inhabit water-logged, partially submerged wood in seeps and springs; both are xylophagous and have overwintering larvae and a multi-year life cycle with adult emergence in spring. It is worth mentioning that no "gills" or osmoregulatory papillae were found under the operculum on abdominal segment IX, which is in agreement with Lawrence [1] and contrary to Ivie [8].

The relative "rarity" of larval *A. monachus* specimens (only 13 specimens are known to us) may be due to a lack of appropriate collecting, with terrestrial beetle collectors usually not examining wood in seeps and aquatic beetle collectors usually not examining wood above the water line. Adults are uncommonly collected (average = 2.6/year) probably due to the species being restricted to small spring habitats and the seasonality of the adults. Most people have only collected one or a few specimens, while only several people have collected multiple adults. These people include those from the 1910s–1950s, and likely had jobs involving collection building. They include Van Dyke, Stace-Smith, Foxlee, Perry, Van Duzee, and Leech (see Appendix A). More recent collectors who have collected multiple specimens have had jobs that supported their avocational collecting. They include Barr, Shepard, and Richards (see Appendix A). A recent exception is J. Stockbridge, who collected *A. monachus* while doing an ecological study for her PhD in Alaska [32].

One of the unanswered questions regarding *A. monachus* is its systematic placement. Although it is currently widely accepted as a member of the family Ptilodactylidae, its relationships remain unclear due to the unique larval morphology, lack of a stable phylogenetic hypothesis for Dryopidea, and widely questioned monophyly of the family Ptilodactylidae [4–6,20,23,28]. Lawrence and Newton [26] (p. 278) stated that "the adult

of *Araeopidius* differs from other ptilodactylids in prothoracic structure and wing folding, but its larva, originally described as that of *Helichus* Erichson, 1847 (a genus in Dryopidae [66]), is so distinct that the group probably should be given family rank". The available phylogenetic analyses, which included *A. monachus*, are relatively old and based solely on morphology [20,23,28]. They placed *Araeopidius* in a clade with Cladotominae, Chelonariidae, Dryopidae, Psephenidae, Lutrochidae, and Elmidae (sharing an abdominal operculum) [28], in various clades including various elateriform groups [23], or in clades consisting of a part of Ptilodactylidae, or some Ptilodactylidae and Chelonariidae [20]. Although *A. monachus* has been sequenced in a barcoding project on Alaskan non-marine arthropods [67] and in an unpublished barcoding project at the Canadian National Collection (Appendix A), it has not been included in any molecular phylogenetic or phylogenomic study so far, e.g., [3,4,6,21,68].

We hope that this contribution will help attract the attention of researchers to this enigmatic beetle and that future studies will help with understanding the main questions regarding *A. monachus*.

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Appendix A

Collection locality information for adult and larval *Araeopidius monachus* (LeConte, 1874). M1 and M2 refer to the two adult color morphs (see main text and Figure 2).

