Ecological Specialization in Predatory *Lasiopogon* Robber Flies and its Role in Facilitating Diversification and Species Coexistence

by

Tristan Alexander McKnight

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Ecology and Evolutionary Biology)
in The University of Michigan
2017

Doctoral Committee:

Professor L. Lacey Knowles, Chair
Associate Professor Johannes Foufopoulos
Associate Professor Timothy Y. James
Assistant Professor Stephen A. Smith

Tristan A. McKnight

trismckn@umich.edu

ORCID iD: 0000-0001-9400-3445

ACKNOWLEDGMENTS

Authorship for chapters II and III is shared with Dr. Robert A. Cannings (Royal BC Museum, Victoria, BC, Canada), who generously shared specimen records, personal experience, taxonomic insights, and encouragement to assist this work. However, the taxonomic decisions, specimen review, molecular work, and vast majority of the writing in these chapters are my own responsibility.

Funding for collecting trips and molecular lab work was provided by the National Science Foundation (DEB-1601389), the Society for the Study of Evolution Rosemary Grant Award, the Smithsonian Williston Dipterology Fund, the University of Michigan Rackham Graduate School, Department of Ecology and Evolutionary Biology, and Museum of Zoology, and the Royal BC Museum Research Associate program.

Labmates at the University of Michigan provided technical and theoretical assistance at various stages of this project: Dr. L. Lacey Knowles, Dr. Raquel Marchan, Dr. Jen-Pan Huang, Andrea Thomaz, Carlos Muñoz, Dr. Rob Massatti, Dr. Diego Alvarado Serrano, Pascal Title. Other associates at the University of Michigan were instrumental in shaping this work: Dr. Barry O'Connor, Dr. Jo Kurdziel, Dr. Pavel Klimov, Dr. Ted Cohn, Dr. Dan Rabosky and the EEB administrative staff (Robbin Murrell, Cynthia Carl, Jane Sullivan, Carol Solomon, Amber Stadler). Sean Ooi assisted with transcribing specimen labels and measurements, Dr. Andre Bochkov (ZIN) photographed type specimens of *Stackelberginia* in St. Petersburg, Dr. H. Don Cameron helped us coin new species etymologies from a sound classical foundation, Kirsten Ruth McKnight Ward prepared figures for the tabular key, Heather Myler helped edit the manuscript, and my mother Joan Boyce McKnight transcribed thousands of specimen labels and helped add new identification labels.

Many friends, colleagues, and extended family members opened their homes and assisted me on collecting trips: Bill and Cheryl Boyce, Dr. Eric Fisher, Dr. Martin Hauser, Dan Swanson, Mark and Suzy McKnight, Dana, Susan, and Edward Fleming, Charlotte Herbert, Shelle Hyde, Bruce Conn, Brent and Kris Gardner, Tom and Karen Tingey, Garth Tingey, Stephen and

Shauna Allen, Sherry Ward, Alma Boyce, Larry and Kathy McKnight. Friends from the online entomology community contributed specimens and ecological data: Alice Abela, Giff Beaton, Paul Bedell. Many curators and collection managers went out of their way to personally assist us during visits: we note the RBCM staff, Dr. Doug Yanega (UCRC), Larry Stevens (MNAZ), Dr. Scott Shaw (ESUW), Gary Shugart and Peter Wimberger (University of Puget Sound), Dr. Rod Crawford (UWBM).

Finally, my father, Dr. Karl B McKnight, provided immeasurable logistical and moral support as a camping, driving, and collecting assistant, analytical partner, and mentor.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Nearctic species of *Lasiopogon* Loew (Diptera: Asilidae) assigned to the *bivittatus* group by Cannings 2002 are revised, with the description of 13 new species, elevation of 1 subspecies to species, and redescriptions of 13 previously described taxa. Keys to adults are updated, notes on taxonomy, distribution, and ecology are provided, and a Bayesian species tree for 67 species of *Lasiopogon* is estimated from one mitochondrial (*COI*) and three nuclear protein-coding loci (*AATS, PEPCK, wingless*), and compared to the previous phylogeny. The following new species of *Lasiopogon* are described: *L. anaphlecter* **sp. nov.**, *L. apoecus* **sp. nov.**, *L. asilomar* **sp. nov.**, *L. bitumineus* **sp. nov.**, *L. canningsi* **sp. nov.**, *L. condylophorus* **sp. nov.**, *L. esau* **sp. nov.**, *L. karli* **sp. nov.** (assigned to *cinereus* group of *opaculus* section), *L. nelsoni* **sp. nov.**, *L. odontotus* **sp. nov.**, *L. sierra* **sp. nov.**, *L. tumulicola* **sp. nov.**, *L. wilcoxi* **sp. nov.**; *L. puyallupi* Cole & Wilcox 1938 **stat. nov.** is elevated from subspecies. *Stackelberginia* Lehr is proposed as the sister taxon to *Lasiopogon* based on morphological and genetic evidence, and *Stackelberginia cerberus* **sp.n**. is described from the Nevada desert (USA) and compared to congeners.

The ecology of 59 Nearctic *Lasiopogon* species is characterized from museum specimens and field observations, and trait divergences for sympatric and allopatric species are compared. Subclades of the *Lasiopogon* tree reveal signatures of different ecological processes: the *bivittatus* and *opaculus* groups show character displacement for seasonal phenology and perch behavior and environmental filtering for habitats; while species from the other half of the phylogeny show no significant associations with those environmental traits but do have a strong correlation with color. Allopatric species pairs have weaker trait associations than sympatric species pairs, supporting the hypothesis that competitive interactions are shaping ecological divergence in these taxa. Bioclimatic variables do not provide meaningful resolution of species niche differences. Given the complexity of trait divergence in *Lasiopogon* flies, evolution is likely proceeding along multiple niche axes which require more complex data collection and modeling to reasonably understand.

CHAPTER I

Introduction

Background

Understanding the processes that produce, maintain, and structure diversity on this planet is one of the central goals of biology. The fight for survival intuitively links the principles of competition and coexistence (Diamond 1975, MacArthur and Levins 1967), but we still struggle to understand the drivers of coexistence in community-level patterns because of potentially confounding signals from the processes of environmental filtering, character displacement, or dispersal limitations. Phylogenetic information can be useful for teasing apart these patterns, especially when working in conjunction with detailed organismal ethology and biogeography. Consequently, my dissertation aims to develop connections between community ecology and evolutionary biology by pairing tests of species-specific ecological evolution with systematic phylogenetics in a continentally distributed taxonomic group: robber flies in the genus *Lasiopogon* Loew.

Robber flies (Diptera: Asilidae), also known as assassin flies, are a diverse, widespread, and well-established radiation of insectivorous predators, with more than 7500 described species and a fossil record extending back to the Cretaceous (Dikow 2009a, Dikow and Grimaldi 2014). Many species are largely considered to be generalist ambush predators, but different taxa coexisting in a region frequently have characteristic behaviors that include preferred habitats, perch positions, seasonal phenology, or prey types (Londt 1994, Shelly 1985); resource partitioning facilitated by this ecological specialization may help shape their remarkable diversification (Haupt 2002, Lehr 1984b).

Unfortunately, researchers have barely begun to touch the interesting evolutionary or ecological developments in this group, for incomplete knowledge of species boundaries and phylogeny hampers downstream questions of evolutionary ecology (Pybus and Harvey 2000). The paucity of asilid research may be attributed to several factors, including a sizable taxonomic gap even in well studied regions, the lack of direct agricultural or medical applications to incentivize funding, and the inherent difficulty of field identification. In some cases, messy

taxonomy and poorly delimited species have left a legacy that dampened asilid research (Cannings 2002, Dikow 2009a). Most publications on robber flies have been confined to purely descriptive taxonomy or ecology, making only occasional passing references to evolutionary history based on intuitive expert opinion. A handful of studies have postulated phylogenetic relationships within a clade using cladistic analyses of morphological similarity (Dikow 2009a, Cannings 2002, Fisher 1986, Adisoemarto and Wood 1975), but molecular phylogenetics have been employed sparingly, and only to evaluate broad tribal relationships across the family (Bybee et al. 2004, Dikow 2009b). This dissertation provides the first estimation of a species tree from molecular data in robber flies.

The focal group of this dissertation is the genus *Lasiopogon*, which was chosen for three primary reasons: a) it is a diverse and broadly distributed group in a clade (the subfamily Stichopogoninae) which is believed to show repeated episodes of ecological specialization, character displacement, and biogeographic expansions (Lehr 1984b, 1975b); b) it has already been a focal group for recent cladistic revisionary taxonomy (Cannings 1996, 2002), which reduced the risk that cryptic undescribed species would ambush the new investigator and provided an opportunity for me to grow in expertise and continuity while working with the incumbent generation of asilidologists; and c) though relatively small and drab, these are elegant flies, easily dissected and straightforward to collect.

Chapter summaries

In **Chapter II**, I estimated the phylogenetic relationship of *Lasiopogon* to the rest of the subfamily Stichopogoninae from molecular data, to establish the broader perspective for this clade and to compare against previous morphology-based cladograms (Cannings 2002, Dikow 2009a). An undescribed species initially thought to be a highly unusual *Lasiopogon* is instead described as the first New World representative to the genus *Stackelberginia* Lehr, which had been overlooked in previous phylogenies, and is likely the sister taxon to the genus *Lasiopogon*. This species provided an ideal outgroup for subsequent work on *Lasiopogon*, and illustrates the multi-continental diversification of this subfamily.

Cannings (2002) sorted most taxa of *Lasiopogon* into species groups based on genitalia morphology, and provided a detailed revision of approximately one-third of the Nearctic taxa (the *opaculus* section). For **Chapter III**, I revised the next-largest group of Nearctic *Lasiopogon* (also approximately one-third): the *bivittatus* group, and described many new species. I also

estimated a species tree from molecular data for all *Lasiopogon* available for Sanger sequencing, sampling nearly 90% of the Nearctic taxa.

In **Chapter IV** I worked from the molecular phylogeny and a comprehensive specimen occurrence database to examine ecological traits that influence species coexistence in Nearctic *Lasiopogon*. By comparing trait divergences of seasonal phenology, habitat, perching behavior, and color differences in sympatric and allopatric species, I reveal how both ecological character displacement and environmental filtering have affected community assembly and diversification in the light of phylogenetic limiting similarity. This represents the ecological capstone of the phylogenetic and systematic work.

Chapter V provides a short discussion of the conclusions and limitations of this work, the value of integrative specimen-based evolutionary ecology, and suggests avenues for fruitful future research arising from this dissertation.

Terminology of asilid morphology

This dissertation is written using the language for asilid morphology (Fig. I.1) developed by Cannings (2002), which mostly follows McAlpine (1981). Stichopogonine flies follow the typical asiloid body plan, with a slender abdomen, long legs, wings extending roughly to the apex of the abdomen, and moderate setation.

The head in lateral view has the antennae inserted just above midpoint. The face has a protuberant gibbosity ventral to the antennal bases, which bears a **mystax** composed of long, strong setae. In the oral cavity ventral to the gibbosity are short cylindrical palps and a strongly sclerotized labial proboscis, which houses the golden hypopharynx used for stabbing prey and feeding. Like all asilids, the compound eyes of both sexes are dichoptic (separate dorsally), with enlarged anterior facets, and like other stichopogoninae, the posterior margin of the compound eye is gently sinuate in the ventral half while the anterior margins of the eyes diverge strongly from the point of antennal insertion to the vertex. The antennae is comprised of four apparent segments: the **scape**, **pedicel**, first flagellomere (called **F1** in this dissertation), and arista (actually comprised of two segments and called the **F2+3** in this dissertation). The scape and pedicel are short, semiglobular or cylindrical; F1 is less that twice as long as the scape and pedicel together, slightly flattened, and varies from rectilinear to oval; F2+3 tapers to a sharp point, varying from much shorter to slightly longer than F1.

The thorax is divided into several sclerites, usually covered in tomentum dorsally and bare on ventral sides. The **scutum** is a slightly rounded shield with a seam (the "**suture**") running from side to side near the midpoint, and is usually covered with tomentum and some longitudinal stripes near the midline: the **medial stripe**, the **acrostichal stripes**, and the **dorsocentral stripes**. The dorsocentral stripes usually have a row of strong bristles (**dorsocentral bristles**) running along their length, these are counted separately anterior and posterior of the suture. Other important bristles are found along the perimeter of the scutum, from anterior to posterior called the **posthumeral, presutural, supraalar, and postalar bristles**. Major sclerites that bear taxonomically significant bristles on the sides of the thorax (pleura) include the **anepisternum**, **anepimeron**, and **katatergite**.

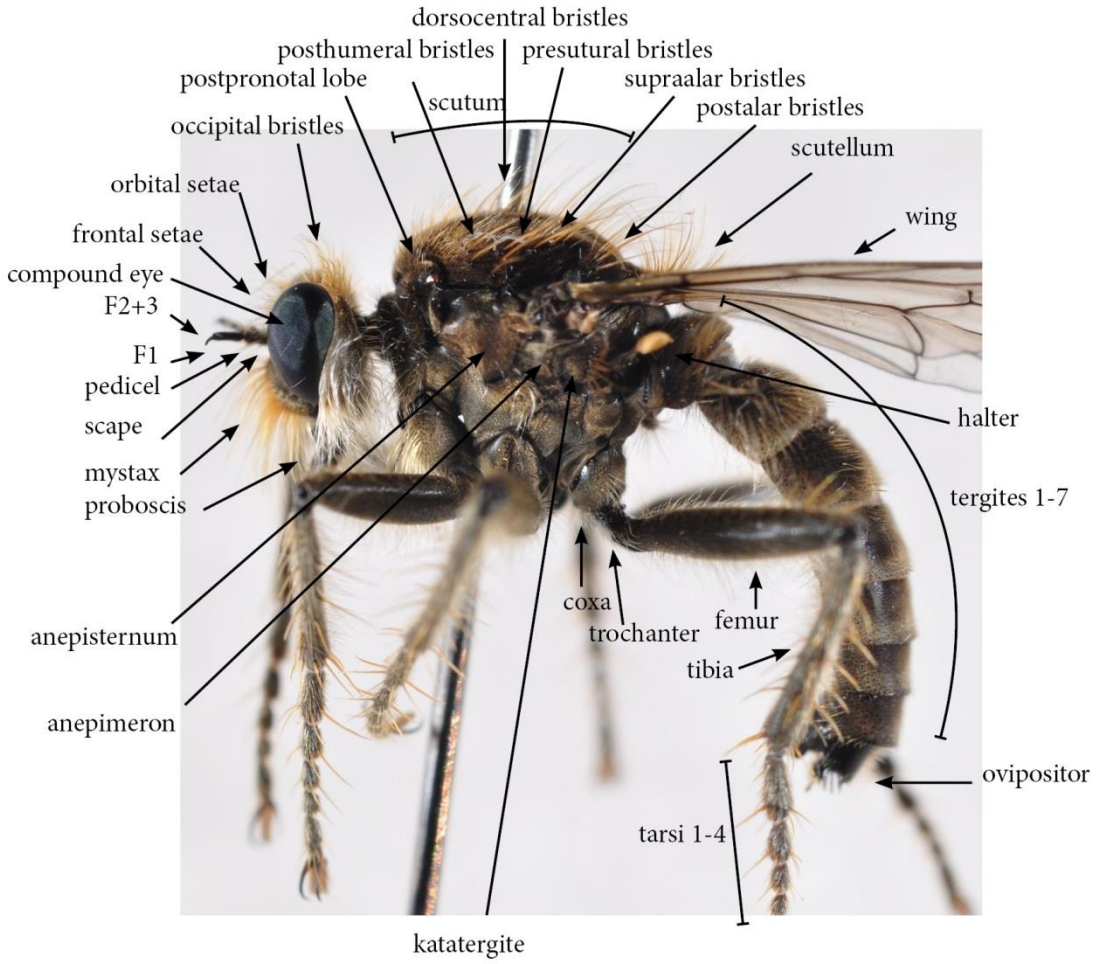


Fig. I.1. Morphological terminology for asilids discussed in this dissertation, as illustrated with a female *Lasiopogon asilomar*.

The legs are fairly long, with the standard segments: the **coxae** are short, extending ventrally from the thorax, with thick tomentum and usually thick setae, some taxa have a spine or peg produding anteriorly from the third pair of coxae; the **trochanter** is short and sandwiched ventrally between the coxa and femur, usually of reddish brown cuticle bare of tomentum; the **femur** and **tibia** are fairly long, not strongly swollen or club-shaped, clothed with fine hairs and some bristles, and with thin tomentum; there are five short **tarsi**, with short decumbent hairs and bristles, the fifth tarsomere has two long curved claws.

The wings are about one third as wide as long, usually fairly clear, but microtrichia on the membrane sometimes give a milky brown tint. Venation does not vary much from species to species, though the relative length of the *d* cell and *rm* crossvein are useful among some taxa. The **halter** varies in color from cream to brown, some species (none in the *bivittatus* group) have the knob marked with a dark brown spot.

The abdomen is slightly tapered from base to apex, with seven apparent undifferentiated segments before the genitalia (segment 8 in the male is hidden under segment 7); the dorsal and ventral halves of each segment are respectively called **tergites** and **sternites**. Tergites 1 to 7 are marked with tomentum patterns useful for species identification, usually with a narrow pale apical ring and basally with dark brown tomentum or the exposed bare dark cuticle. The basal dark area is frequently divided by pale tomentum along the midline, especially in females. Tergite 1 has several long lateral bristles; all tergites have very short fine setae on dorsal surface and some longer hairs along lateral edge.