CANADA

BRITISH COLUMBIA

[no other data] (NHMUK) (A, M2)
Agassiz, 24 IV 1924, R. Glendenning (CNC) (♂, M2)
Agassiz, 2 V 1926, R. Glendenning (CNC) (♂, M2)
Agassiz, 26 IV 1927, H. H. Ross (CNC) (♀, M2)
Alouette Lake, Garabaldi Pk. 2 July 1971, N. M. Downie (FMNH) (♂, ♀, A, M2)
Alouette Lake, Golden Ears Prov. Park, 6-24-1982 24 June 1982, N. M. Downie (FMNH) (2♀, M2)
Alouette Lake, Golden Ears Prov. Park, 6-27-1982, N. M. Downie (FMNH) (♀, A, M2)
Alouette Lake, Golden Ears Prov. Park, 16 June 1987, N. M. Downie (FMNH) (♀, M2)
Brit. Columb. [no other data] (NHMUK) (A, M2)
Brit. Columbia, 24·5·1928, W. H. A. Preece (NHMUK) (♂, M1)
Canoe, 33·VI·1978, Lot 3, BF & JL Carr (CNC) (A, M2)
Capilano Timber Company, 4.vii.1933, J. K. Jacobs, [5 m], 49.321 –123.139 (SEM-UBC) (♀, M2)
Central Kootenay, 13 June 2020, [778 m], 49.627069 –117.814283 (iNaturalist) (A, M2)
Columbia Highway, 27-V-30, R. Hopping (CAS) (♂, M2)
Columbia Highway, 27.V.1930, R. Hopping (CNC) (♂, M2)
Creston, 15.vi.1932, G. Stace-Smith, [2013 m], 49.096 –116.514 (SEM-UBC) (♀, M2)
Creston, 5 mi W, Hwy 3, 24.v.1967, J. Shepard, [623 m], 49.083 –116.62 (SEM-UBC) (A, M2)
Cypress Prov. Park, 8-VII-1980, El. 1500 m, N. M. Downie (FMNH) (♀, M2)
Diamond Head Mt., 27.v.1971, J. L. Gordon, [1663 m], 49.844 –123.033 (SEM-UBC) (2♀, M1 and M2)
Diamond Head Mt., 27.v.1971, B. Thompson, [1663 m], 49.844 –123.033 (SEM-UBC) (♂, M2)
Duricu, 11-VI-1953, Edith Mason (CNC) (♂, M2)
Eagle R., 26-V-32, Buckell (CAS) (♂, M2)
Fauquier, 19 VI 1944, W. Coleorave coll. [20] (UCRC) (♀)
Hatzic, 11.VI.53, S. D. Hicks (CNC) (♀, M1)
Hedley, 21.iii.1955, R. Stace-Smith, [527 m], 49.357 –120.077 (SEM-UBC) (♀, M2)
Hot Springs Area, Lakelse Lake, 14·VI·1960, G. E. Shewell (CNC) (♀, M2)
Indian River, 22-VI-30, H. Leech (CAS) (♀, M2)
Lynn Valley, 3 VII 30, H. Leech (CAS) (5♀, 1♂, M2)
Maple Ridge, Golden Ears, [no date], Mike Lake (iNaturalist) (A, M2)
Mara, V-VI·1922, K. F. Auden collection (INHS) (♂, M2)
Metro Vancouver, Golden Ears Provincial Park, 19 June 2020, on goat's beard (Bridget Spencer; BugGuide) (A, M2)
Mission City, 9·VI·53, S. D. Hicks (CNC) (♂, M2)
Mission City, 17·VI·53, W. R. M. Mason (CNC) (A, M2)
Mission City, 19.VI.53, S. D. Hicks (CNC) (♀, M2)
Nanaimo, Departure Bay, 26.v.1925, G. J. Spencer, [1.2 m], 49.192 –123.954 (SEM-UBC) (♀, M1)
Nanaimo, Biol. Station, 23 June 20, E. P. Van Duzee (CAS) (4♀, M1)
Nanaimo, Biol. Station, 25 June 20 (CAS) (1A, 1♀, M1)
Paxton Valley, 25-V-33, A. Thrupp (CAS) (A, M2)
Peachland, 28.IV.18, W. R. S. Metcalfe (CNC) (♀, M2)
Pemberton, Squamish-Lillooet District, 19 May 2020 (Trevor Van Loon; BugGuide) (A, M2)
Pender Harbour, 19 V 1985, S. G. Cannings, 49.63 –124.04 (SEM-UBC) (A, M2)
Port Coquitlam, Crystal Falls Trail, 12 June 2010, on flowering bush (Tim Loh; BugGuide) (2A, M1 and M2)
Prince Rupert, 23·IV·1923, W. B. Anderson (CNC) (♂, M2)
Prince Rupert, VI.1925, P. W. Pillsbury (SEM-UBC) (♀, M1)
Prince Rupert Island, North Coast, 9 June 2020; on cow parsnip flowers (GreenIsland; BugGuide) (A)
Robson, 22.V.1948, H. R. Foxlee (CNC) (♂, M2)
Robson, 20 IV 1949, H. R. Foxlee (CNC) (♂, M2)
Robson, 10-V-1949, H. R. Foxlee (CNC) (♂, M2)
Robson, 12 V 1949, H. R. Foxlee (CNC) (♂, M2)
Robson, 8 V 1968, H. R. Foxlee (SEM-UBC) (♀, M2)

Salmo, 2 mi S, 9.VI.1968, Campbell & Smetana, on driftwood in stream (CNC) (A, M2)
Salmon Arm, 26·IV·36, Hugh Leech (CNC) (♀, M2)
Sanca, 12.v.1933, G. Stace-Smith, [543 m], 49.39 –116.736 (SEM-UBC) (A, M2)
Sanca, 27.v.1933, on *Ceanothus sanguineus*, G. Stace-Smith, [543 m], 49.39 –116.736 (SEM-UBC) (A, M2)
Sanca, 2.vi.1933, *Cornus pubescens*, G. Stace-Smith, [543 m], 49.39 –116.736 (SEM-UBC) (A, M2)
Seymour Cr., 9-VI-30, H. Leech (CAS) (♀, M1)
Sicamous, 2.VI.78, Lot 1, BF & JL Carr (CNC) (A, M2)
Squamish-Lillooet, 9 June 2019, [970 m], 50.146535 –123.121791 (iNaturalist) (A, M2)
Squamish-Lillooet, 3 August 2020, [878 m], 10.21 AM, 50.52628 –123.503725 (Chloe and Trevor; iNaturalist) (A, M2)
Steelhead, 2·VI·1933, H. B. Leech (CAS) (♀, M1)
Sumas Pr., 3·VI·1933, Ralph Hopping (CAS) (♂, M1)
Terrace, 1927, Mrs. Hippisley, [68 m], 54.518 –128.599 (SEM-UBC) (♀, 1A, M2)
Terrance [probably Terrace], 23 mi N of, Mt. Allard, 28·VI·1960, J. G. Chilcott (CNC) (♀, M2)
Terrance [probably Terrace], S of, Lakelse Lake Bog, 11-VII-1960, B. Heming, CNC COLEO DNA Barcode voucher 00152769 (CNC) (♀, M2)
Three Valley, 4·VI·78, Lot 2, BF & JL Carr (CNC) (♂, M2)
Trinity Valley, 19-6-[19]68 [50°23′59″ N 118°55′0″ W] (MFNB) (A, M2)
Tyee, SE Prince Rupert, 8.VI.1958, Lindroth (CNC) (♀, M2)
U. B. C. Forest, Garibaldi Park, nr. Haney, 7·VII·53, S. D. Hicks (CNC) (♀, M2)
Vancouver, 13-V-04 (CAS) (♂, M2)
Vancouver, 1.vi.1924, F. Perry, on flowers of *Pyrus occidentalis*, [84 m], 49.251 –123.137 (SEM-UBC) (2A, M2)
Vancouver, 1·VI 1924, F. Perry, on flowers of *Pyrus occidentalis* (CNC) (♀, M2)
Vancouver, 1·VI·1924, F. Perry, on flowers of *Pyrus occidentalis*, K. F. Auden collection (INHS) (♂, M1 and ♀, M2)
Vancouver, 1·VI·1924, F. Perry, K. F. Auden collection (INHS) (1♂and 2♀, M2)
Vancouver, May 1926 (INHS) (♀, M2)
Vancouver, June 1926 (INHS) (♀, M1)
Vancouver, 29·4·6, K. F. Auden collection (INHS) (A, M2)
Vancouver, 13·V·1931, H. B. Leech (CNC) (♂, M2)
Vancouver, 30·V·1931, H. B. Leech (CAS) (A, M2)
Vancouver, 1·VII·1931, Hugh B. Leech (CNC) (♀, M2)
Vancouver, Lynn Cr., 1·VII·1932, H. B. Leech, *Aruncus sylvester*—goat's beard (CNC) (♂, M2)
Vancouver, 12-V-36, W. A. Mathers (CAS) (♂, M2)
Vancouver, 6-22-1971, N. M. Downie (FMNH) (♂, ♀, M2)
Vancouver, Howe Sound, 24·V·30, E. E. Peden (CNC) (A, M2)
Vancouver, Howe Sound, McNab Cr., 19·VI·30, H. Leech (CAS) (A, M1; A, M2; 1 ♀, M1; 3♀, M2)
Vancouver, Howe Sound, McNab Cr., 19·VI·30, H. Leech (CNC) (3♀, ♂, M2)
N. Vancouver, 13-V-04 (CAS) (A, M2)
Vancouver, UBC, 4.v.1954, B. Hardy, [92 m], 49.265 –123.253 (SEM-UBC) (A, M1)
Vancouver, UBC, 23.v.1955, B. Hardy, [92 m], 49.265 –123.253 (SEM-UBC) (♂, M1)
Vancouver, UBC, 2.vii.1954, B. Hardy, [92 m], 49.265 –123.253 (SEM-UBC) (♀, M2)
Vancouver, UBC, 1.viii.1954, B. Hardy, [92 m], 49.265 –123.253 (SEM-UBC) (♀, M1)
Vancouver, 1-VII-1973, N. M. Downie (FMNH) (♀, M2)
Vancouver Island, Upper Jordan River, 14 May 2016, on Western Mountain Ash—*Sorbus sitchensis* (Jeremy Gatten; BugGuide) (A, M1)
Vernon, 28·IV·1915, Max H. Bühmann (CAS) (A, M2)
Vernon, 17-V-25, E. A. Redell (CAS) (♀, M2)
Vernon, 10 V 1929, H. B. Leech (CNC) (♂, M2)
Wellington, 18.vi.1947, R. Guppy, [96 m], 49.214 –124.044 (SEM-UBC) (A)
Wellington, 24.v.1948, R. Guppy, [96 m], 49.214 –124.044 (SEM-UBC) (♂, M1)