The genitalia of the male are usually rotated 90–180° around the long axis of the body; this rotation happens shortly after the adult fly emerges, perhaps after the initial mating (Weinberg 1978). As a result, the **epandrium** ("superior forceps" of some authors) is found ventrally instead of dorsally. The epandrium is completely divided into two somewhat curved rectangular lobes. The **hypandrium** and **gonocoxite** ("basistylus" or "inferior forceps") are fused into a round bowl-shaped device opposite the epandrium, with the **gonostylus** ("claspers" or "dististyle") inserted apically. The gonostylus is varies from long hooks to short paddles with various fins and teeth, and is very useful for species diagnosis. The **phallus** ("aedeagus") is attached to the medial surface of the hypandrium/gonocoxite, and the fins and teeth are similarly invaluable for species identification. Opposite the phallus, centered between the epandrium lobes and usually bearing many ventral spines is the **subepandriual sclerite**. The genitalia of the

female begins with the 8th abdominal segment, which is polished and somewhat elongated to form a keel-like **ovipositor**. At the apex of sternite 8 are two flat plates called the **hypogynial valves**, while the apex of tergite 10 is crowned with 12-20 heavy blunt **acanthophorite spines**; these structures are likely used for digging during oviposition. The **spermathecae** extend anteriorly inside the abdomen and are useful for species identification, but have not been described in this work.

Setation in asilids is important but more variable than in many other Diptera. Taxonomically relevant color differences (usually merely pale (white/yellow) vs dark (black/brown)) occur primarily in setae of the mystax, scutum, katatergites, scutellum, legs, and tergite sides. In this dissertation, the word **setae** is used to refer generally to setae of all sizes, whereas if a size distinction is relevant, the term **hairs** is used for fine setae and **bristles** for macrosetae (i.e., where a socket is evident). The following groups of setae are used for species descriptions. On the head: mystax, beard, frontal setae, orbital setae, occelar setae, occipital setae, labial setae. On the thorax:

Descriptions of colors are not based on a standardized code, but are kept as simple as possible and where two colors are named the dominant color is listed first. Caution must be taken when working with teneral (recently emerged) specimens, as the cuticle and setae can appear significantly paler (sometimes even reddish) than in mature specimens; colors in the descriptions refer to mature adults. Furthermore, color of the cuticle must be differentiated from color of the **tomentum** (also called pollinosity or pruinosity). The matte shine effect of tomentum is made from microscopic extensions of the cuticle and is distinct from the polished shine of bare cuticle. In most *Lasiopogon*, the base cuticle is black or dark brown, sometimes reddish; tomentum adds greys, golds, browns, whites, and blacks that can vary based on the angle of light. While the texture of tomentum can still be made out in wet-preserved specimens, the color is usually not apparent, though it usually returns upon drying. “Greased” specimens are similarly problematic, as their colors look uniformly black and can usually only be restored by soaking in an organic solvent.

CHAPTER II

Stackelberginia cerberus sp. n. (Diptera: Asilidae): morphological description, phylogenetic placement and first Nearctic records of the genus

TRISTAN A. MCKNIGHT & ROBERT A. CANNINGS

Abstract

Stackelberginia cerberus **sp.n**. (Diptera: Asilidae) is described from the Nevada desert (USA) and compared to related taxa. This is the first record of the genus in the Western Hemisphere; other species live in the deserts of central Asia. *Stackelberginia* Lehr is proposed as the sister taxon to *Lasiopogon* Loew in the robber fly subfamily Stichopogoninae based on morphological similarities and a Bayesian species tree estimated from one mitochondrial (*COI*) and three nuclear protein-coding loci (*AATS*, *PEPCK*, *wingless*). *Stackelberginia* has the diverging frons and divided, rotated epandrium of *Lasiopogon*, but the facial gibbosity is flat, macrosetae are unusually long, and phenology peaks in late autumn.

Introduction

Robber flies, also known as assassin flies (Diptera: Asilidae), are a major modern radiation of predators with more than 7000 species and 500 genera described and representatives in almost every terrestrial ecosystem (Geller-Grimm 2013). Reliable systematic treatments are essential for downstream analyses of ecology and evolutionary biology; however, most asilid taxa still await modern revisionary work. Diversity patterns in the subfamily Stichopogoninae have suggested repeated bouts of specialization and morphological and ecological character displacement (Lehr 1984), unfortunately, further exploration of these ideas has been hampered by our limited knowledge of phylogenetic relationships in this group.

While preparing forthcoming phylogenetic revisions for the genus *Lasiopogon* Loew and other Stichopogoninae, we discovered an undescribed species with unusual morphology from the southwestern Nevada desert. Classifying this new species provided an opportunity to revise our

understanding of the long-overlooked genus *Stackelberginia* Lehr and consider its place in the Stichopogoninae lineage of robber flies.

Material and Methods

Specimens were obtained from the personal collections of Eric Fisher and the first author; material has been deposited in the following collections: California Academy of Sciences, San Francisco, CA, USA (CAS); Eric Fisher private collection, El Dorado Hills, CA, USA (FISH); National Museum of Natural History, Washington D.C., USA (USNM); Royal BC Museum, Victoria, BC, Canada (RBCM); University of Michigan Museum of Zoology, Ann Arbor, MI, USA (UMMZ). Type specimens of *Stackelberginia gracilis* Lehr and *S. tsharykulievi* Lehr were photographed by associates at the Russian Zoological Institute of Science, St. Petersburg, Russia (ZIN). Relevant passages from the original Russian literature were translated by the first author and are available on request.

The known specimens of Asian *Stackelberginia* are more than 50 years old and beyond the capabilities of our molecular lab, so we only used specimens from the American *Stackelberginia* to estimate its position in the species tree. To reduce computational complexity and uncertainty not essential for the intergeneric scope of this study, six *Lasiopogon* taxa were selected as representatives of the major species groups, based on a phylogenetic revision of that genus currently in preparation. Species of *Stichopogon* Loew and *Townsendia* Williston, with multiple nuclear loci sequenced, were included to represent the other major branches of North American Stichopogoninae, and four robber flies from other subfamilies and one mydas fly (Mydidae) were used as outgroups. Specimens used for genetic analysis are summarized in Table II.2.

Morphological processing

Formats of the species description, descriptive terminology, and label transcription follow Cannings (2002), as does the protocol for genitalia dissection and measurements. The following abbreviations are used for measurements: HW= head width, FW= face width, VW= vertex width, VD= vertex depth, GH= gibbosity height, GL= gibbosity length, LF1= length of flagellomere 1, WF1= width of flagellomere 1, LF2+3= length of flagellomeres 2+3, DCI= length from r-m crossvein to base of discal cell divided by overall length of discal cell. All

specimens were measured for body length; two males and two females were used for other measurements. Images were taken with the Image-Pro Plus software via a Leica DC 300 camera mounted on a Leica MZ 16 dissecting microscope and measurements made in Adobe Photoshop CS5 12.0.4 after calibration with a stage micrometer.

Molecular processing

Specimens for molecular work were stored in 95% ethanol promptly after capture. At least the head, terminalia, wings, and one set of fore/mid/hind limbs were preserved as morphological vouchers for DNA-extracted specimens; these have been deposited at the UMMZ. Genomic DNA was extracted using Qiagen DNeasy Blood and Tissue or QIAamp DNA Micro kits respectively for larger or smaller specimens (QIAGEN Inc., Valencia, CA, USA), following the manufacturer's protocols; extractions were eluted into H_2O and stored at -20°C.

Loci from one mitochondrial and three nuclear protein coding genes were amplified: cytochrome oxidase I (*COI*; 658 bp), phosphoenolpyruvate carboxykinase (*PEPCK*; 585 bp), wingless (*wg*; 553 bp), and alanyl-tRNA synthetase (*AATS*; 550 bp); primers for the PCR reactions are presented in Table II.1. PCR amplifications were performed on an Eppendorf epgradient Mastercycler using this universal recipe: 1 µL DNA template, 5.69 µL H_2O, 1 µL 10x PCR buffer, 0.5 µL dNTPs, 0.2 µL BSA, 0.4 µL each primer, 0.75 µL 50 mM $MgCl_2$, 0.06 µL Platinum Taq. Thermocycler protocols were as follows: *COI* : 35 cycles of 30 sec at 94°C, 30 sec at 46°C, 30 sec at 72°C; *wg* :35 cycles of 45 sec at 94°C, 45 sec at 58°C (first 5 cycles touchdown from 64–60°C) , 1 min at 72°C; *PEPCK* and *AATS*: 35 cycles of 45 sec at 94°C, 45 sec at 50°C (first 5 cycles touchdown from 56–52°C) , 1 min at 72°C. Cycle steps for all samples were preceded by a denaturing step of 5 min at 94°C and followed by an extension step of 7 min at 72°C. Amplification success was verified by visualization on a 2% agarose gel; products were then purified with Affymetrix ExoSAP according to manufacturer's protocols and sequenced by the University of Michigan Sequencing Core on an Applied Biosystems 3730xl DNA Analyzer. All sequence files were visually inspected and cleaned in Sequencher 4.2 (GeneCodes Corp., Ann Arbor, MI, USA) and aligned in MEGA6 (Tamura *et al.* 2013) or MESQUITE 3.02 (Maddison and Maddison 2016). The *wg* alignment contained one variable-length intron that was removed before analysis, a short variable repeat section at amino acid (AA) positions 42–58, and a single AA indel at position 89; the other loci lack indels and were trivial to align.

A species tree was estimated using the random local clock species tree template in BEAST 2.4.3 (Bouckaert *et al.* 2014, Drummond and Suchard 2010), with *Mydas clavatus* (Drury) (Mydidae) set as the outgroup. Each locus was partitioned independently during phylogenetic analysis; the third codon position in *COI* was unlinked from (1+2) to allow independent site and clock models but linked tree models with 0.5 ploidy (versus 2.0 ploidy for the nuclear loci). Optimal nucleotide substitution models compatible with the *BEAST software for each locus and partition were determined following AIC and BIC in jModelTest 2.1.5 (Darriba *et al.* 2012, Guindon and Gascuel 2003): *AATS*, *PEPCK*, *COI* (1+2): GTR+G; *wg*: TrN+G; *COI* (3): HKY+G; in all cases gamma was estimated with 4 categories. Default settings were kept for most parameters and priors, except setting the birth death tree model and constant populations. Two chains were run with length set to 200 million and sampling every 10 thousand. Parameter distributions and convergence of MCMC runs were assessed using Tracer 1.6 (Rambaut *et al.* 2014); chains were combined using LogCombiner, discarding the first 10% of each run as burn-in and resampling half as often (ESS for all priors was >200). Trees were visualized in FigTree 1.4 (Rambaut 2012).

Table II.1. Primers used for genetic sequencing.

Locus	**Primer name**	**Primer sequence**	**Reference**
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer *et al.* 1994
COI	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al.* 1994
Wingless	WG550F	ATGCGTCAGGARTGYAARTGYCAYGGYATGTC	Wild and Maddison 2008
Wingless	WGABRZ	CACTTNACYTCRCARCACCARTG	Wild and Maddison 2008
PEPCK	PK282F	GAAGGATGGCTBGCNGARCAYATG	Wild and Maddison 2008
PEPCK	PK485R	GCAGCVGTNGCYTCRCTYCTCAT	Wild and Maddison 2008
AATS	AATS1F40	GNATGAAYCARTTYAARCCNAT	Dikow 2009b
AATS	AATS1R244	CATNCCRCARTCNATRTGYTT	Dikow 2009b

Figure II.1. *Stackelberginia cerberus* **sp.n.** female habitus and head detail.

Taxonomy

Stackelberginia cerberus **sp.n.** McKnight

Diagnosis. A small grey species similar to *Lasiopogon* but with mostly flattened facial gibbosity; reduced mystax; bristles of ocellar triangle, thorax, and legs extremely long and strong; tarsal claws unusually large; numerous strong, straight macrosetae behind dorsal and lateral margins of compound eyes; metacoxae with anterior blunt peg; cuticle dark except for ferruginous tibiae and tarsi, mostly covered in grey tomentum; genitalia ferruginous, epandrium completely divided as in *Lasiopogon*, narrow. (Figs II.1, II.2)

Description. *Body length* ♂ 8.5–10 mm; ♀ 8.5–11.5 mm.

Head. Cuticle black; tomentum of face silver, vertex and occiput grey. Facial gibbosity greatly reduced, leaving only a slightly swollen angle above oral margin but otherwise not extending beyond eyes in lateral view. All setae on head white except ocellar and orbital bristles, which are typically chestnut brown. Mystax setae long, loosely clumped over oral margin with a small gap

dorsomedially; frons with a clump of short, thick setae midway between antennae and ocellar triangle; one long, strong orbital seta anteriorly inclined, occasionally with another short fine seta; ocellar triangle with two long, strong setae and several short fine hairs anteriorly inclined along posterior edge, longest bristle to 0.7mm; occipital bristles behind posterior margin of eye erect, relatively short and straight, in lateral view extending ventrally to midpoint of eye. Palps with fine white hairs along length; robust setae on postgena.

HW ♂ 1.48–1.88mm; ♀ 1.64–1.88mm. FW ♂ 0.28–0.34mm; ♀ 0.32–0.35mm. VW ♂ 0.66–0.73mm; ♀ 0.67–0.77mm. GL ♂ 0.25–0.28mm; ♀ 0.25–0.33mm. VW/HW = ♂ 0.39–0.45; ♀ 0.41. FW/VW = ♂ 0.42–0.46; ♀ 0.46–0.48. VD/VW = ♂ 0.10–0.14; ♀ 0.12–0.13. GH/GL = ♂ 0.43–0.52 ♀ 0.42–0.48.

Antennae. Dark brown, base of pedicel paler. Robust white setae on scape and pedicel. F1 rectangular with a slight bulge at midlength; F2+3 long, with pronounced apical spine. WF1/LF1 = ♂ 0.22; ♀ 0.20–0.21. LF2+3/LF1 = ♂ 0.50; ♀ 0.67–0.70.

Thorax. Thoracic cuticle dark brown, covered in thick grey tomentum. Prothorax with hairs white; postpronotal lobes chestnut brown with lateral angle reddish, hairs white; postalar lobes reddish. Scutum tomentum grey, without stripes or spots; short hairs sparse, white around perimeter and brown/black over dorsum. Dorsocentral bristles brown, prominent (longest 0.85mm), 1 anterior, 2 posterior. One each of postalar, supra-alar, presutural, and posthumeral bristles, all brown and very long (longest 1.3mm). Scutellum covered in grey tomentum, without impressed rim, bare on disc, 5-6 long white bristles apically with a few short fine hairs just inside.

Pleural tomentum grey, all hairs and bristles white. Katatergite setae 6–7 with a few finer hairs mixed dorsally; katepisternal setae fine, short; anepisternum with 2 long, prominent setae (longest 1.2mm) at posterior edge and a patch of fine hairs along dorsal margin; anepimeron without setae. Antepronotum with 8–12 fine setae; proepisternum with 4–6 strong long setae and 0–2 fine hairs.

Legs. Cuticle black except reddish tibia, trochanters, extreme medial and apical tips of femorae, and tarsal bases; tomentum grey, very thin below femora. Pronounced coxal peg with rounded

apex, does not taper, 2 fine setae projecting ventrally at base of peg. All hairs and bristles of legs white except on tarsi, where mostly brown. Coxae with dense, long, strong bristles facing anteriorly (on procoxa) or laterally (on meso- and metacoxae); 40+ on procoxa, 3–12 on mesocoxa, 4 on metacoxa. Femora with fine, short procumbent hairs and strong erect bristles; 5–6 ventral bristles longer than adjacent hairs on pro- and mesofemur, metafemur with only fine hairs just longer than surrounding setae. Apical and dorsolateral bristles strong, numerous: profemur with 3–5, mesofemur with 2–4, metafemur with 5–7. Bristles on tibiae and tarsi strong, long; protibia with longest bristle 3.5 x longer than tibial width. Tarsal claws huge, with reddish base and black apices.

Wings. Veins yellow to dark brown, darker apically; membrane hyaline, slightly brown in oblique view. DCI = 0.52–0.58; cell m3 broadly open; cell cu*p* barely closed at wing margin (varies from slightly stalked to slightly open). Halter cream to light brown; knob without dark spot.

Abdomen. Tergite base color dark brown, lighter apically; covered in pale grey tomentum without other patterning. Tergite 1 with 6–8 strong bristles basolaterally, other tergites with strong short lateral setae, longest apically. Lateral setae white, dorsal setulae white laterally, black near midline. Sternite tomentum grey; setae white; sternite 1 with clump of 5–8 prominent erect setae. Tergite 8 red, visible between tergite 7 and terminalia. Terminalia red, with long hairs (white in male, black in female), in male rotated to one side.

Male genitalia. Epandrium and hypandrium/gonocoxite complex reddish-orange with darker apices, without tomentum, clothed in long white setae. Setal brush on hypandrium/gonocoxite complex white, hairs long but comparatively sparse. Epandrium completely divided, in lateral view each half with width about 0.48x length, widest at apex, ventral and dorsal margins mostly parallel, slumping ventrally, apex truncate with rounded corners. In dorsal view, medial margins of epandrial halves very shallowly concave, almost straight. Epandrial apodeme shallow. Basal sclerite absent.

Gonostylus elongate, slender, curved dorsally like a hooked finger, with another point dorsolaterally at the base. Long hairs over basal part of gonostylus. Hypandrium/gonocoxal

complex in ventral view with width about 0.86x length, transverse slit a prominent semicircle with apex pointing distally. Gonocoxal apodemes long, in lateral view exposed length about 0.7x the basal width of the hypandrium; apodeme with sclerotized web ventrally.