West Vancouver, Capilano, 9.vi.1963, G. G. E. Scudder, [115 m], 49.343 –123.116 (SEM-UBC) (A, M1)

Wynndel, 10.v.1931, G. Stace-Smith, [575 m], 49.18 –116.553 (SEM-UBC) (3♂, 2♀, 2A, M2)

Wynndel, 19.v.1946, G. Stace-Smith, [575 m], 49.18 –116.553 (SEM-UBC) (2♀, 1♂, M2)

Wynndel, 16.vi.1946, G. Stace-Smith, [575 m], 49.19 –116.553 (SEM-UBC) (3♀, 1A, M2)

Wynndel, 18.v.1947, G. Stace-Smith [575 m], (SEM-UBC) (3♀, 1A, M2)

Wynndel, 6-VI-48, G. S. Smith (CAS) (♀, M2)

USA

ALASKA

Annette Island, 27-V-1945, R. Sanders (WSUC) (♀, M2)

Dall Island, 2 VII 47, G. D. Hanna (CAS) (A, M2)

Etolin Island, 20 July 2011, [895 m], 56.13203 –132.3293 (UAM) (1A)

Etolin Island, Steamer Bay, 26 VI 1977, T. F. Hansen, [109 m], 56.15014 –132.68453 (UAM) (♀, M2)

Mitkof Island, 15 mi South of Petersburg, Whale Pass, 16-VII-1962, J. R. Planck (UCDC) (♀, M2)

Prince of Wales Island, Hatchery Ck. 4, 30 May–14 June 2010, J. Stockbridge, 78 m el., old growth, pitfall 3, 55.88602 –132.8607 (UAM) (♀, M2)

Prince of Wales Island, Luck Lake, Rd. 1, 18 May–4 June 2010, [98 m], 55.97805–132.75456 (UAM) (♀, M2)

Prince of Wales Island, Luck Lake, Rd. 3, 4–29 June 2010, J. Stockbridge, C. Bickford, 117 m el., old growth, pitfall 4, 55.95347 –132.7708 (UAM) (♀, M2)

Prince of Wales Island, Luck Point, 18 May 2010 (UAM; Derek Sikes; BugGuide) (A, M2)

Prince of Wales Island, Luck Point 1A, 27 June–11 July 2012, J. Stockbridge et al., 174 m el., 55.98452 –132.78786 (UAM) (♀, M2)

Prince of Wales Island, Luck Point 1B, 20 June–5 July 2011, J. Stockbridge et al., 169 m el., clear cut, pitfall 1, 55.98497 –132.787 (UAM) (♀, M2)

Prince of Wales Island, Luck Point 1B, 20 July–5 July 2011, J. Stockbridge, B. Wong, 169 m el., clear cut, pitfall 2, 55.98497 –132.787 (UAM) (♀, M2)

Prince of Wales Island, Luck Point 1B, 11–26 July 2012, [180 m], 55.98497–132.787 (UAM) (♀, M2)

[Revillagigedo Island], Ketchikan, 13-VI-39, E. C. Johnston (CAS) (♂, M2)

CALIFORNIA

Butte Co.: 5 mi NE Butte Meadows, Cherry Hill Campground, V-24 through 27-1974, Fred G. Andrews (CDFA) (♂, A, M1)

Butte Co.: Skyway Bridge at mile marker 24, 06/10/2012, A. Brady Richards, 865 m, 39.89707 –121.56713 (ABRC) (1A)

Butte Co.: Pulga, 12 IV.1990, unnamed spring seep, Cheryl Barr & William D. Shepard (EMEC) (♂, M1)

Butte Co.: 2.5 mi NE Pulga on Dixie Rd. off Camp Creek Rd., 12 IV 1990, William D. Shepard and Cheryl B. Barr, 2500 ft. [762 m], spring seeps at unnamed stream, WDS-A-689 (EMEC) (5♂, M1)

Butte Co.: flume entering De Sabla Reservoir, along Hwy 32, 5/8/2010, A. Brady Richards, 849 m, 39.87695 –121.61250 (ABRC) (1A)

Colusa Co.: Mendocino N Forest, Rd M10, 0.6 mi W Sanborn Cabin turn off, 5.4 mi W Fouts Spring turn off, unnamed spring, 5 IV 87, W. D. Shepard, 3290′ [1056 m], WDS-A-458, [N39°19.987′ 122°43.065′] (EMEC) (1L)

Colusa Co.: Mendocino N Forest, Rd M10, 5.4 mi W Fouts Spring turn off, unnamed spring, 21 IX 2021, W. D. Shepard, 3290′ [1056 m], [N39°19.987′ 122°43.065′] WDS-A-2153, (EMEC) (2L)

Colusa Co.: Mendocino N Forest, Rd M10, 5.4 mi W Fouts Spring turn off, unnamed spring, 11 X 2021, W. D. Shepard, 1056 m, [N39°19.987′ 122°43.065′], WDS-A-2153, (EMEC) (2L)

Colusa Co.: Mendocino N Forest, Rd M10, 5.4 mi W Fouts Spring turn off, unnamed spring, 7 XII 2021, 1056 m, [N39°19.987′ 122°43.065′], WDS-A-2157 (EMEC) (1L)

Colusa Co.: Mendocino N Forest, Rd M10, 5.4 mi W Fouts Spring turn off, unnamed spring, 31 III 2022, 1056 m, [N39°19.987′ 122°43.065′], WDS-A-2158, (EMEC) (2L)

Del Norte Co.: 4 mi S Mill Creek Campground, 26-VI-1978, A. J. Gilbert & M. E. Gilbert (CDFA) (2A, M1)

Del Norte Co.: line Hwy 101, 1-VIII-1975, A. J. Gilbert & M. E. Gilbert (CDFA) (♀, M1)

Humboldt Co.: McKinleyville, bog area nr Azalea Avenue, 25-VI-1980, Thomas W. Davies (CAS) (2♀, M1)

[Lake Co.]: Brtltt. Springs, 4 June 23 (CAS) (A, M1)

[Marin Co.]: Alpine Dam, 10-IV-33, E. S. Ross (CAS) (A, M1)

Marin Co.: Lagunitas, 30-IV-05, Van Dyke Coll., [#] 3934 (CAS) (A, M1)

Marin Co.: Lagunitas, 24-IV-1910 (CAS) (♂, M1)

Marin Co.: Lagunitas, 2-V-1927 (CAS) (♀, M1)

Marin Co.: Mt. Tamalpais, 16-V-1920 (CAS) (♀, M1)

Mendocino Co.: NCCRP, 3 mi N. Branscomb, 17 May 1975, J. Benson, 1400′ el. [427 m] (EMEC) (♂, M1)

Mendocino Co.: NCCRP, 3 mi N Branscomb, 30 May–1 Jun 80, L. Kawakani (EMEC) (♂, M1)

Mendocino Co.: NCCRP, 3 mi N. Branscomb, 21–23 May 1982, C. Besette, 1400′ el. [427 m] (EMEC) (♂, M1)

Mendocino Co.: Angelo Coast Range Reserve, 8 km N of Branscomb, Essig Field Trip, 25-V/2-VI-2003, Sugar Creek near Headquarters, 1-VI-2003, C. B. Barr, sweep (EMEC) (♀, M1)

Plumas Co.: 1.6 mi N Caribou, campground off Caribou Road, Lassen National Forest, 21 June 2003, Aaron D. Smith, [1476 m], 40.1020 –121.1500 (Mike Caterino; SBMNH; BugGuide) (♀, M1)

Plumas Co.: hillside spring tributary of Lake Davis, Plumas Hwy 113, 5/18/2007, A. Brady Richards, 1767 m, 39.90084 –120.48002 (ABRC) (1A)