Phallus. Paramere sheath long and slender, curved ventrally like a goose neck. Dorsal carina a low ridge (no wider than the paramere sheath itself) that follows the curvature of the paramere sheath and terminates without a notch before the apex.
Subepandrial sclerite of V-shaped type (Cannings 2002); broad unsclerotized portion in basal 0.65; spines slender, attenuate, sparsely scattered over surface.

Female genitalia. (Undissected) Hairs dark brown/black, erect, abundant. Tergite 8 black, sternite 8 red/yellow, hypogynial valves darker, with many dark hairs. Lateral lobe with dark setae. Acanthophorite spines black.

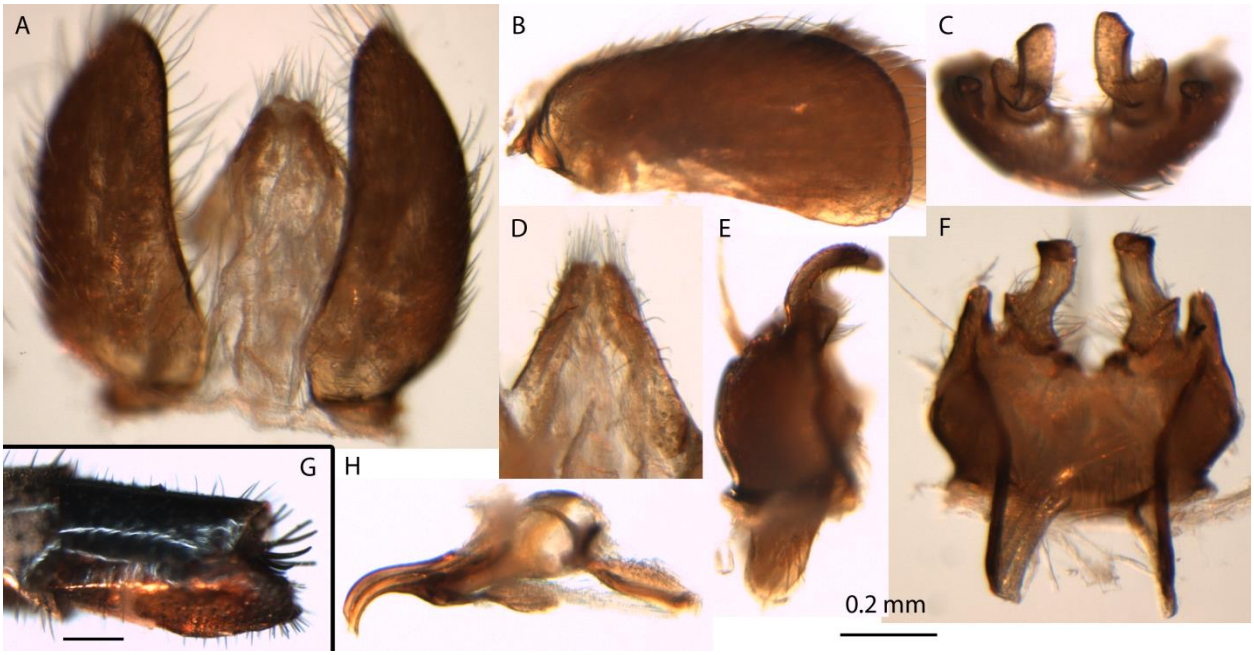


Figure II.2. *Stackelberginia cerberus* **sp.n.** genitalia detail: A) epandrium, dorsal; B) epandrium lateral; C) gonostylus, apical; D) subepandrial sclerite, ventral; E) hypandrium complex + gonosylus, ventral; F) hypandrium complex + gonosylus, lateral; G) female ovipositor, lateral; H) phallus, lateral. Scale bars are 0.2 mm.

Type Material.
HOLOTYPE. ♂ labelled: "[rectangular white label] NEV: Nye Co: NTS [Nuclear Test Site]/ Rock Valley/ IX-12-76, can tr./E.L. Sleeper et al." My holotype label "HOLOTYPE/ Stackelberginia ♂/ cerberus/ des. T.A. McKnight 2017 [red, black-bordered label]" has been attached to this specimen. USNM label: USNMENT01295437.

PARATYPES (6 designated). **U.S.A.: Nevada**, Clark Co: Wheeler wash 6 mi NE of Pahrump, N 36.24678° W 115.89428°, elev: 1251 m, 5.x.2013, T.A. McKnight (1♂, 1♀, CAS); Nye Co: NTS [Nuclear Test Site] Rock Valley can tr., 3.x.1975, E.L. Sleeper (1♀, FISH), 12.ix.1976, E.L. Sleeper (1♂, RBCM); Rock Valley wash jct Hwy 95, 5 mi E of Amargosa Valley city, N of hwy, N 36.63359° W 116.31018° elev: 878 m, 6.x.2013, T.A. McKnight (1♀, RBCM, 1♀, UMMZ).

Type Locality. USA; Nevada, Nye Co., Nuclear Test Site, Rock Valley.

Taxonomic Notes. This species was included in Cannings (2002) as "L. unc-7 sp.n." and had been assigned a manuscript name of "mirus" because it was thought to be a miraculously unusual *Lasiopogon*. This epithet was changed after reclassification outside *Lasiopogon*.

Etymology. Latin *Cerberus,* from the Greek Κέρβερος, noun in apposition, named in similarity to the hound guarding the gates of the underworld in Greek mythology. The type locality for this predator is just outside the boundaries of both Death Valley National Park (the lowest site in North America) and the Yucca Mountain nuclear waste facility—sites with a suitably Hadean flair.

Distribution. Nearctic: USA; known only from the Amargosa desert in southwestern Nevada. The other species of *Stackelberginia* are known from Kazakhstan and Turkmenistan.

Natural History. Habitat: sandy dry desert washes, usually found perching on fist-sized rocks in sandy areas near clumps of vegetation (Fig. II.3). One female was observed preying on a slightly-smaller fly (not collected). The fall flight period (12 September–6 October) is distinctive within the subfamily.

Other assassin flies were also active at the *Stackelberginia* sites at the same time. These were identified using keys in Wood (1981) and Wilcox (1961, 1965, 1966) and voucher specimens have been deposited at the RBCM and UMMZ: *Hodophylax basingeri* Pritchard, *Cophura fisheri* Wilcox, *Efferia (Aridefferia) basingeri* Wilcox.

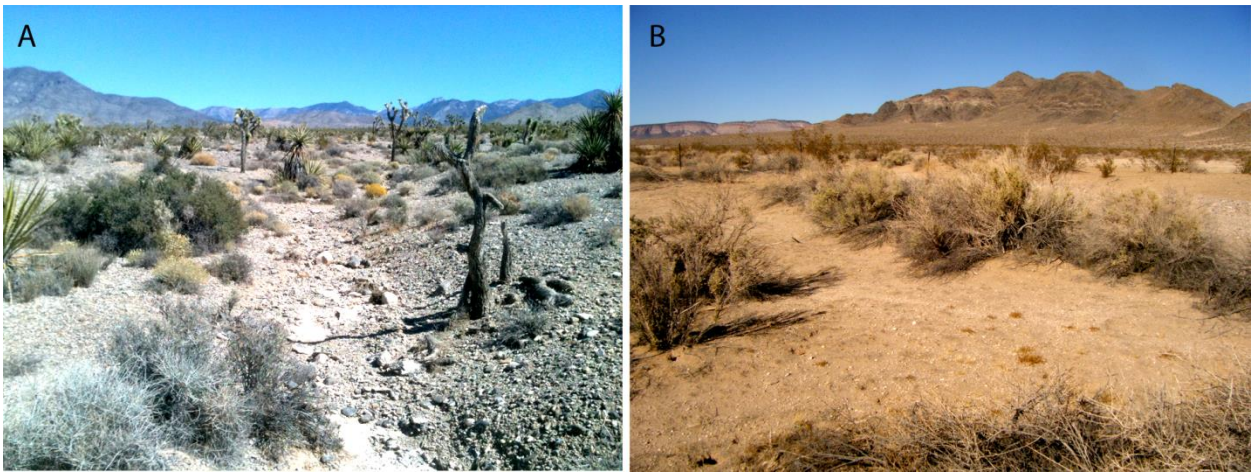


Figure II.3. Habitat of *Stackelberginia cerberus* **sp.n.** in Nevada (see paratype list for more precise locality data): A) Clark Co.: Wheeler wash; B) Nye Co.: Rock Valley wash. Specimens were caught on small stones and sand along the washes.

Phylogeny

The species tree supports *Stackelberginia* as sister to *Lasiopogon*, and this clade as sister to the rest of the subfamily (Fig. II.4); these relationships were also recovered in each of the four individual gene trees (not shown). Bayesian support values are high (≥ 0.92) throughout the tree, except for some uncertainty for phylogenetic relationships within *Lasiopogon* and at the Stichopogoninae root. Lower support values for the subfamily root appear to stem from a basal polytomy in COI; this locus is known to have trouble resolving deeper level phylogenetic relationships (Matsuda *et al.* 2014). Intrageneric relationships within *Lasiopogon* and *Stichopogon* will be covered in future publications with more comprehensive taxon sampling, but the overall genus-level topology matches our prior expectations from morphology—e.g., *Townsendia* grouping with *Stichopogon*, and the Asilinae (*Proctacanthus* Macquart) and Ommatiinae (*Ommatius* Wiedemann) clustering together in the outgroup.

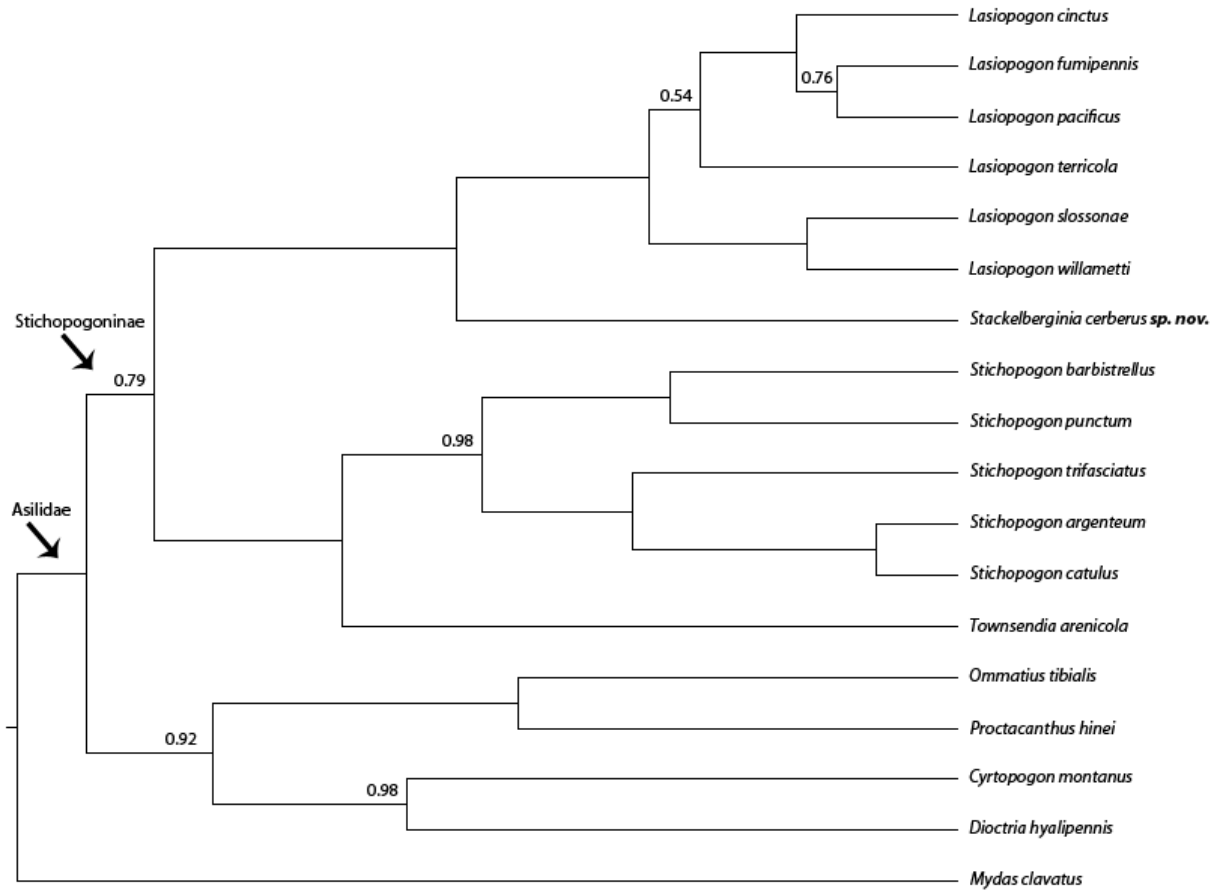


Figure II.4. Species tree for representatives of *Stackelberginia*, *Lasiopogon*, *Stichopogon*, *Townsendia*, and Asilidae and Mydidae outgroups, estimated via Bayesian inference in STARBEAST2 from one mitochondrial locus (COI) and three nuclear protein coding loci (wingless, PEPCK, AATS). Branch labels show support for nodes when posterior probability <1.

Discussion

These specimens were initially thought to represent an extraordinary new *Lasiopogon* species (hence its inclusion in Cannings, 2002 as "L. unc-7") but comparison to the text and figures of *Stackelberginia* descriptions (Lehr 1964, 1984) and to photographs of the type specimens at St. Petersburg (Fig. II.5) suggest a closer affinity to *Stackelberginia*. Rationale for this taxonomic decision is enumerated below. Whether these disparately distributed taxa actually constitute a single monophyletic group or are merely similar but independent relic branches left from the early diversification of the Stichopogoninae lineage cannot be positively ascertained until newer specimens of the Central Asian taxa are collected and made available for DNA analysis or genitalia dissection, and we invite entomologists collecting in these areas to collaborate in this hunt.

Figure II.5. Holotypes of *Stackelberginia tsharykulievi* Lehr (A, B, E) and *S. gracilis* Lehr (C, D, F); lateral, dorsal and head detail.

Higher level relationships in the Asilidae have been repeatedly addressed over the last century, but *Stackelberginia* remained largely forgotten on the sidelines, likely because the genus is known from only a few specimens collected long ago in a region now difficult to access. Following Karl's (1959) cladistic insights on male genitalia in the Asilidae, Lehr (1984) recognized two separate branches of Stichopogoninae: one with unrotated genitalia and the epandrium halves fused into a single hood-like structure (as in *Stichopogon* and most of the group); the other with genitalia inverted and the epandrium halves completely divided (e.g., *Lasiopogon* and *Stackelberginia*). This hypothesis was described verbally, not statistically tested, but it represents the only prior supposition and justification of *Stackelberginia* phylogeny. Morphological and molecular parsimony analyses in recent years (Cannings 2002, Dikow 2009a, 2009b) passed over *Stackelberginia* due to lack of specimens but otherwise supported a monophyletic subfamily with *Lasiopogon* as the sister taxon to the rest of the subfamily.

The American new species and the Central Asian *Stackelberginia* do indeed share the primary defining characters of the Stichopogoninae subfamily (Dikow 2009a, Cannings 2002): dorsally widening frons, sinuate lower posterior margin of the compound eye (albeit slightly), anterior anepisternal setae absent, and female sternite 8 platelike with flattened and separated hypogynial valves. The fused prosternum and proepisternum are not visible in photographs of

Central Asian *Stackelberginia*, but are confirmed in *S. cerberus* **sp.n.** Unusually for this subfamily (Dikow and Grimaldi 2014), the wing cell cu*p* is open in a few individuals of the type series for *S. cerberus* **sp.n.**

The case for classifying this new species with the Central Asian *Stackelberginia* is based on similarities in morphology, phylogeny, and ecology. (i) Morphology: key characters shared by these taxa include: rotated male genitalia; completely divided epandrium; medial tuft of hairs on the hypandrium; facial gibbosity mostly flattened; mystax loosely clumped just above oral margin; numerous macrosetae extending around posterior margin of compound eye; bristles of the mesonotum, mesopleuron, coxae, and legs unusually long and strong; body covered in thick tomentum; and strong claws. The divided and rotated male genitalia are also found in *Lasiopogon*, but not in combination with all the other characters. (ii) Phylogeny: as noted above, Lehr did not publish a cladogram that included *Stackelberginia*, but his text (Lehr 1984) suggests grouping the genus with *Lasiopogon* and not *Stichopogon*, *Townsendia*, or others. Our molecular analysis strongly supports the placement of *S. cerberus* **sp.n.** as sister to all Nearctic and Palearctic *Lasiopogon*, but with a substantial branch length between the genera. (iii) Ecology: although little is known of the ecology of these species, they are notably similar for emerging during the autumn (Sept–Oct) instead of the spring or summer; this phenology is almost unknown in *Lasiopogon* species, which primarily fly in spring. Habitats for *Stackelberginia* from both continents (Lehr 1964, 1980, 1984, 1988) can be characterized as desert areas where sandy and gravely patches mix near intermittent water (e.g., dry washes, alkali flats); they are found perching directly on the sand or on nearby rocks or plants.

Despite these similarities, there are some differences, most notably in the morphology of the antenna and the coxal pegs. The flagellum of *S. tsharykulievi* is longer and narrower than in *S. cerberus* **sp.n.** and has the arista shortened and inset apically; the flagellomeres of *S. gracilis* are missing. Neither of the Central Asian species appears to have a metacoxal peg in the photographs on hand, nevertheless, the stout rounded coxal peg of *S. cerberus* **sp.n.** is unlike those of *Lasiopogon* (sharp and short, if present, Fig II.6); it instead resembles the pegs found in certain groups of *Stichopogon*, *Lissoteles* Bezzi, *Rhadinus* Loew, and many outgroup taxa and probably represents an ancestral state. Similar blunt metacoxal knobs are also thought to be pleisiomorphic in stiletto flies (Winterton 2004).

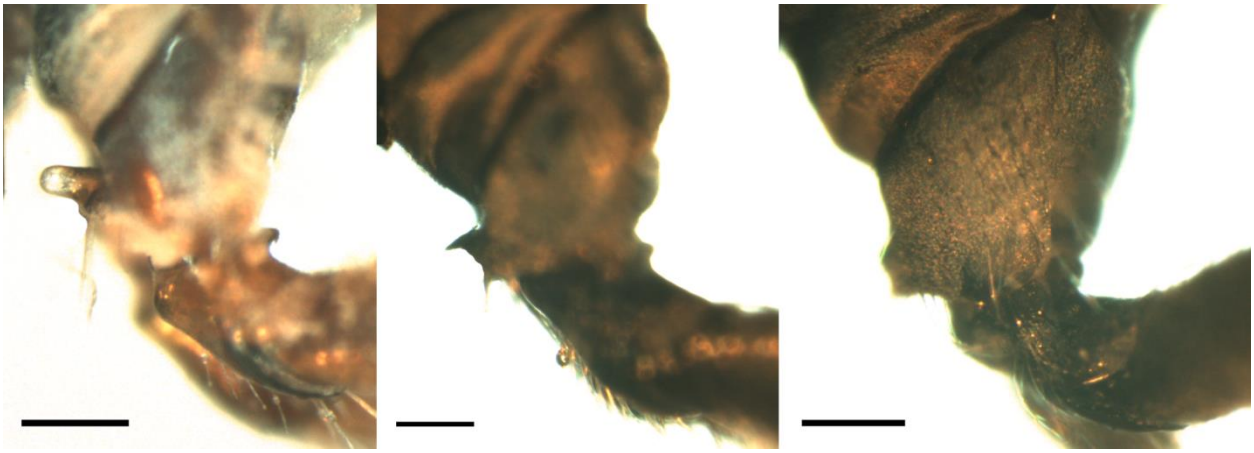


Figure II.6. Coxal peg types in Stichopogoninae: A) blunt, robust (*Stackelberginia cerberus* sp.n.); B) sharp, short (*Lasiopogon canus* Cole and Wilcox); C) no peg (*Lasiopogon schizopygus* Cannings). Scale bar is 0.2 mm.

In the commonly used key to genera from the Manual of Nearctic Diptera (Wood 1981), *S. cerberus* **sp.n.** runs to couplet 22a (*Stichopogon*); it can be distinguished from *Stichopogon* by having two presutural bristles (instead of one), ocellar macrosetae continuing ventrally to midpoint of eye, viewed laterally (instead of ending in the dorsal quarter), and the divided epandrium in the male (instead of a fused hoodlike sclerite).

Coming on the heels of a recent review of southern Nevada robber flies that documented many new state records (Stevens and Scarbrough 2015); it is evident that undescribed fly diversity abounds even in the relatively well-sampled United States. The extremely patchy nature of robber fly distributions is undoubtedly both a blessing and a curse for biologists: it may help species diversify and allow these flies to persist in fragmented habitats, but it also may prevent their discovery, even by specialists. The collections of *S. cerberus* **sp.n.** fall just outside the main areas studied by Stevens and Scarbrough, i.e., Ash Meadows National Wildlife Refuge and Spring Mountains National Recreation Area. It is possible that other undescribed species of *Stackelberginia* remain in the deserts of the American Southwest.

Table II.2. Taxonomy, collection data, genetic sampling, and voucher location for specimens used in the Stichopogoninae species tree.

Taxon	Locality	GenBank #				Specimen Voucher #
		AATS	COI	PEPCK	WG	
Cyrtopogon montanus Loew	USA: Oregon: Clackamas Co., Mt. Hood, Timberline lodge area; N 45.3326° W 121.7056°, 15 Jul 2014, col. T. & K. McKnight.	KY906309	KY914526	KY914509	-	UMMZ-TAM-692-1
Dioctria hyalipennis (Fabricius)	USA: Michigan: Washtenaw Co., Ann Arbor, Bird Hills Nature Area, forest trail; N 42.3081° W 83.7600°; 31 May 2012; col. T. McKnight.	KY906300	KY914516	KY914499	-	UMMZ-TAM-347-1
Lasiopogon cinctus (Fabricius)	Sweden: SÖ: Nyköping Strandbadet Byggninge, path to beach near parking; N 58.7801° E 17.3917°; 30 May 2009; col. K.C. Holston.	KY906298	KY914514	KY914497	KY914530	UMMZ-TAM-RBCM-17
Lasiopogon fumipennis Melander	USA: Oregon: Hood River Co., Sherwood cmpgd, 6 mi E of Mt. Hood peak; N 45.3943° W 121.5698°; 15 Jun 2013; col. T. McKnight.	KY906304	KY914521	KY914504	KY914536	UMMZ-TAM-472-3
Lasiopogon pacificus Cole and Wilcox	USA: Oregon: Lane Co., Sutton Creek cmpgd, forest trail to Alder dunes, 6 mi N of Florence; N 44.0555° W 124.1060°; 21 Jun 2013; col. T. McKnight.	KY906305	KY914522	KY914505	KY914537	UMMZ-TAM-488-1
Lasiopogon slossonae Cole and Wilcox	USA: New York: Essex Co., W Branch Ausable River at 118 River Rd; N 44.2659° W 73.9590°; 2 Jun 2014; col. K. McKnight.	KY906297	KY914513	KY914496	KY914529	UMMZ-TAM-KBM2014060202
Lasiopogon terricola (Johnson)	USA: Michigan: Washtenaw Co., sandy blowout in oak forest SW of Pickerel Lake; N 42.4120° W 83.9882°; 10 May 2013; col. T. McKnight.	KY906303	KY914520	KY914503	KY914535	UMMZ-TAM-404-1

Lasiopogon willametti Cole and Wilcox	USA: Oregon: Marion Co., Willamette River sandbars at Willamette Mission SP, 4 mi W of Waconda; N 45.0821° W 123.0618°; 18 May 2012; col. T. & K. McKnight.	KY906299	KY914515	KY914498	KY914531	UMMZ-TAM-338-8
Mydas clavatus (Drury)	USA: North Carolina; Wake Co., 4.8 km E Angier; N 35.5167° W 78.6667°; 5 Jul 2003; col. D. Pritchard.	EF650269	KT733514	-	-	USNMENT00914563
Ommatius tibialis Say	USA: Rhode Island, Washington Co., South Kingstown, Great Swamp; N 41.4611° W 71.5864°; 16 Jul 2006; col. T. Dikow, M. Thomas, K. Bayless.	EF650302	KT733263	-	-	USNMENT00914193
Ommatius tibialis Say	USA: Michigan: Oakland Co., Kensington Metropark, Martindale Dr. glade; N 42.5403° W 83.6295°; 14 Jul 2012; col. T. McKnight.	-	KY914519	KY914502	KY914534	UMMZ-TAM-379b-2
Proctacanthus hinei Bromley	USA: Michigan: Berrien Co., Warren Dunes SP; N 41.9123° W 86.6014°; 14 Jul 2012; col. T. McKnight.	KY906301	KY914517	KY914500	KY914532	UMMZ-TAM-360-1
Stackelberginia cerberus **sp.n.**	USA: Nevada: Clark Co., Wheeler wash, 6 mi NE of Pahrump; N 36.2468° W 115.8943°; 5 Oct 2013; col. T. McKnight.	KY906307	KY914524	KY914507	KY914539	UMMZ-TAM-509-1
Stackelberginia cerberus **sp.n.**	USA: Nevada: Nye Co., Rock Valley wash N of jct Hwy 95, 5 mi E of Amargosa Valley city; N 36.6336° W 116.3102°; 6 Oct 2013; col. T. McKnight.	KY906308	KY914525	KY914508	KY914540	UMMZ-TAM-512-1
Stichopogon argenteus (Say)	USA: Michigan: Leelanau Co., dunes W of D.H. Day group cmpgd; N 44.8949° W 86.0472°; 17 Aug 2013;	KY906306	KY914523	KY914506	KY914538	UMMZ-TAM-502-1

	col. T. McKnight.					
Stichopogon barbistrellus Loew	Mongolia: Bayan-Olgii/Khovd Aimag: Bulgan Soum, stream confluence of Deed Nariin Gol with Bulgan Gol ~55 km N Bulgan; N 46.5531° E 91.3885°; 10 Jul 2009; col. Mongolian Aquatic Insect Survey, C.R. Nelson.	KY906296	KY914512	KY914495	-	UMMZ-TAM-CRN-9251-1
Stichopogon catulus Osten Sacken	USA: New Mexico: Grant Co., Gila River below Grapevine campsite; N 33.1779° W 108.2015°; 6 May 2015; col. T. & K. McKnight.	KY906310	KY914527	KY914510	-	UMMZ-TAM-754-1
Stichopogon punctum Loew	South Africa: KwaZulu-Natal; Cumberland Nature Reserve; S 29.5069° E 30.5064°; 13 Jan 2004; col. J. Londt, T. Dikow.	EF650315	KT733193	-	-	USNMENT00914067
Stichopogon trifasciatus (Say)	USA: Michigan: Mason Co., Ludington SP, dunes S of Skyline dune; N 44.0318° W 86.4966°; 15 Jun 2012; col. T. McKnight.	KY906302	KY914518	KY914501	KY914533	UMMZ-TAM-366-2
Townsendia arenicola Scarbrough	USA: Florida: Polk Co., Broussard Catfish Creek SP, site 8; N 27.9827° W 81.4947°; 24 Jun 2010; col. M. & N. Deyrup, J. Dunlap.	-	KY914511	KY914494	KY914528	UMMZ-TAM-ARCH-2

CHAPTER III

Molecular phylogeny of the genus *Lasiopogon* (Diptera: Asilidae) and a taxonomic revision of the *bivittatus* group

TRISTAN A. MCKNIGHT & ROBERT A. CANNINGS

Abstract

Nearctic species of *Lasiopogon* Loew assigned to the *bivittatus* group by Cannings 2002 are revised, with the description of 13 new species, elevation of 1 subspecies to species, and redescriptions of 13 previously described taxa. Keys to adult *Lasiopogon* are updated, and notes on taxonomy, distribution, phylogeny, and ecology are provided. A Bayesian species tree for 67 species of *Lasiopogon* is estimated from one mitochondrial (*COI*) and three nuclear protein-coding loci (*AATS*, *PEPCK*, *wingless*), and compared to the previously published morphological phylogeny. The following new species of *Lasiopogon* are described (assigned to the *bivittatus* group except as noted): *L. anaphlecter* **sp. nov.**, *L. apoecus* **sp. nov.**, *L. asilomar* **sp. nov.**, *L. bitumineus* **sp. nov.**, *L. canningsi* **sp. nov.**, *L. condylophorus* **sp. nov.**, *L. esau* **sp. nov.**, *L. karli* **sp. nov.** (assigned to *cinereus* group of *opaculus* section), *L. nelsoni* **sp. nov.**, *L. odontotus* **sp. nov.**, *L. sierra* **sp. nov.**, *L. tumulicola* **sp. nov.**, *L. wilcoxi* **sp. nov.**; *L. puyallupi* Cole & Wilcox 1938 **stat. nov.** is elevated from subspecies; and the following existing species are considered valid: *L. actius* Melander 1925, *L. albidus* Cole & Wilcox 1938, *L. arenicola* (Osten Sacken 1877), *L. bivittatus* Loew 1866, *L. californicus* Cole & Wilcox 1938, *L. dimicki* Cole & Wilcox 1938, *L. drabicola* Cole 1916, *L. gabrieli* Cole & Wilcox 1938, *L. littoris* Cole 1924, *L. ripicola* Melander 1923, *L. willametti* Cole & Wilcox 1938, *L. zonatus* Cole & Wilcox 1938. The species *L. martinensis* Cole & Wilcox 1938 is considered valid but transferred to the *tetragrammus* group of the *opaculus* section.

Introduction

Assassin flies, also known as robber flies (Diptera: Asilidae), are one of the largest radiations of modern predators, with more than 7000 species and 500 genera described and inhabitants in nearly every terrestrial biome (Geller-Grimm 2013). Asilid species tend to have characteristic behaviors that include preferred habitats, perch positions, activity patterns, and prey types, and ecological competition and niche partitioning are thought to have played a role in asilid diversification and species sorting (Haupt 2002). Diversity in the subfamily Stichopogoninae suggest repeated patterns of specialization and character displacement at fine ecological scales (Lehr 1984), unfortunately, further exploration of such ideas has been hampered by incomplete knowledge of asilid species boundaries and phylogeny (Dikow 2009). In this chapter we follow up on recent work (Cannings 2002) to estimate phylogeny for one of the largest genera of Stichopogoninae flies, *Lasiopogon* Loew 1847 (Fig. III.1), and provide a taxonomic revision of the *bivittatus* group.

Fig. III.1. *Lasiopogon drabicolum* female eating a beetle (Scarabaeidae c.f. Aphodiinae). U.S.A.: California: Riverside Co., Santa Ana River at Mt. Rubidoux, 4.iii.2013.Photo: T.A. McKnight.

Most species of *Lasiopogon* were described in the pre-code era; revisionary work is now ongoing to bring the genus up to modern taxonomic standards and properly recognize cryptic diversity. A complete taxonomic history for the genus was summarized by Cannings (2002); we mention only actions pertinent to the *bivittatus* group here. Throughout the late 19th and early 20th century, species in this group were described slowly and in piecemeal fashion by several authors (Loew 1866, Osten Sacken 1877, Cole 1916, Melander 1923, Cole 1924). The revision of North American *Lasiopogon* collections by Cole and Wilcox (1938) proved to be a major landmark, doubling the number of known species and taking some consideration for external genitalia morphology. This taxonomy then sat mostly undisturbed for half a century until Cannings (1996, 2002) began revising the genus on the basis of internal genitalia morphology. Approximately a quarter of the world fauna received detailed treatment at that time; most other species were assigned to putative species groups. The *bivittatus* group was established on the basis of a two morphological synapomorphies from male genitalia: the strongly bifid phallus apex and the strongly apically ridged medial lobes of the gonocoxite.

Most publications on robber flies have been confined to purely descriptive taxonomy or ecology, making only occasional passing references to evolutionary history based on intuitive expert opinion. A handful of studies have postulated phylogenetic relationships within a clade using cladistic analyses of morphological similarity (Dikow 2009a, Cannings 2002, Fisher 1986, Adisoemarto and Wood 1975), but molecular phylogenetics have been employed sparingly, only to evaluate broad tribal relationships across the family (Bybee et al. 2004, Dikow 2009b). This paper provides the first estimation of a species tree from molecular data in robber flies.

Materials and Methods

Sources of Material: Approximately 4500 specimens of *Lasiopogon* were examined for this study, using material loaned from or inspected while visiting the following museums (curators or collection managers assisting this work are listed in parentheses). Repository abbreviations are adopted from Evenhuis (2016), with some additions.

BEZA: L.G. Bezark Collection (private), Sacramento, California, U.S.A.

BPBM: Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A. (N.L. Evenhuis, K. Arakaki)

BYU: Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, U.S.A. (C.R. Nelson)

CAS: Department of Entomology, California Academy of Sciences, San Francisco, California, U.S.A. (G.E. Griswold, A. Carmichael)

CNC: Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada (J.H. Skevington, J.E. O'Hara)

CSUC: C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado, U.S.A. (B.C. Kondratieff)

CUAC: Clemson University Arthropod Collection, Clemson, South Carolina, U.S.A. (M.S. Caterino)

EMEC: Essig Museum of Entomology, Department of Entomology, University of California, Berkeley, California, U.S.A. (P.T. Oboyski)

ESUW: Department of Plant, Soil, and Insect Sciences, University of Wyoming, Laramie, Wyoming, U.S.A. (S. Shaw)

FISH: E.M. Fisher Collection (private), Sacramento, California, U.S.A.

FSCA: Florida State Collection of Arthropods, Florida Department of Agriculture, Gainesville, Florida, U.S.A. (W.C. Whitehill)

INHS: Insect Collection, Illinois Natural History Survey, Champaign, Illinois, U.S.A. (C.C. Grinter)

LACM: Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A. (B. Brown, W. Xie)

MCZ: Entomology Department, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. (P.D. Perkins)

MNAZ: Museum of Northern Arizona, Flagstaff, Arizona, U.S.A. (L.E. Stevens)

OSUC: C.A. Triplehorn Insect Collection, The Ohio State University, Columbus, Ohio, U.S.A. (L. Musetti)

RBCM: Royal British Columbia Museum, Victoria, British Columbia, Canada. (R.A. Cannings, K. Sendall)

SDMC: San Diego Natural History Museum, San Diego, California, U.S.A. (M. Wall, J. Berrian)

UCDC: R.M. Bohart Museum of Entomology, University of California, Davis, California, U.S.A. (S.L. Heydon)

UCRC: Entomology Research Museum, University of California, Riverside, California, U.S.A. (D. Yanega)

UMMZ: Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A. (M.F. O'Brien)
USNM: National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A. (T. Dikow)
UTST: Department of Biology, Utah State University, Logan, Utah, U.S.A.
UWBM: Burke Museum, University of Washington, Seattle, Washington, U.S.A. (R. Crawford)
WSUC: James Entomological Collection, Washington State University, Pullman, Washington, U.S.A. (R.S. Zack)

This revision is based primarily on pinned, dried specimens, but records known only from alcohol-preserved specimens have also been included. Protocols for specimen preparation and genitalia dissection were adopted from Cannings (2002): genitalia were usually cleared overnight in cold 10% KOH, then rinsed in glacial acetic acid and distilled water, and then dissected and photographed while mounted in a watch glass with a water-based gel (KY personal lubricant). After examination, dissections of pinned specimens were placed in a microvial containing glycerol and pinned underneath the specimen, while dissections of wet-preserved specimens were placed in a small shell vial placed inside the vial of ethanol. Images of genitalia dissections were taken with Image-Pro Plus software via a Leica DC 300 camera mounted on a Leica MZ 16 dissecting microscope; tergite tomentum photographs were taken with a Nikon D200 digital camera. Measurements were made in Adobe Photoshop CS5 after calibration with a stage micrometer. Measurements of the epandrium do not include the basal apodeme so they can be applied to undissected specimens. Phallus length was measured from the apex of the aedeagal sheath to the farthest point on the sperm sack, thus excluding the ejaculatory apodeme and dorsal carina.