Plumas Co.: Meadow Valley, 3500–4000 ft alt, 1-VI-1924, E. C. Van Dyke (CAS) (♀, M1)

Shasta Co.: 15 mi S McCloud, McCloud R. Preserve, A. E. Hajek, 1975 May (EMEC) (M1)

Shasta Co.: 3.5 mi WSW Vollmers, along Dog Creek Rd., 30·V·1994, unnamed stream, William D. Shepard, 2767′ [843 m], 40°56.48′N 122°31.35 W, WDS-A-1099, sweeping steep drainage upstream of road (EMEC) (♂, M1)

Sierra Co.: New York Ravine, ca. 2 mi E Downieville, 1-V-1993, C. B. Barr & W. D. Shepard, WDS-A-964 (EMEC) (♂, M1)

Siskiyou Co.: Summer 1959, Ex. Frick trap (CDFA) (A, M1)

Tehama Co.: spring along CA Hwy 32, 21 June 2009, Brady Richards (BugGuide) (A, M1)

Tehama Co.: spring tribs of Big Chico Creek along CA Hwy 32, 6/21/2009, A. Brady Richards, ~1105 m, 40.0781 –121.59568 (ABRC) (6A)

Tehama Co.: spring tribs of Big Chico Creek along CA Hwy 32, 6/27/2010, A. Brady Richards, ~1105 m, 40.0781 –121.59568 (ABRC) (1♀)

Tehama Co.: spring tribs of Big Chico Creek along CA Hwy 32, 15/5/2022, A. Brady Richards, ~1105 m, 40.0781 –121.59568 (ABRC, EMEC) (8A, M1)

Tehama Co.: spring tribs of Big Chico Creek along CA Hwy 32, 28/5/2022, A. Brady Richards and William D. Shepard, ~1105 m, 40.0781 –121.59568 (ABRC, EMEC) (2♂, 3♀, 1A, M1)

Trinity Co.: 4 mi W Forest Glenn, berlesing flood debris along stream, 1.vii.1975, 3300′ [1005.8 m], A. Newton & M. Thayer [1] (2L)

Trinity Co.: 8 mi SE Trinity Ctr., along East Side Rd., small spring creek, 30·V·1994, WDS-A-1096, William D. Shepard, 3364′ [1025 m], 40°56.61′ N 122°34.32′ W (EMEC) (♂, M1)

IDAHO

[Bonner Co.]: 12 mi NE Sand Point, Trout Cr, 18-V-66, R. L. Westcott (WFBM) (A, M2)

[Bonner Co.]: 12 mi SE Sand Point, Trout Creek, 9-VI-1971, W. F. Barr (WFBM) (♀, M2)

Bonner Co.: Schweizer Basin, 6-15-1982, N. M. Downie (FMNH) (♂, M2)

Boundary Co.: Moyie Springs, Lindgren [funnels with] A-pinene and ETOH lure, 17-V-2007, L. H. Dersch (WFBM) (2A, M2)

Idaho Co.; 12 mi SE Grangeville, Hwy 14 above S. Fk. Clearwater River, June 1980s, Albert Allen, sweeping vegetation around seepage/wet areas (AAC) (A)

Idaho Co.; 18 mi SE Grangeville, Hwy 14 above S. Fk. Clearwater River, June 1980s, Albert Allen, sweeping vegetation around seepage/wet areas (AAC) (A)

[Kootenai Co.]: C. D. Alene, 6 July 1963, N. Jorgensen (WSUC) (♀, M1)

Kootenai Co.: Beauty Cr., nr Lake Cd' A, 11-VI-75, D. F. Veirs (WFBM) (♂, M2)

Kootenai Co.: Twin Lakes, 19-V-63, C. P. Markin (WFBM) (A, M2)

Shoshone Co.: Hobo Cedar Gr.[ove], 6-VI-1987, T. D. Miller (WFBM) (♀, M1)

Shoshone Co.; Hobo Creek Grove, 8-VI-2007, on low vegetation, F. W. Merickel (WFBM) (A, M1)

MONTANA

Glacier N. Pk., VII 35, J. E. Blum (CAS) (5A, 1♀, M1)

Mineral Co.: small tributary of Two Mile Creek, 47°16.39′ N 115°14.97′ W 1115 m, 14.VIII.2015, coll. G.W. Courtney (GWCC) (1L)