Species concept: Our philosophy for systematics follows the general lineage concept (de Queiroz 1998) that species are populations or groups of populations with an independent evolutionary trajectory. Operationally, we have used morphospecies as the criterion for judging evolutionary independence, by identifying consistent gaps across multiple morphological characters in the adults. Historically, most *Lasiopogon* species were defined using attributes of external morphology (e.g., colors of body tomentum or setae); unfortunately, this left many cryptic species unrecognized. Internal structures of the male and female genitalia provide much

better resolution of the distinct lineages that apparently share a common gene pool (Theodor 1976, Cannings 2002).

Morphological and molecular data were developed simultaneously for this project. Genetic distance or clustering of individuals from different populations in preliminary gene trees were occasionally used as a heuristic to guide our search for morphological gaps between taxa, but species were accepted only if there was significant phenotypic differentiation on a scale comparable to established taxa, helping us avoid the trap of oversplitting molecular lineages as species instead of populations (Sukumaran and Knowles 2017).

Virtually nothing is known about immature life stages of *Lasiopogon* flies; in fact, larvae and pupae have only been described from a single species to date (the European *L. cinctus*). As a result, immature stages play no role in the systematics or ecology described herein, but a few recently discovered immature stages will be described in a future publication.

Presentation of species descriptions: Descriptions or redescriptions for each species are presented in alphabetical order and follow the general format and terminology of recent work in this group (Cannings 2002, McKnight and Cannings 2017); however, descriptions of female internal genitalia and some body measurements have been omitted, and whereas previous work detailed the three-dimensional array of knobs, flanges, and other informative characters on the gonostylus, we have instead focused our descriptions on the phallus and epandrium as these are easier to consistently orient and compare between taxa and between taxonomists. When a size distinction for setae is relevant, the term hairs is used for fine setae and bristles for macrosetae. Descriptions were prepared from a subset of individuals (usually 6–10) selected to sample across the geographic and morphological range of each species, and then further refined by random spot checks against the rest of the available material. Images of dissected genitalia and tergite tomentum in the tabular key should be consulted for further detail; these are a composite of best images from all individuals examined for a given species.

Allotypes have not been designated for new species but are included where originally designated. Labels for primary types are copied verbatim following the system described by O'Hara (1982): listed from the top label downward, with data from each label enclosed in quotation marks and the lines of each label delimited by oblique slash marks. Information not found on the labels is given in square brackets. Other specimen records are not presented verbatim; all relevant locality information is included but localities have been edited for

consistency and are listed alphabetically by country, state, and county. Most localities have been georeferenced with latitude and longitude for utility in future biogeographic analyses, this was done by incorporating data from labels, notes from the original collectors, or (in most cases) intuition from the first author's field experience to select an area of suitable habitat near the stated locality. For example, a species known to inhabit beach dunes will not have coordinates estimated at a city's post office or centroid but rather at that city's beach access. Estimated information (including coordinates) is written in square brackets and estimated coordinates have been truncated to three decimal places to avoid the appearance of false precision. Abbreviations used in localities: cpgd = campground, crk = creek, E = east, fk = fork, hwy = highway, jct = junction, km = kilometer, mi = mile, mtn(s) = mountain(s), N = north, r = river, S = south, W = west. Distribution maps were generated using ArcGIS 10.4 software by Esri, with species arranged into the same groups as the tabular key and plotted on an elevation background (Hijmans et al. 2005). Prey items were identified using keys in Hardy (1961), Huckett (1975), McAlpine et al. (1981, 1982), and Merritt et al. (2008).

Molecular processing: Most specimens for molecular work were stored in 95% ethanol promptly after capture; a few had genetic material extracted from a leg of a pinned, dried specimen. For ethanol specimens, at least the head, terminalia, wings, and one set of fore/mid/hind limbs were preserved as morphological vouchers; these have been deposited at the UMMZ. Genomic DNA was extracted using Qiagen DNeasy Blood and Tissue or QIAamp DNA Micro kits respectively for larger or smaller samples (QIAGEN Inc., Valencia, CA, USA), following the manufacturer's protocols; extractions were eluted into H_2O and stored at -20°C. Taxonomy, collection data, genetic sampling, and voucher location for specimens used in the *Lasiopogon* species tree are presented in Table III.1.

Loci from one mitochondrial and three nuclear protein coding genes were amplified: cytochrome oxidase I (COI; 658 bp), phosphoenolpyruvate carboxykinase (PEPCK; 585 bp), wingless (wg; 553 bp), and alanyl-tRNA synthetase (AATS; 550 bp); primers for the PCR reactions are presented in Table II.1. PCR amplifications were performed on an Eppendorf epgradient Mastercycler using this universal recipe: 1 µL DNA template, 5.69 µL H2O, 1 µL 10x PCR buffer, 0.5 µL dNTPs, 0.2 µL BSA, 0.4 µL each primer, 0.75 µL 50 mM MgCl2, 0.06 µL Platinum Taq. Thermocycler protocols were as follows: COI : 35 cycles of 30 sec at 94°C, 30 sec at 46°C, 30 sec at 72°C; wg :35 cycles of 45 sec at 94°C, 45 sec at 58°C (first 5 cycles

touchdown from 64–60°C) , 1 min at 72°C; PEPCK and AATS: 35 cycles of 45 sec at 94°C, 45 sec at 50°C (first 5 cycles touchdown from 56–52°C) , 1 min at 72°C. Cycle steps for all samples were preceded by a denaturing step of 5 min at 94°C and followed by an extension step of 7 min at 72°C. Amplification success was verified by visualization on a 2% agarose gel; products were then purified with Affymetrix ExoSAP according to manufacturer's protocols and sequenced by the University of Michigan Sequencing Core on an Applied Biosystems 3730xl DNA Analyzer. All sequence files were visually inspected and cleaned in Sequencher 4.2 (GeneCodes Corp., Ann Arbor, MI, USA) and aligned in MEGA6 (Tamura et al. 2013) or MESQUITE 3.02 (Maddison and Maddison 2016). The *wg* alignment contained one variable-length (117-132 bp) intron that was removed before analysis, a short variable repeat section in the Brachycera expansion zone at amino acid positions 42–58, and a single amino acid indel at position 89. Other loci lacked introns or indels and were trivial to align.

A species tree was estimated using the UCLN species tree template in BEAST 2.4.3 (Bouckaert et al. 2014, Drummond and Suchard 2010). *Stichopogon trifasciatus* (Say), *S. argenteus* (Say), and *Stackelberginia cerberus* McKnight served as outgroup taxa to root the tree, but this was not hard-coded in the input file. Each locus was partitioned during phylogenetic analysis to allow independent nucleotide site, clock, and tree models; ploidy for the nuclear loci was 2.0, for COI it was 0.5. Optimal nucleotide substitution models compatible with *BEAST software for each partition were determined following AIC and BIC in jModelTest 2.1.5 (Darriba et al. 2012, Guindon and Gascuel 2003): AATS, COI, WG: TrN+G; PEPCK: HKY+G; in all cases gamma was estimated with 4 categories. The species tree was estimated using the Yule branching model and constant population sizes, with default settings retained for most parameters and priors. Four chains were run with length set to 300 million and sampling every 10,000. Parameter distributions and convergence of MCMC runs were assessed using Tracer 1.6 (Rambaut et al. 2014); chains were combined using LogCombiner, discarding the first 10% of each run as burn-in and resampling only every 100,000. ESS for most priors was >200, except for priors on TreeHeight and TreeLength, which had ESS >190. Trees were visualized in FigTree 1.4 (Rambaut 2012). New species that are still formally undescribed at this time are included using placeholder names following Cannings (2002), to better capture the true diversity of each clade.

Species Accounts

Lasiopogon actius Melander

Lasiopogon actius Melander, 1923. *Psyche* 30: 138–139.

Diagnosis. A medium-sized pale species from the beach dunes of Oregon, Washington and British Columbia; most setae white except bristles black along sides of scutum and on lower leg segments, some individuals also with black bristles in dorsocentral, occipital, and occellar groups; tergites with basal brown tomentum usually as lateral spots (especially in female) but occasionally as a dark band; apical 40% covered in grey tomentum. Epandrial halves moderately concave medially, with long white hairs; phallus dorsal carina protruding with apex swollen into rounded process. Ovipositor dark brown/black, acanthophorite spines black.

Description.

Head. Face with silver-yellow tomentum; vertex with silver/light brown tomentum. Mystax, frontal, and most orbital and occipital setae straw-colored; a few black occipital bristles behind eye; beard and labial hairs white. Occipital bristles relatively straight and of average length, those behind the dorsomedial angle of the eye and most curved; lateral and ventral bristles shorter, straighter. Frontal and orbital setae fine and long.

Antennae. Black, F1 dark brown at base; Setae usually straw-colored, F1 never with setae. F1 rectangular, F2+3 broadly tapering.

Thorax. Prothorax light grey/brown, hairs white; postpronotal lobes grey to brownish grey, lateral angle ferruginous, hairs white. Scutum tomentum grey/tan, darker around the perimeter. Dorsocentral stripes dark brown; acrostichal stripes absent, cuticle subshining. Dorsocentral bristles and shorter setae straw-colored, some dorsocentral bristles occasionally black; lateral bristle groups black, some postalars occasionally straw-colored. Anterior dorsocentral bristles 8, mixed with finer setae; 5 posteriors. Postalars 2–5, with a few shorter hairs; supra-alars 2–4; presuturals 2–4; posthumerals 1–2. Scutellar tomentum yellow; rim inflated, leaving a semi-

circular line impressed inside the dorsal edge; apical bristles straw-colored, very abundant (10+ on each side) and mixed with many other long hairs.

Pleural tomentum gold. Katatergite bristles straw-colored, 8–13, with a few weaker hairs; katepisternal setae sparse, moderately long, white; anepisternal setae 6–9, relatively strong and mixed with other short hairs, a patch of short white hairs on dorsal margin of sclerite; anepimeron with 1–3 short wispy setae.

Legs. Cuticle dark brown to black, tomentum grey. No coxal peg. Bristles on femur usually white, sometimes brown, bristles of tibia and tarsi dark brown/black; all finer setae white. Ventral hairs on femur dense, longest are longer than femur width. Dorsolateral bristles mixed with finer hairs: 8–11 on profemur but difficult to distinguish from surrounding finer hairs, bristles more prominent on mesofemur (4–8) and metafemur (12–18). Protibia with ventral bristles about 4 times longer than tibial width. Claws dark brown over basal 60%, apically black.

Wings. Veins dark brown; membrane faintly grey from microtrichia. Halter pale brown, with no spot.

Abdomen. Cuticle dark brown/black; subshining brown tomentum at bases of tergites 1–7, bands of grey tomentum cover apical 40–50% of each tergite, extending anteriorly along lateral margins, and in some individuals anteromedially to divide brown into lateral spots (especially in females). Setae yellow-white/white; all tergites in male with long lateral setae; females with long setae along tergites 1–3 and shorter hairs on 4–7. Lateral bristles on first tergite 8–9, long but not strongly differentiated from surrounding hairs. Sternite tomentum grey; hairs long, yellow-white/white.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown; covered in thin grey tomentum except polished medially on hypandrium and sometimes apically on epandrium; with long straw hairs, setal brush light brown, dense. Epandrium elongate, in lateral view the width about 45% the length, widest in basal third; apex rounded with ventral tooth. In dorsal view, medial margins of epandrium moderately curved, curvature starts about 35% from base, outer margins gradually tapered; basal sclerite prominent.

Phallus paramere sheath dorsally 55% the length of phallus; paramere sheath without ventral ornamentation; dorsal carina divergent from aedeagal tube and extending slightly farther, apex hemispherically rounded. Ejaculatory apodeme in lateral view strongly to moderately bent dorsally in basal quarter, with broad dorsal carina. Subepandrial sclerite with triangular central unsclerotized area in basal 28% narrowing to a parallel-sided gap in central portion; spines parallel-sided, blunt, densely arranged apically and medially, more sparse elsewhere.

Female genitalia. Undissected: Hairs white, abundant, erect. Tergite 8 dark brown/black, occasionally lighter at apex; sternite 8 dark brown; lateral lobe setae strong; hypogynial valves with fine hairs concentrated basally. Cerci brown/black with pale setae; acanthophorite spines black.

Type Material. LECTOTYPE (examined) ♂ labelled: "[rectangular white label] IlwacoWash/ July 1917/ ALMelander"; "[rectangular red label] TYPE/ Lasiopogon/ actius/ Melander"; "[rectangular white and green label] ALMelander/ Collection/ 1961"; "[rectangular beige label] Lasiopogon/ actius/ Mel."; "[rectangular white label] USNMENT/ 01071654".

PARALECTOTYPES: **USA: Washington: Pacific Co.**, Nahcotta [46.501 -124.059], 24.v.1917, A.L. Melander (1♂ CNC).

Other Material Examined (285 specimens). **CANADA: BRITISH COLUMBIA**: Haida Gwaii, Graham Island, Masset, 3.vi.1957, E.E. MacDougall (1♂ RBCM); Graham Island, Masset, Skokum Point [54.031 -132.078], 9.vi.1987, D. & J.M. Cooper (1♀ RBCM), 6.vi.1988, J.M. Cooper (1♀ LACM, 1♂ 1♀ RBCM); Graham Island, Tlell, 53.611278 -131.936351, 25.vi.2009, R. Bennett, M. Connelly, C. & D. Copley, J. Heron, J. Miskelly, (2♂ 2♀ RBCM), vii.2014, B. Wijdeven (1♂ RBCM); **U.S.A.: OREGON:** no loc, 1929, F.J. Spuijt (1♂ FSCA); **Clatsop Co.**, Gerhart Beach [46.031 -123.929], 16.ix.1991, S. & S. Frommer (2♂ 3♀ UCRC); Seaside [45.999 -123.929], 29.v.1933, W.W. Baker (4♂ 1♀ CAS); Sunset Beach [46.099 -123.942], 6.viii.1938, S.E. Crumb (4♂ 4♀ FSCA); **Douglas Co.**, Ziolkouski Beach Park, 2 mi W of Winchester Bay, 43.66264 -124.2067, 16.v.2012, T.A. McKnight (2♂ 1♀ TAM); **Lane Co.**, Baker Beach, dunes behind [44.0853 -124.11778], 27.vi.2012, J.D. Pinto (1♀ UCRC);

Florence [44.024 -124.129], 21.vi.1960, E. Ball (1♂ 2♀ FSCA); **Lincoln Co.**, Beachside State Park [44.381 124.089], 11.vi.1988, D.W. Webb (4♂ INHS); Devil's Lake [44.9674 -124.0151], 2.ix.1932, W.W. Baker (1♀ CAS); Gleneden Beach, NW tip of Salishan Spit, 44.920078 -124.026942, 17.v.2012, T.A. McKnight (5♂ 2♀ TAM); Governor Patterson State Park, beach, 44.408 -124.085, 24.vi.2006, J.D. Pinto (1♂ UCRC); Newport, S side Yaquinna River mouth, dunes E of South Jetty Rd, 44.612546 -124.069057, 17.v.2012, T.A. McKnight (1♂ 1♀ TAM), 21.vi.2013, T.A. McKnight (1♂ TAM); Waldport [44.4333 -124.0836], 5.vi.1925, H.A. Scullen (1♀ OSUC), 7.vi.1925, J.E. Davis (1♂ CAS), vii.1938, E.C. Van Dyke (1♂ CAS), 15.vii.1938, E.C. Van Dyke (8♂ 3♀ CAS, 1♂ 1♀ FSCA); **Tillamook Co.**, Nehalem Bay, 3 mi S Manzanita [45.6641 -123.9345], 7.vii.1971, J.R. Powers (1♂ 5♀ CAS); Pacific City, Bob Straub State Park, dunes W of parking lot, 45.192474 -123.968284, 18.v.2012, T.A. McKnight (2♂ TAM); Rockaway [45.612 123.946], 27.vi.1920, L.P. Rockwood (1♂ 1♀ USNM), 27.v.1965, C. Henne (4♂ 1♀ CAS); **WASHINGTON: Grays Harbor Co.**, Ocean City State Park, sand dunes [47.032 124.172], 26–27.v.1996, M. Kippenhan (2♂ 3♀ CSUC); Ocean Shores, Taurus Blvd SW [46.9721 -124.1704], 16.v.1994, R.A. Cannings (1♂ 2♀ CSUC, 2♂ 2♀ RBCM); Twin Harbor State Park, beach [46.857 124.114], 22.v.2003, B. Kondratieff, J. Schmidt (1♀ CSUC); Westhaven State Park, dunes 2 mi NW of Westport, 46.90241 -124.12839, 20.vi.2013, T.A. McKnight (3♂ 2♀ TAM); Westport [46.902 -124.128], 8.v.1931, J. Wilcox (1♂ CNC), 8.v.1932, J. Wilcox (4♂ 1♀ CAS, 1♂ CUAC, 1♂ EMEC, 1♂ MCZ), 12.v.1932, J. Wilcox (1♂ OSUC), 15.v.1932, J. Wilcox (1♂ 2♀ CAS, 1♀ CUAC, 1♂ MCZ), 17.vii.1932, C.W. Getzendaner (1♀ CAS), 31.vii.1932, W.W. Baker (4♂ 2♀ CAS, 1♀ CNC, 1♀ EMEC, 1♂ 1♀ FSCA), 24.v.1933, C.H. Martin (1♂ FISH), 28.v.1933, C.H. Martin (2♂ 1♀ FSCA), 29.v.1933, C.H. Martin (1♂ ESUW, 3♂ 2♀ FSCA), 18.vi.1933, C.W. Getzendaner (4♂ 4♀ CAS), W.W. Baker (1♂ FSCA), 5.vii.1933, G.P. Engelhardt (1♂ CAS), 7.vii.1933, I. Wilcox (4♂ 7♀ CAS, 1♂ FISH, 1♂ UCRC), J. Wilcox (1♂ BEZA, 13♂ 6♀ CAS, 2♂ 2♀ FISH, 2♂ 4♀ MCZ), W.W. Baker (5♂ 9♀ CAS, 2♂ 2♀ FISH, 1♂ 1♀ FSCA, 1♀ UCRC), 19.vii.1933, W.W. Baker (2♂ CAS, 1♀ FSCA), 5.v.1935, W.W. Baker (1♀ CAS), 24.vi.1935, C.W. Getzendaner (1♂ 1♀ CAS, 1♀ FISH), 21.vii.1935, C.W. Getzendaner (1♀ BEZA, 5♂ 8♀ CAS, 1♀ FISH), 8.ix.1935, W.W. Baker (2♀ CAS), 28.iv.1936, J. Wilcox (1♀ CAS), 16.v.1994, R.A. Cannings (2♀ RBCM); **Pacific Co.**, Ilwaco [46.316 -124.067], 28.vi.1925, A.L. Melander (10♂ 11♀ USNM); Klipsan Beach [46.466 -124.058], 26.v.1981, C.V. Nidek (2♂ BEZA); Long Beach [46.353 -124.063], 1.vii.1949, C.B.

Philip (9♂ CAS), 23.viii.1972, E.I. Schlinger (1♂ BEZA), 19.v.1977, V.F. Lee (3♂ 2♀ CAS, 4♂ 2♀ FISH); Ocean Park [46.490 -124.058], 9–10.viii.1950, M.T. James (1♀ RBCM), 29.vi.1957, M.T. James (1♂ RBCM); Seaview [46.331 -124.066], 27.iv.1998, G.E. Hutchings (4♂ RBCM); Seaview, beach dunes at end of 38th Pl., 46.331 -124.066, 30.v.1995, R.A. Cannings (1♂ CSUC, 3♂ LACM).

Type Locality. USA: Washington: Pacific Co., Seaview.

Taxonomic Notes. Melander's original description noted 16 specimens as "types" (i.e., syntypes in modern usage), but one male in the USNM type collection has been traditionally interpreted as the primary type, including receiving a red label by an unknown worker at some point. For future stability, I am hereby designating this specimen as the lectotype, and others in this series as paralectotypes.

Etymology. No explanation given in the original description, but evidently from the Greek *aktaios* = of the coast or shore.

Distribution (Fig. III.3). Nearctic; coast of Pacific Northwest in USA: Oregon, Washington, and Canada: British Columbia (Haida Gwaii). This distribution skips over Vancouver Island and the Puget Sound area, where *L. actius* is apparently replaced by *L. puyallupi* stat. nov.; some individuals of *L. puyallupi* stat. nov. even have similar coloration (e.g., predominantly white mystaces).

Phylogenetic Relationships. Member of the *actius* group within the *bivittatus* section, likely as sister to *L. puyallupi* stat. nov. (not closely related to *L. arenicola* despite Melander's (1923) comment). The close genetic and morphological similarity and complimentary geographical distributions of *L. actius* and *L. puyallupi* stat. nov. suggest that these taxa are likely either a recent divergence with shared ancestral polymorphisms, or a case of introgression.

Natural History. Habitat: coastal sand dunes, especially on the foredune. Usually perches on bare sand adjacent to beachgrass (*Ammophila*) and other low, scraggly vegetation (Fig. III.6a,

III.6b), occasionally found on riprap boulders. Dates collected: April 21 to September 16, most in May and June. Frequently found flying simultaneously with *L. tumulicola* sp. nov., though the latter species was typically encountered in the backdune field or backside of the foredune, whereas *L. actius* was typically on the beach side.

***Lasiopogon albidus* Cole and Wilcox**

Lasiopogon albidus Cole and Wilcox, 1938. *Entomologica Americana* 18:21–22.

Diagnosis. A medium-sized pale grey species from inland sand dunes of Oregon and Washington; all setae white to golden; bristles well developed; trochanters and femur/tibia joint ferruginous; tergites with faint basal spots of brown tomentum, otherwise covered in thick silvery-grey tomentum. Epandrial halves strongly concave medially, with long hairs; ovipositor dark brown with yellow acanthophorite spines.

Description.

Head. Face with silver-grey tomentum; vertex with gold-grey tomentum. Mystax, frontal, and occipital setae straw-colored; beard and labial hairs usually white. Occipital bristles relatively straight and of average length, those behind the dorsomedial angle of the eye and most curved; lateral and ventral bristles shorter, straighter. Frontal setae fine and short; orbital setae long, erect.

Antennae. Dark brown, F1 darker; Setae straw-colored, F1 never with setae.

Thorax. Prothorax grey/brown, hairs white; postpronotal lobes grey to brownish grey, lateral angle ferruginous, hairs white. Scutum tomentum pale grey, brown around the perimeter. Dorsocentral stripes pale gold-brown with dark cuticle subshining; acrostichal stripes absent. Bristles straw-colored, shorter hairs white. Notal and acrostichal setae. Anterior dorsocentral bristles 5–6mm, mixed with finer setae; 4 posteriors. Postalars 4, with about 7 shorter hairs;

supra-alars 3 with 3 shorter hairs; presuturals 3–4; posthumerals 1–2. Scutellar tomentum grey; rim strongly inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles straw-colored, abundant (usually 8–10+ on each side) and mixed with many other long hairs.

Pleural tomentum gold. Katatergite bristles straw-colored, 8, with a few weaker hairs; katepisternal setae sparse, moderately long, white; anepisternal setae 4–5, moderately strong and mixed with other hairs, a patch of short white hairs on dorsal margin of sclerite; anepimeron with a single fine hair, white.

Legs. Cuticle dark brown to black, trochanter and base of femur ferruginous, sometimes reddish at joints of femur/tibiae and tarsal bases; tomentum sparse, grey. No coxal peg. Bristles on legs dirty white, finer setae white. Ventral setae on femur somewhat sparse and short, as long or shorter than width of femur; dorsolateral bristles on femur strong, 7–8 on profemur, mixed with many finer hairs; 4–5 on mesofemur; longer and more numerous on metafemur (15–16). Protibia with longest bristles about 3–4 times longer than tibial width. Claws chestnut over basal 40–50%, black apically.

Wings. Veins brown, paler in apical half; membrane transparent, milky white when viewed obliquely. Halter yellow, with no spot.

Abdomen. Cuticle dark brown/black basally, covered in grey tomentum except for very faint and broadly separated patches of brown tomentum at bases of tergites 2–7, apical light grey tomentum covers about 50% the length of each tergite and extends medially and laterally to the tergite base; tergite 1 completely covered in light grey tomentum. All tergites in male with long lateral setae; tergites 4–7 in female with short lateral setae, anterior tergites as in male. Lateral bristles on first tergite long but relatively weak, 8–9. Sternite tomentum grey, hairs straw-colored/white.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle brown/chestnut; covered in thin grey tomentum and long white hairs, setal brush yellowish white, dense. Epandrium elongate, in lateral view the width about 45% the length, widest in basal third, dorsally and ventrally sinuate; apex right-angled ventrally, straight-edged apically, and rounded

dorsally. In dorsal view, medial margins of epandrium moderately curved, curvature starts around 35% from base; basal sclerite prominent.

Phallus paramere sheath dorsally 45% the length of phallus; paramere sheath with a strong subapical ventral tooth; dorsal carina jutting out like a thin fin near apex, leaving only a narrow gap between apex of dorsal carina and gonopore. Ejaculatory apodeme in lateral view moderately bent dorsally in basal quarter, strongly recurved at apex, dorsal carina narrowly filling the gap. Subepandrial sclerite with triangular central unsclerotized area in basal 50% narrowing to a parallel-sided gap in central portion; spines parallel-sided, blunt, densely arranged apically, sparse elsewhere.

Female genitalia. Undissected: Hairs white, abundant, erect. Tergite 8 dark brown/black; sternite 8 dark brown, paler medially at bases of hypogynial valves; lateral lobe setae strong. Hypogynial valves with fine hairs, concentrated basally and apically. Cerci brown/black with pale setae; acanthophorite spines yellow.

Type Material. HOLOTYPE. (photos examined) ♂ labelled: "[rectangular white label] Kiona, Wn./ IV-23 1933";"[rectangular white label] J. Wilcox/ Coll."; "[rectangular salmon label] HOLOTYPE/ Lasiopogon/albidus/Cole & Wilcox";"[rectangular white label] California Academy/ of Sciences, Type No. 6407".

ALLOTYPE. (examined) ♀ labelled: "[rectangular white label] Kiona, Wn./ IV-23 1933"; "[rectangular white label] Itol Wilcox/ Coll."; "[rectangular salmon label] ALLOTYPE/ Lasiopogon/ albidus/Cole & Wilcox". CAS.

PARATYPES. (55 examined). **USA: Washington, Benton Co.**, Kiona [46.2540 -119.2890], 23.iv.1933, Itol Wilcox (3♂ 2♀ CAS, 1♂ CNC, 1♀ EMEC, 2♂ 1♀ FISH, 1♀ UCRC, 2♂ 1♀ USNM), J. Wilcox (2♂ BEZA, 16♂ 4♀ 1? CAS, 1♀ CNC, 1♂ EMEC, 1♀ FISH, 1♂ LACM, 2♂ 2♀ MCZ, 2♂ 2♀ OSUC, 1♂ UCRC, 2♂ 3♀ USNM).

Other Material Examined (32 specimens). **USA: Oregon: Harney Co.**, Alvord Basin T41S R35E S155E¼ [42.006 -118.594], 29.iv.1979, Cobb & Lightfoot (1♂ FISH); **Lake Co.**, Alkali

Lake, 2.5 km N on Hwy 395, 43.0217 -119.9896°, 30.iv.2014, T.A. McKnight (1♀ TAM); Fossil Lake [43.353 -120.436], 16.v.1957, W.J. Hogg (2♂ 2♀ RBCM); **Washington: Benton Co.,** Hanford Site, sand dunes W of Columbia River, 46.5203 -119.3477, 25.iv.1995, R.S. Zack (1♂ 1♀ WSUC); **Franklin Co.**, Juniper Dunes Wilderness, N entrance 18 mi NE of Pasco, 46.4249 -118.8301, 20.iv.2014, T.A. McKnight (9♂ 4♀ TAM); juniper forest 30 mi NE Pasco [46.533 -118.584], 2.v.1970, E. Gage (1♀ BEZA); **Walla Walla Co.,** Wallula 1 mi W [46.080 -118.908], 30.iv.1960, M.T. & H.B. James (2♀ RBCM, 2♂ 6♀ WSUC).

Type Locality. USA: Washington: Benton Co., 8 mi E of Kiona (Cole and Wilcox 1938).

Taxonomic Notes. Because of their similar pale appearance, specimens of *L. quadrivittatus* Jones have occasionally been misidentified as this species, as in Nelson (1987).

Etymology. No explanation given in the original description, but evidently from the Latin *albus* = white; referring to the overall pale coloration of the body tomentum and setae.

Distribution (Fig. III.3). Nearctic; USA, inland sagebrush dunes of eastern Oregon and Washington; reports from Utah and Arizona are likely erroneous. All specimens that I have found identified as *L. albidus* from Utah and Arizona have proven to instead be *L. quadrivittatus*, and while I have not personally inspected every specimen listed as *L. albidus* in Nelson's (1987) checklist of Utah asilids, the remaining records match entries for *L. quadrivittatus* in Cannings (2002).

Phylogenetic Relationships. Member of the *bivittatus* section, likely basal to the *drabicolum* group.

Natural History. Habitat: inland sand dunes and sagebrush steppe. Found perching on bare sand dunes far from water with sparse grasses, sagebrush, and juniper (Fig. III.7d) and "far from the dunes on a loamy-clay flatland interspersed by sandy patches… vegetated largely by halophyte shrubs" (Cobb et al. 1981). Dates collected: April 20 to May 2 (an unverified report extends to May 16). Found in the same localities and habitats as *L. chaetosus* Cole and Wilcox,

but no specimen records coincide in phenology, suggesting that *L. albidus* may have an earlier emergence season. One male with prey: Cicadellidae nymph.

***Lasiopogon anaphlecter* McKnight sp. nov.**

Diagnosis. A medium-sized brown species from the Sierra Nevada in California; most setae black, including mystax, antennal setae, and scutal bristles; dorsocentral and acrostichal stripes brown; metafemur with short appressed dorsal setae black apically; tergites in male with brown tomentum in basal bands and grey tomentum covering apical 30–50% of each tergite; females with brown tomentum divided by grey along midline. Epandrial halves in dorsal view moderately concave medially, with long black hairs; phallus dorsal carina long, slender, and curving far past gonopore; ventral margin of paramere sheath with buttress-like flange. Ovipositor dark brown, reddish at base of hypogynial valves, acanthophorite spines black.

Description.

Head. Face grey, vertex brown-grey. Ventral hairs (on beard, labium, palps) white; mystax and all dorsal setae black. Frontal and orbital setae long (reach midpoint of F1), dense; occellar setae indistinct among other hairs; occipital setae relatively straight.

Antennae. Black, with thin grey tomentum. Setae black (rarely 1–2 white hairs ventrally on scape), abundant; 0–1 black hairs on F1. F1 short, widest at midpoint with ventral margin curved. Arista long.

Thorax. Prothorax grey, with white hairs; postpronotal lobes grey, the lateral angle yellow-brown, hairs variable from white to black. Scutum tomentum grey to chocolate brown except patches of grey lateral of dorsocentral stripes near suture and along posterior margin; dorsocentral stripes rich satiny dark brown, acrostichal stripes fainter but still distinct. Setae and bristles of scutum black; anterior dorsocentral bristles fine, 3–8, with several finer hairs,

posteriors 3–4, prominent; postalars 2–3, with several finer hairs; supra-alars 1–3, with several finer hairs; presuturals 2–3; posthumerals 1–2. Scutellar tomentum grey to greyish brown; rim inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, abundant (8–12 on each side), with shorter hairs; short vertical hairs on uppermost edge of rim black, about half as long as main bristles.

Pleural tomentum grey. Katatergite setae black, long, 8–10, with a few shorter white hairs; katepisternal setae white, curved; anepisternal setae 5–9, black, with several very short black hairs along dorsal margin and a few fine white hairs in posteroventral corner; anepimeron with 2 short white hairs.

Legs. Cuticle black, with thin yellow/grey tomentum except bare at femur joints. No coxal peg; coxae with white setae. Fine hairs on femur and tibia yellowish white, black on tarsi and dorsal side of protibia; bristles black. Ventral setae on femur as long or slightly longer than femur width; dorsolateral bristles on profemur 6–10, fine and relatively indistinct amidst long hairs; on meso- and metafemur short and robust, respectively 4–9 and 11–15. Ventral setae just longer than width of femur. Dense patch of short pale yellow bristles along inside of protibia. Claws chestnut over basal half, black apically.

Wings. Veins brown; membrane hyaline but brown when viewed obliquely. Halter knob cream, without spot, stem brown.

Abdomen. Male. Tergite cuticle dark brown/ black. Brown tomentum on tergite bases; bands of grey tomentum cover apical 30–50% of each tergite and extend along lateral margins (tergite 1 fully covered in grey); grey apical tomentum rarely extends to anterior margin along midline to divide brown tomentum into two lateral spots. Tergite 1 with 3–5 black and 2–3 yellow-white lateral bristles; lateral hairs white, on tergites 1–3 as long as halter, on tergites 4–7 as long as scape + pedicel; dorsal setulae black, short. Sternite tomentum grey, hairs white.

Female. As in male, except brown tomentum along midline greyish, leaving two indistinct lateral spots; lateral hairs on tergites 4–7 black, usually no longer than scape.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown/black, with yellow-grey tomentum except polished medially on hypandrium; long black erect hairs on epandrium and hypandrium. Epandrium elongate, in lateral view the width about 40% the length, eidest in basal third; apex rounded with ventral tooth. In dorsal view, medial margins of epandrium moderately curved, curvature starts about 35% from base, tapering to apex; basal sclerite prominent.

Phallus paramere sheath dorsally 45% the length of phallus; paramere sheath with long buttress-like ventral flange along basal half; dorsal carina very long, slender, and curving far past gonopore. Ejaculatory apodeme in lateral view moderately bent dorsally in basal quarter, slightly recurved at apex, dorsal carina broadly filling the gap. Subepandrial sclerite with triangular central unsclerotized area in basal 25% narrowing to parallel-sided gap in central portion; spines parallel-sided, blunt, densely arranged apically and medially.

Female genitalia. Undissected: Cuticle of tergite 8 polished dark brown/ black; sternite 8 dark brown or reddish brown, especially near base of hypogynial valves, which are short and wide. Short fine erect hairs abundant, white everywhere except occasionally on hypogynial valves; cerci with white hairs, lateral lobes with black bristles; acanthophorite spines black.