OREGON

[No specific locality or date], Lord Walsingham [15] (MCZ) (M1) [type specimen] (A, M1)

Alice Lake, Garabaldi Pk., 6-30-1974, N. M. Downie (FMNH) (♂, M2)

19 mi W of Suttle Lake, 5-30-41, Schuh & Gray, on bear grass raceme (FMNH) (A, M1)

20 mi SW of St. Helens, 21 May 1938, K. Gray & J. Schuh (CNC) (♀, M1)

[Benton Co.]: Alsea, 11 May 2021, 5:52 PM, [389 m], 44.46738 –123.50652 (corndog; iNaturalist) (A)

[Benton Co.]: Corvallis, 3-V-1936, G. Ferguson (FMNH) (2♂, M1)

Benton Co.: McDonald Forest, 12 April 1975 (FMNH) (♂, M1)

Cannonville, 26-V-1930, R. Hopping (CAS) (A, M2)

[Clatsop Co.]: Cannon Beach, 12 June 1927, E. C. Van Dyke (CAS) (A, M1)

[Clatsop Co.]: Cannon Beach, 14 June 1927, E. C. Van Dyke (CAS) (♂, M1)

[Clatsop Co.]: Seaside, 20 June 64, RW (WFBM) (♂, M1)

Douglas Co.: Umpqua Nat. F., Headwater tribs to Squaw Creek & Donegan Cr, 27 Sep 1990, R. W. Wisseman (EMEC) (1L)

Douglas Co.: Umpqua R., 14 mi N of Tiller, VI-1 through 5–48, D. P. Frechin (CNC) (A, M2)

Douglas Co.: Whitehorse Falls, Diamond Lake Road, Umpqua River, 14 June 2017, on *Ceanothus* (John & Jane Balaban; BugGuide) (A, M2)

Hood River Co.: Bill Williams Creek [no date], G. Ulrich (Costa et al. 1999) (L) [This locality is questionable because Gary Ulrich often collected in CA: Marin Co. Bill Williams Creek and there is no Bill Williams Creek in Oregon.]

Jackson Co.: Ashland/Ashland Mt, 6 June 2015, mixed forest on flowers (*Ceanothus*) (Andrew McKorney; BugGuide) (A, M1)

Josephine Co., Caves Natl. Monument, 27-VI-1974, A. J. Gilbert & M. E. Gilbert (CDFA) (♀, M1)

Lane Co.: 3 mi W Florence, 6-III-71, H. P. Stene (WSUC) (A, M2)

Lane Co.: HJ Andrews Experimental Forest, 11 mi NE Blue River, 9 June 1982, G. L. Parsons (SBMNH) (♂, ♀, M2)

[Lane Co.]: Oakridge, 40 mi NNE, [no date], L. N. Herman (ANIC) (♂)

Lane Co.: 0.8 mi E Hwy 101, 42 m, Tenmile Creek, 15 May 2014, R. L. Westcott, 44.22° –124.09°, flowers of *Heracilium maximum* [=*Heracleum maximum* W. Bartram] (WFBM) (A and ♀, M1)

Lane Co.: Waldo Lake, 6-VII-1980, L. R. Bronson (CDFA) (A, M1)

Lincoln Co.: Van Duzer Corridor, 18 VII 1982, R. L. Penrose (WFBM) (♀, M1)

[Linn Co.]: Cascadia, 19 May 1935, H. A. Scullen (CNC) (A, M1)

Linn Co.: HJ Andrews Experimental Forest, 15 May 2014 (Bill Gerth; BugGuide) (A, M1)

Linn Co.: 1.5 mi S Marion Forks, 2-VII-1974, R. L. Westcott (WFBM) (♂, M2)

Linn Co.: Monument Peak, 21-VII-1968, R. L. Westcott (WFBM) (♀, M2)