Type Material. HOLOTYPE (here designated) ♂ labelled: "[rectangular white label] Fish Camp, Calif./ Mariposa Co./ V-10-1942"; "[rectangular white label] E. G. Linsley/ Collector"; "[white and pink label] UCB"; "[rectangular white label] FISH". My holotype label "HOLOTYPE/ *Lasiopogon* ♂/ *anaphlecter* McKnight/ des. T.A. McKnight 2017 [red, black-bordered label]" has been attached to this specimen.

PARATYPES (53 specimens designated). **U.S.A.: CALIFORNIA: Madera Co.**, Willow Creek, pools by Angle Falls parking lot, 1 mi N of Bass Lake, 37.33519 -119.57029, 22.v.2016, T.A. McKnight (1♂ 1♀ TAM); **Mariposa Co.**, Big Creek, 22.v.1985, M. Elliott, J. Welch (1♂ RBCM); Fish Camp [37.478 -119.637], 10.v.1942, E.G. Linsley (1♂ 1♀ FISH), S.H. Benedict (1♀ CAS), 21.v.1942, A.J. Walz (1♀ FISH), E.G. Linsley (2♂ FISH), 29.v.1942 (1♂ FISH), E.G. Linsley (6♂ 2♀ FISH); Mariposa [37.497 -119.956], 23.v.1956, R.P. Allen (1♂ FISH); Summerdale campground, Big Creek, 37.48948 -119.63408, 11–15.vi.1973, D.K. & D.C. Young

(1♂ BEZA), 28.vi.1973, P.H. Arnaud, Jr. (2♀ FISH), 22.v.2016, T.A. McKnight (6♂ 5♀, 4 pr in cop, TAM); **Tuolumne Co.**, Basin Creek campground [37.994 -120.182], 31.v.1963, P.H. Arnaud, Jr. (2♂ FISH), 2.vi.1963, P.H. Arnaud, Jr. (1♂ 2♀ FISH); Big Trees State Park, Beaver Creek, S Grove [38.245 -120.267], 8/12.vii.1991, E.M. Fisher (1♂ 1♀ FISH); Carlon, S Fork Tuolumne River, 37.81243 -119.85957, 25.v.1969, P.H. Arnaud, Jr. (1♀ FISH), 20.v.2016, T.A. McKnight (8♂ 4♀, 4 pr in cop, TAM); Fraser Flat campground, South Fork Stanislaus River, 23.v.2016, T.A. McKnight (5♂ 1♀, 1 pr in cop, TAM); Middle Fork campground, Middle Fork Tuolumne River, 4 km S Mather [37.857 -119.864], 24.v.1969, P.H. Arnaud, Jr. (1♂ 1♀ FISH); Strawberry [38.195 -120.015], 23.vi.1951, P.D. Ashlock (1♀ FISH), 18.v.1953, J.G. Rozen (1♂ 4♀ FISH).

Type Locality. USA: California: Mariposa Co., Fish Camp.

Etymology. From the agent noun based upon the Greek verb αναφλέγω, anaphlego, meaning to kindle; used as a noun in apposition with reference to the peculiarly curved shape of the phallus dorsal carina which resembles an automobile spark plug.

Distribution (Fig. III.3). Nearctic; USA, California, Sierra Nevada.

Phylogenetic Relationships. Member of the *bivittatus* section, *drabicolum* group.

Natural History. Habitat: banks of mountain rivers. Found perching on bare sand, boulders, and fallen logs <1–10 m from the water (Fig. III.8c, III.8d). Dates collected: May 10 to July 12 (most in May). Two males and one female with prey: Peltoperlidae c.f. *Yoraperla*, Fanniidae c.f. *Fannia*, and Muscidae c.f. Phaoniinae.

***Lasiopogon apoecus* McKnight sp. nov.**

Diagnosis. A medium-sized dark species from mountain meadows of southern California and Baja California; with mystax black, thoracic tomentum grey to golden brown with distinct dorsocentral stripes, thoracic setae black, legs black; tergite tomentum in male starts out as mostly separate spots of basal brown that fuse into a single band on later segments, female with spots only. Epandrial halves strongly curved over medial margins, phallus dorsal carina comes to a hemispherical apex parallel to gonopore; ovipositor dark brown, acanthophorite spines black.

Description.

Head. Face and vertex with grey tomentum. Ventral hairs (on beard, labium, palps) white; mystax and all dorsal setae black. Occipital bristles fine, longest and most strongly curved forward posterior of frons, lateral bristles slightly hooked. Frontal setae average length, erect, reach basal quarter of F1; orbital setae fine, average length, slightly curved over eye margin; occelar setae slightly longer than surrounding hairs.

Antennae. Black, with thin grey tomentum. Setae black, 0–1 short hairs on F1. F1 widest at midpoint, tapering to apex. F2+3 moderately short.

Thorax. Prothorax brown-grey, with white hairs; postpronotal lobes grey, the lateral angle dark chestnut, hairs white except a few black laterally. Scutum tomentum grey, slightly brownish on lateral margin; dorsocentral stripes brown, acrostichal stripes usually faint or absent (sometimes brown). All bristles and hairs of scutum black; short notal hairs very fine; dorsocentral bristles not particularly distinct; anterior dorsocentrals 3–5; posteriors 3–4; postalars 3, with several shorter hairs; supra-alars 2–3, with a few shorter hairs; presuturals 2–3; posthumerals 0–1. Scutellar tomentum grey; apical bristles black, long, 8–9 on each side, with several other long hairs; a few sparse hairs on uppermost edge of rim less than half as long as apical bristles.

Pleural tomentum yellow-grey. Katatergite bristles black, 6–8, with 0–2 long and a few short white hairs; katepisternal setae of moderate length, white; anepisternum with 4–6 fine setae and several shorter hairs along dorsal margin; anepimeron with 0–3 short white hairs.

Legs. Base color dark brown/black; covered in thin grey tomentum except at both femur joints. No coxal peg. Coxae with all white setae. Bristles of legs black except 1–2 white at base of femur; finer hairs black except white hairs ventrolaterally on femur. Ventral setae on femur long and abundant; dorsolateral bristles indistinct, profemur with 8–13 bristles; mesofemur 5–6; metafemur 7–10. Protibia with ventral bristles very fine, 3 times as long as tibial width. Dense patch of short yellow hairs along inside apical half of protibia. Claws chestnut over basal 60%, black apically.

Wings. Veins light brown; membrane hyaline but brown when viewed obliquely. Halter knob cream, without spot, stem slightly darker.

Abdomen. Male. Tergite cuticle dark brown/black. Thin brown tomentum faintly on tergite bases, grey tomentum in bands that cover apical 50–60% of each tergite (tergite 1 completely covered) and sometimes faintly extend anteriorly along the midline leaving pattern indistinct. Tergite 1 laterally with 4–5 black bristles, 1–3 white bristles. Lateral hairs on tergites white, on tergites 1–3 as long as scape + pedicel, on tergites 4–7 a little shorter; dorsal setuale short, brown. Sternite tomentum grey, hairs white.

Female. Apical grey tomentum does extend anteriorly along the midline, splitting basal brown into two lateral spots.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown/black, covered in thin grey/brown tomentum except medially on hypandrium, where reddish-brown cuticle is bare; hairs long and black, setal brush dark brown. Epandrium elongate, in lateral view the width 43% the width, widest in basal third, slightly sinuate along ventral margin, gently curved to straight along dorsal margin; apex rounded with ventral subapical tooth. In dorsal view, medial margins of epandrium moderately curved, curvature starts about 35% from base; basal sclerite prominent.

Phallus paramere sheath dorsally 48% the length of phallus; paramere sheath with long buttress-like ventral flange along basal half; dorsal carina extending parallel to gonopore, with rounded apex slightly compressed dorsoventrally. Ejaculatory apodeme in lateral view strongly

bent dorsally in basal quarter, dorsal carina narrow. Subepandrial sclerite with triangular central unsclerotized area in basal 45%; spines parallel-sided, blunt, densely and evenly distributed.

Female genitalia. Undissected: cuticle dark brown except reddish at base of hypogyinal valves. All setae dark brown/black except short white hairs on cerci; weak but erect hairs on tergite and sternite 8; lateral lobes with short black bristles; acanthophorite spines black.

Variation. Specimens from the north are usually more richly brown-colored, with more distinct acrostichal stripes and less apical grey tomentum on tergites.

Type Material. HOLOTYPE (here designated) ♂ labelled: "[rectangular white label] Sierra San Pedro Martir/ LaGrulla, 6500'/ Baja Calif., MEX. V-29-58"; "[rectangular white label] J. Powell/ Collector"; "[rectangular white and pink label] UCB"; "[rectangular white label] FISH"; "[rectangular white label] RBCM-46". My holotype label "HOLOTYPE/ *Lasiopogon* ♂/ *apoecus* McKnight/ des. T.A. McKnight 2017 [red, black-bordered label]" has been attached to this specimen.

PARATYPES (16 specimens designated). **MEXICO: BAJA CALIFORNIA NORTE:** Sierra San Pedro Martir, 4 mi S Encinas, 6000' [30.793 -115.598], 2.vi.1958, J. Powell (1♂ FISH); Sierra San Pedro Martir, La Grulla, 6500' [30.892 -115.464], 29.v.1958, J. Powell (4♂ 3♀ FISH), 30.v.1958, J. Powell (4♀ FISH); **U.S.A.: CALIFORNIA: Riverside Co.**, Hurkey Creek [33.684 -116.676], 23.iv.1937, A.J. Basinger (3♂ CAS, 1♂ RBCM).

Type Locality. Mexico: Baja California Norte: Sierra San Pedro Martir, La Grulla.

Taxonomic Notes. This species was included in Cannings (2002) as "L. biv-1 sp. nov."

Etymology. From the Greek ἄποικος, apoikos, meaning colonist or resident in a settlement far from home; noun in apposition; befitting because this species ranges farther south than all others known from this hemisphere.

Distribution (Fig. III.3). Nearctic; mountains of northern Baja California Norte and southern California.

Phylogenetic Relationships. No samples were found with viable DNA, however, based on genitalia morphology this species is likely a member of the *bivittatus* section, related to *L. condylophorus* sp. nov. and *L. gabrieli*, especially the former.

Natural History. Habitat: unknown, but the original collecting localities in Baja California were described as a "small lush meadow among oaks… cool clear stream… downstream, lupine was in bloom in abundance… steep walled canyon of heavy vegetation… beautiful meadow which stretches amongst conifer [Ponderosa pine] forest in a sinuate expanse of green grass" (Patterson and Powell 1959). Dates collected: April 23 to June 2.

***Lasiopogon arenicola* (Osten Sacken)**

Lasiopogon arenicola Back, 1909. *Trans. Amer. Ent. Soc*. 35:297–298.
Daulopogon arenicola Osten Sacken, 1877. *Western Diptera*, p. 310. Unecessary emendation.

Diagnosis. A medium-sized species from central California coastal dunes; all bristles and hairs light-colored (white/gold); thoracic tomentum light grey with golden brown perimeter and brown dorsocentral stripes; abdominal tergites with brown tomentum basally and grey tomentum covering apical 50% of each tergite and extending laterally and up the midline in both sexes to divide brown tomentum into lateral spots. Epandrium strongly concave medially, curvature starts 35% from base; apical 20% bare of tomentum, with squared ventral edge. Ovipositor dark brown/black, acanthophorite spines yellow.

Description. Body length ♂ 7–10 mm; ♀ 8–10.5 mm.
Head. Face and vertex with grey tomentum. Beard, labial, frontal and occipital setae all white; mystax usually somewhat darker: dingy white. Occipital bristles of moderate length; those

behind the dorsomedial angle of the eye and moderately curved anterolaterally; lateral and ventral bristles shorter, straighter. Frontal setae fine and short; orbital setae longer, extend just beyond the edge of the eye.

Antennae. Brown to black, base of F1 chestnut in some. Setae dirty white; F1 never with setae. F1 rectangular, with straight dorsal and ventral margins, F2+3 moderately long, tapering.

Thorax. Prothorax grey, hairs dirty white; postpronotal lobes grey to brownish grey, the lateral angle ferruginous, hairs white. Scutum tomentum steelish-grey, sometimes brown around the perimeter. Dorsocentral stripes usually light brown bordered by tan, sometimes darker brown with a grey border; acrostichal stripes absent. Notal and acrostichal setae white. Anterior dorsocentral bristles 5–8mm, white, relatively fine and mixed with finer setae; 3–5 posteriors. Other bristles white with dingy bases; postalars 3, with about 4 shorter hairs; supra-alars 3–5 with 1 or 2 shorter hairs; presuturals 3–4; posthumerals 1. Scutellar tomentum grey, ranging from silvery to brownish; rim strongly inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles whitish, abundant (usually 8–10+ on each side) and mixed with many other long hairs.

Pleural tomentum grey, brownish on the lower anepisternum. Katatergite bristles dirty white, 8–10 with a few weaker hairs; katepisternal setae sparse, moderately long, white; anepisternal setae 4–7, usually moderately strong and mixed with other hairs, a patch of short white hairs on dorsal margin of sclerite; anepimeron with a single fine seta, white.

Legs. Base color usually dark brown to black, sometimes reddish at joints of coxa/femur, femur/tibiae, and tarsal bases; tomentum of coxae and rest of legs grey, sparse. No coxal peg. Bristles on legs dirty white, finer setae white. Ventral hairs on femur longer than femur width; dorsolateral bristles strong, mixed with many finer hairs, 5–7 on profemur; longer on mesofemur (3–6) and metafemur (8–9). Protibia with longest bristles about 3 times longer than tibial width. Claws reddish brown over basal 70%, apically black.

Wings. Veins dark brown, lighter in apical half; membrane transparent, milky white when viewed obliquely. Halter yellow, with no spot.

Abdomen. Cuticle dark brown/black basally, covered in grey tomentum except for semicircular patches of brown tomentum at tergite bases. Tergite 1 completely covered in light grey tomentum; on other segments, apical bands of light grey tomentum cover about half the length of the tergite and extend medially and laterally to the tergite base in both sexes. Tergites 2–5 each show a clear pair of brown spots; tergites 6 and 7 have the brown patches reduced to minor smudges. All tergites with relatively prominent and dense lateral hairs. Abundant bristles on each side of tergite 1, setae on sides of tergites 2–3 longer than basitarsus, erect. Setae on side of tergies 4–7 about length of scape+pedicel. Sternite tomentum grey, hairs white.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown/chestnut; epandrium polished over apical 20%, otherwise covered in thin grey tomentum; covered in long white hairs, setal brush yellowish white. Epandrium elongate, in lateral view the width about 45% the length, widest in basal third, dorsally and ventrally sinuate; apex right-angled ventrally, straight-edged apically, and rounded dorsally. In dorsal view, medial margins of epandrium strongly curved, curvature starting 35% from the base of the epandrium; basal sclerite prominent.

Phallus paramere sheath dorsally 60% the length of phallus; paramere sheath with small ventral flange near base; dorsal carina a narrow wave-like fin with rounded apex not projecting apically and ending well short of the gonopore. Ejaculatory apodeme in lateral view moderately bent dorsally in basal quarter, slightly recurved at apex; dorsal carina broadly fills gap. Subepandrial sclerite with triangular central unclerotized area in basal 75%; spines blunt, sparsely distributed, especially basally.

Female genitalia. Undissected: Hairs white, abundant, erect. Tergite 8 dark brown/black with posterior margin paler; sternite 8 dark brown/black laterobasally, yellowish brown/chestnut along midline; lateral lobe setae strong; hypogynial valves with fine hairs, concentrated basally; cerci brown with pale setae; acanthophorite spines brown.

Variation. Most individuals have white or dingy-white hairs and bristles, but a few specimens are completely clothed in golden hairs, yet otherwise indistinguishable in morphology or

genetics. Similar golden morphs have been observed in several other *Lasiopogon* species (*L. canningsi* sp. nov., *L. monticola*, *L. zonatus*).

Type Material. LECTOTYPE (here designated) ♂ labelled: "[rectangular white label] Lone Mt. S. Francisco/ June 29 O.Sacken"; "[rectangular white label] O. Sacken/ West. Dipt"; "[square red label] Type/ 12802"; "[rectangular white label] Museum of/ Comparative/ Zoology". My lectotype label "LECTOTYPE/ Daulopogon ♂/ arenicola Osten Sacken/ des. T.A. McKnight 2017 [red, black-bordered label]" and my determination label "Lasiopogon ♂/ arenicola/ (Osten Sacken) / det. T.A. McKnight 2017 [white, black-bordered label]" have been attached to this specimen. MCZ.

PARALECTOTYPES. **USA, California,** San Francisco [37.784 -122.444], 6.iv.[1876], Osten Sacken (3♂ 2♀ [2 pr in cop] MCZ); Lone Mountain [37.772 -122.463], 29.vi.[1876], Osten Sacken (1♀ CNC). My paralectotype and determination labels have been attached to these specimens.