Linn Co.: Monument Peak G. S., Sec 21, T10S, R4E, 3-VII-1974, R. L. Westcott (WFBM) (6♀and 1A, M1)
Linn Co.: Monument Peak G. S., Sec 21, T10S, R4E, 16-VII-1974, W. F. Barr (WFBM) (A, M2)
Marion Co.: Monument Peak, 21 July 1974, Wayne N. Mathis & D. C. Carlson (CDFA) (♂, M1)
Mt. Hood, [no other data] (ANIC) (♀)
Mt. Hood, 2 VII 1927, P. J. Darlington (NHMUK) (♂)
Mt. Hood, Gov't Camp, 6 July 1938, R. W. Jones, 4000′ [1219 m], K. E. Gibson collection (WFBM) (♀, M1)
Mt. Hood NF, Bull Run watershed, Bull Run R headwaters spring, Oct 1995 (EMEC) (1L)
Multnomah Co.: Larch Mt, 6 June 2016 (Jensanford; BugGuide) (A, M2)
Multnomah Co.: Multnomah Cr. at Falls Scenic Route S I-84, 30-VI-1985, C. B. Barr (EMEC) (♀, M1)
[Washington Co.]: Dilley, [no date], Leng coll. (CAS) (A, M1)
WASHINGTON
[no other data] (CNC) (A, M2)
W. T. [Washington Territory], 3984, Bolter coll., No. E7615a, Univ. of Ill. (INHS) (♀, M2)
[Clallam Co.]: Crescent Lake, 27 VI 1936 (Van Dyke Coll.) (CAS) (♀, M1)
[Clallam Co.]: Sol Duc Hot Spgs, 23-VI-36 (CAS) (♀, M1)
[Cowlitz Co.]: Stella, 27 April '15 (NHMUK) (A, M1)
[Grays Harbor Co.]: Lake Quinault, 31-V-1914 (CAS) (9♀, 1♂, M1)
[Grays Harbor Co.]: Quinault, 30-V-1914, E. C. Van Dyke (CAS) (3♀, 1♂, M1)
[King Co.]: Seattle, [no date], O. B. Johnson, [#] 3984 (WSUC) (A, M1)
[King Co.]: Seattle, [no date], O. B. Johnson (WSUC) (♀, M2)
[King Co.]: Seattle, [no date] (CAS) (♀, M1)
[King Co.]: Seattle, [no date] (CAS) (A, M1)
[King Co.]: Seattle, [no date] (CAS) (A, M2)
[King Co.]: Seattle, [no date] (CAS) (A, M1)
[King Co.]: Seattle, [no date] (CAS) (♀, M2)
[King Co.]: Seattle, [no other data] (WSUC) (♀, M2)
[King Co.]: Seattle, 5-V-1907 (CAS) (♀, M2)
[King Co.]: Seattle, 27-V-1933 (CAS) (♂, M1)
[King Co.]: Seattle, V or X 35 [month of collection illegible], Liebeck Collection (NHMUK) (♂)
Kitsap Co.: 6-4-98 (EMEC) (1L) [date should be 4 June 98]
[Kitsap Co.]: Bremerton, 25·V·47, Don Frechin (CNC) (♀, M1)
[Kitsap Co.]: Bremerton, 30-V-48 (CNC) (♀, M1)
[Kittitas Co.]: Easton K, [no date] (CAS) (♀)
[Lewis Co.]: Longmires, Rainier N Pk, 11-VII-36 (CAS) (3♀, M2)
[Lincoln Co.]: Sherman (CAS) (♀, M1)
Mason Co.: Stimson Cr., 22.V.48, Don Frechin (CNC) (A, M1)
Mason Co.: 21·V·49 (CNC) (♂, M1)
Mt. Rainier, 10-V-1931, Arthur J. Hanson (WSUC) (♂, M2)
Mt. Rainier National Park, June 16, 1951 (UWIM) (♂, M2)
Mt. Rainier Natl Pk, Misqually R., 4000′, 16.V.1968, Campbell & Smetana, CNC COLEO DNA Barcode voucher 00152771 (CNC) (♂, M2)
North Cascades National Park, NE of Marblemount (https://irma.nps.gov/NPspecies) (accessed on 20 June 2021)
Snohomish Co.: 17 July 2018 (Chloe and Trevor; iNaturalist) (2A, M1 and M2)
Snohomish Co.: Verlot, 14·V·49, E. C. Johnston (CNC) (♂, A, M2)
Whatcom Co.: Mt. Baker, 19 Jun 1987, el. 750 m, N. M. Downie (FMNH) (A, M2)
[Whitman Co.]: Pullmann, [#] 3984, Leng Coll (CAS) (♀, M2)
Yakima Co.: Mount Adams, Klickitat River, 3000 ft [914 m], 21 VI 1935, J. Wilcox [20] (A) (UCRC)

[Yakima Co.]: Signal Peak?, 21 VI 1935, S. E. Crumb coll. [20] (A) (UCRC)

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