Other Material Examined (51 specimens). **USA: California: San Francisco Co.**, no loc, vi, (1♀ USNM), 4.vi.1905, E.C. Van Dyke (1♀ CAS), 10.iv.1907, E.C. Van Dyke (1♂ CAS), 24.iii.1920, A.J. Basinger (1♀ RBCM); Fort Funston [37.717 -122.504], 16.iv.1960, G.I. Stage, R.R. Snelling (1♀ BPBM), 5.iv.1987, R.L. Zuparko (1♀ EMEC); Golden Gate Park [37.767 -122.511], 6.vi.1920, F.R. Cole (1♀ CNC); 6.vi.1928, F.R. Cole (1♂ LACM); San Francisco [37.784 -122.444], 12.v.1915, M.C. Van Duzee (2♂ 2♀ OSUC, 1♀ CAS), 22.v.1915, M.C. Van Duzee (1♀ CAS), 29.iii.1920, A.J. Basinger (1♂ FSCA), 4.iv.1920, A.J. Basinger (1♂ FSCA), 6.vi.1920, E.P. Van Duzee (1♂ CAS), 18.iii.1933, E.S. Ross (1♀ CAS), 30.v.1933, E.S. Ross (1♀ CAS), 1.v.1947, E.L. Kessel (1♂ 1♀ CAS, 1♂ ESUW), E.S. Ross (1♂ 1♀ CAS, 1♀ FSCA, 1♂ RBCM), 21.v.1949, C. Hildebrand (1♀ CAS), 23.v.1949 (1♀ FISH), 2.vi.1949 (1♂ FISH), 9.v.1951, E.L. Kessel (1♀ CAS), 18.iii.1960, G.I. Stage (1♂ 3♀ CAS, 1♂ FISH); San Francisco beach [37.763 -122.511], 16.v.1951, E.I. Schlinger (1♂ CNC, 1♂ FSCA, 1♂ FISH), R.C. Bechtel (1♀ FISH); San Francisco sand dunes, 2.vi.1923, Carl D. Duncan (1♂ 1♀ UMMZ), 12.vi.1923, Carl D. Duncan (1♂ OSUC, 1♂ 1♀ UMMZ); **San Mateo County.**, Half Moon Bay [37.462 -122.445], 23.v.1937 (1♀ UCRC), R.C. Dickson (1♀ CSUC), 24.v.1979, J. Powell (1♀

BEZA); Half Moon Bay State Park, 37.47997 -122.45096, T.A. McKnight (2♂ 2♀ [2 pr in cop] TAM); Santa Clara Co., Palo Alto [37.435 -122.095], 11.v.1893, R.W. Doane (2♀ EMEC).

Type Locality. USA, California, San Francisco, "... on the sands about Lone Mountain..." (Osten Sacken 1877).

Taxonomic Notes. Osten-Sacken's original description referenced 8 specimens that would be syntypes according to the modern code. Prior to this publication, the accepted species concept of *L. arenicola* included *L. asilomar* sp. nov., a similar species from the south that is readily distinguished by comparing tergite tomentum patterns. For future stability, I am hereby designating one of Osten-Sacken's specimens as a lectotype, and others in this series as paralectotypes.

Etymology. No explanation given in the original description, but evidently from the Latin *arena* = sand, *cola* = inhabitant of; referring to the sand dune habitat of the species.

Distribution (Fig. III.3). Nearctic; USA: California; beach dunes of the San Francisco peninsula.

Phylogenetic Relationships. Member of the *bivittatus* section, *drabicolum* group; likely the sister species to *L. asilomar* sp. nov.

Natural History. Habitat: sand dunes. Perches on bare sand adjacent to low, scraggly vegetation (Fig. III.6e). Dates collected: 29 March to 12 June. One specimen with a tiny arachnid speared on the proboscis, possibly prey.

***Lasiopogon asilomar* McKnight sp. nov.**

Diagnosis. A medium-sized species from central California coastal dunes; all bristles and hairs white/gold; thoracic tomentum thin, brown cuticle shining through in dorsocentral stripes; abdominal tergites with basal brown tomentum very thin, male with tergite bases broadly subshining dark, grey tomentum in straight bands over apical 30% of each tergite; female with grey tomentum faintly reaching along midline to create basal spots of subshining brown/black. Epandrium strongly concave medially, curvature starting about 25% from base; apical 30% bare of tomentum, with slightly toothed square ventral edge. Ovipositor dark brown/black, acanthophorite spines yellow.

Description. Body length ♂ 8.5–10 mm; ♀ 10–12 mm.
Head. Face and vertex with tan-grey tomentum. Beard, labial, frontal and occipital setae all white; mystax dingy white. Occipital bristles long and steadily curved through 90°, those behind the dorsomedial angle of the eye and most curved; lateral and ventral bristles shorter, straighter. Frontal setae fine and short; orbital setae longer, extend over the eye for half their length.

Antennae. Brown to black. Setae dirty white; F1 never with setae. F1 long and rectangular, with straight dorsal and ventral margins; F2+3 short and tapered.

Thorax. Prothorax brown/grey, hairs dirty white; postpronotal lobes brown, the lateral angle ferruginous, hairs white. Scutum tomentum brownish-grey/grey. Dorsocentral stripes thin dark brown; acrostichal stripes greyish brown. Notal and acrostichal setae white, long. Anterior dorsocentral bristles 4–8mm, white, relatively fine and mixed with finer setae; 5–6 posteriors. Other bristles white; postalars 2–4, with several additional setae; supra-alars 3–4 with 1 or 2 additional setae; presuturals 3; posthumerals 1–2. Scutellar tomentum subshining brownish grey; rim strongly inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles whitish, abundant (usually 9–11+ on each side) and mixed with many other long hairs.

Pleural tomentum grey, brownish on the lower anepisternum. Katatergite bristles dirty white, 9–11 with a few weaker hairs; katepisternal setae sparse, moderately long, white;

anepisternal setae 3–8, usually moderately strong and mixed with other hairs, a patch of short white hairs on dorsal margin of sclerite; anepimeron with a 1–2 fine setae, white.

Legs. Base color usually dark brown to black, dark reddish at joints of coxa/femur, femur/tibiae, and tarsal bases; tomentum of coxae and rest of legs grey, sparse. No coxal peg. Bristles on legs dirty white, finer setae white. Ventral hairs on femur dense, longer than femur width; dorsolateral bristles strong, mixed with many finer hairs, 3–7 on profemur; longer on mesofemur (5–6) and metafemur (10–14). Protibia with longest bristles about 3 times longer than tibial width. Claws chestnut over basal 50–60%, apically black.

Wings. Veins dark brown; membrane transparent, milky white when viewed obliquely. Halter yellow/orange, with no spot.

Abdomen. Male. Cuticle dark brown/black basally; tergite bases subshining dark brown, bands of grey/grey-gold tomentum cover apical 30% of each tergite (tergite 1 fully covered in grey) and extending anteriorly 50% along lateral margins, but only faintly apparent along midline (overall appearance is straight band). All setae yellow/white; tergite 1 with abundant (12+) lateral bristles; lateral setae on tergites 2–3 longer than basitarsus and erect, on tergites 4–7 as long as F1. Sternite tomentum grey, hairs white.

Female. Tomentum along midline of tergites lighter, creating the illusion of diffuse basal subshining brown spots. Setae on sides of tergites 4–7 shorter than in male.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown/chestnut; epandrium polished over apical 30%, otherwise covered in thin grey tomentum; covered in long white hairs, setal brush yellowish white. Epandrium elongate, in lateral view the width about 45% the length, widest in basal third, dorsally and ventrally sinuate; apex right-angled ventrally, straight-edged apically, and rounded dorsally. In dorsal view, medial margins of epandrium strongly curved, curvature starting 25% from the base of the epandrium; basal sclerite prominent.

Phallus paramere sheath dorsally 60% the length of phallus; paramere sheath with small ventral flange near base; dorsal carina a narrow wave-like fin with straight apex not projecting apically and ending well short of the gonopore. Ejaculatory apodeme in lateral view moderately

bent dorsally in basal quarter, slightly recurved at apex; dorsal carina moderately wide. Subepandrial sclerite with triangular central unclerotized area in basal 70%; spines blunt, sparsely distributed.

Female genitalia. Undissected: Hairs white, abundant, erect. Tergite 8 black with posterior margin paler; sternite 8 black, with a lighter spot medially; lateral lobe setae long; hypogynial valves with long fine hairs, concentrated basally and apically; cerci black with pale setae; acanthophorite spines brown.

Variation. Most individuals have white or dingy-white hairs and bristles, but a few specimens are completely clothed in golden hairs, otherwise indistinguishable in morphology or genetics. Similar golden morphs have been observed in several other *Lasiopogon* species (*L. canningsi* sp. nov., *L. monticola, L. zonatus*).

Type Material. HOLOTYPE. (here designated), ♂ labelled: "[rectangular white label] ASILOMAR/ 3/9/45 CAL/ ALMELANDER"; "[rectangular white and green label] ALMelander/ Collection/ 1961"; "[rectangular white label] Lasiopogon/ arenicola/ O.S. '65/ det. J. Wilcox"; "[rectangular white label] USNMENT/ 01100340". My holotype label "HOLOTYPE/ *Lasiopogon* ♂/ *asilomar* McKnight/ des. T.A. McKnight 2017 [red, black-bordered label]" has been attached to this specimen. USNM.

PARATYPES (193 specimens designated). **USA: California: Monterey Co.**, Asilomar [36.626 -121.939], 1.ix.1945, A.L. Melander (2♂ 1♀ USNM), 2.ix.1945, A.L. Melander (2♂ 5♀ USNM), 3.ix.1945, A.L. Melander (2♂ 2♀ RBCM, 13♂ 6♀ USNM), 28.ix.1946, A.L. Melander (2♂ UCRC, 20♂ 14♀ 2? USNM), 29.ix.1946, A.L. Melander (2♂ 2♀ UCRC, 10♂ 12♀ USNM), 2.x.1946, A.L. Melander (2♀ UCRC, 1♂ 2♀ USNM), 3.x.1946, A.L. Melander (1♀ USNM), 26.iv.1947, George Geiwitz (2♂ CAS), 11.vii.1957, A.L. Melander (1♂ USNM), 23.v.1959, J.R. Powers (1♂ 1♀ UYWO); Giberson Beach [36.836 -121.802], 17.v.1959, D. Jamieson (1♂ 1♀ BEZA); Monterey [36.606 -121.864], 25.ix.1934, A.L. Melander (1♂ 1♀ USNM), 24.ix.1938, M. Cazier (2♀ CAS, 2♂ 1♀ CSUC), 20.v.1956, M. Wasbaner (1♂ 1♀ CAS); Moss Landing [36.803 -121.788], 1.iv.1961, Ed Ball (1♂ 1♀ FSCA), 27.v.1969, M.E. Irwin, F.G. Andrews (8♂

3♀ UCRC); Pacific Grove [36.633 -121.936], v.1906, J.M. Aldrich (1♂ 1♀ USNM), 7.v.1906, J.M. Aldrich (2♂ 2♀ USNM), 9.v.1906, J.M. Aldrich (3♂ USNM), 10.v.1906, J.M. Aldrich (1♂ USNM), 27.viii.1957, R.M. Bohart (4♂ 1♀ FSCA, 1♂ RBCM), 17.iv.1965, B.A. McKinley (1♀ CAS); Pacific Grove, dunes in golf course by Sunset Dr, 36.6330 -121.9362, 11.v.2012, T.A. McKnight (2♂ 2♀ TAM); Pacific Grove, Point Pinos [36.634 -121.936], 24.v.1952, P.H. Arnaud (1♂ 2♀ CAS, 1♀ EMEC); Pajaro River mouth [36.851 -121.809], 12.v.1975, D.W. Moss (1♀ FISH), 23.v.1976, D.W. Moss (4♂ 1♀ BEZA); Seaside [36.634 -121.836], 16.vii.1967, M.E. Irwin (1♀ UCRC), 5.ix.1970 (1♀ BEZA); **Riverside Co.**, the Gavilan, 17.v.1951, E.I. Schlinger (1♂ 1♀ FSCA); **San Luis Obispo Co.**, Oceano [35.095 -120.621], 24.iv.1951, R.M. Bohart (1♂ CNC); Oso Flaco Lake [35.032 -120.627], 13.vii.1959, I.L. Bath (1♂ UCRC); Paso Robles, Salinas River E side [35.642 -120.683], 17.iv.1990, D.W. Webb, M.E. Irwin (1♀ INHS); Pismo Beach [35.087 -120.626], 13.v.1956, J. Wilcox (2♂ 1♀ CAS, 1♂ USNM), 5.x.1964, W. Bish (1♂ LACM); **Santa Cruz Co.**, Santa Cruz [36.964 -122.009], 2.v. (2♀ CAS, 2♂ 6♀ FSCA), 29.v. (2♂ CAS, 1♂ 4♀ FSCA).

Type Locality. USA: California: Monterey Co., Asilomar.

Taxonomic Notes. In previous publications, this species was subsumed into the species concept of *L. arenicola*, a similar species found to the north. These species can be readily distinguished by comparing the tomentum patterns of the abdominal tergites.

Etymology. Asilomar is a local name for the beach dune complex at Pacific Grove, coined in 1913 by Helen Salisbury from the Spanish "asilo" (haven, refuge) and "mar" (sea). Used here as a noun in apposition to maintain the phonetic similarity to “Asilidae”.

Distribution (Fig. III.3). Nearctic; USA, California; beach dunes along the central California coast, between Santa Cruz and Pismo. Two specimens labelled “The Gavilan, Cal/Riverside Co” collected 17.v.1951 by E.I. Schlinger (FSCA) are probably mislabelled or anomalous.

Phylogenetic Relationships. Member of the *bivittatus* section, *drabicolum* group; likely the sister species to *L. arenicola*.

Natural History. Habitat: coastal sand dunes. Perches on bare sand adjacent to scraggly vegetation (Fig. III.6f). Dates collected: 1 April to 5 October, with a bimodal emergence pattern. Two females and one male with prey: 2 *Coleopa* (Coleopidae), 1 Anthomyiidae.

***Lasiopogon bitumineus* McKnight sp. nov.**

Diagnosis. A small to medium sized dark brown species with very long and robust black bristles on scutum and legs; both sexes with abdominal tergite tomentum in straight bands, brown basally and grey over apical 30–40% of each tergite. Male terminalia shining black, covered in long hairs, epandrial halves narrow, strongly concave medially. Ovipositor black except for light tan apically and along midline of sternite 8, as well as hypogynial valves.

Description.

Head. Face yellow-grey, vertex brown-grey. Ventral hairs (on beard, labium, palps) white; mystax and all dorsal setae black. Occipital bristles fine, very long; longest posterior to frons, strongly curved anterolaterally; lateral and ventral bristles reduced to short, fine, straight hairs. Frontal setae very long, erect, densely abundant, longest reach apex of F1; orbital setae also fine and long, gently curving over eye margin; occelar setae also long, but fine and indistinct in 'lawn' of hairs.

Antennae. Black, with thin grey tomentum. Setae black, abundant. No hairs on F1. F1 short, widest at midpoint, dorsal edge straight, ventral edge curved. Arista extremely long.

Thorax. Prothorax brown-grey, with yellowish-white hairs; postpronotal lobes brown, the lateral angle dark chestnut, hairs black-brown. Scutum tomentum brown, varying from greyish to copper or chocolate hued. Dorsocentral stripes dark brown; acrostichal stripes lighter but distinct. Notal and acrostichal setae black, widely spaced, long (up to 60% as long as dorsocentrals).

Dorsocentral setae black, extremely long; anteriors 4–7, 3–5 posteriors. Postalars 2–3, with about 4 shorter hairs; supra-alars 2–4 with a few short hairs; presuturals 2–3; posthumerals 1. Scutellar tomentum grey-brown; rim inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, abundant (4–10 on each half), mixed with other long hairs. Hairs on uppermost edge of rim short (30% as long as other bristles), point straight up.

Pleural tomentum grey to brownish grey. Katatergite bristles black, long, 5–8, with a few fine short white hairs; katepisternal setae fairly long, white; anepisternal setae 6–8, black, 0–5 short black hairs along dorsal margin; anepimeron with 1–3 fine white setae.

Legs. Base color dark brown/black, covered in thin grey tomentum; bare at femur-tibia joint and trochanters. No coxal peg. Coxae with long white setae. Main bristles of legs black, finer hairs mostly white except some brown hairs mixed in on femur apicoventrally and on protibia. Bristles on profemur fine, 10+, almost indistinguishable from the surrounding hairs; apicolateral bristles on other femorae strong, short, mesofemur with 2–5, metafemur 6–10. Longest ventral setae longer than the width of the femur. Protibia with ventral bristles about 4 times longer than tibial width; dense patch of short yellow-brown bristles on inside of protibiae indistinct. Claws dark chestnut over basal 60%, black apically; pulvilli longer than claws.

Wings. Veins dark brown; membrane hyaline but pale brown when viewed obliquely. Halter knob cream, without spot, stem brown.

Abdomen. Male. Tergite cuticle dark brown/black. Thin brown tomentum on tergite bases; bands of grey tomentum cover apical 40–50% of each tergite (segment 1 is half to fully covered); ventrolaterally lighter grey-brown. Tergite 1 with 5–6 lateral black bristles. Lateral setae on tergites white, as long as scape+pedicel; dorsal setulae shorter, brown, straight. Sternite tomentum grey, hairs white.

Female. As in male, except basal brown tomentum thicker and covers more of each tergites, grey tomentum only over apical 20–60% of each tergite; lateral setae on tergite 3–7 black, shorter and more sparse than in male.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle shining dark brown/black, devoid of tomentum; with long, prominent dark brown/black hairs, setal brush black. Epandrium long, slender, in lateral view the width 45% the length, widest in basal third, dorsal and ventral margins both constricted medially and flaring apically; apex gently concave with shallow subapical ventral tooth. In dorsal view, epandrial halves wide set, moderately concave; basal sclerite prominent.

Phallus paramere sheath dorsally 48% the length of phallus; paramere sheath without ventral ornamentation; dorsal carina broad, coming to a slight point and then curving to rejoin paramere sheath apically. Ejaculatory apodeme in lateral view gently bent dorsally, with broad dorsal carina. Subepandrial sclerite U-shaped, with central unsclerotized area a tall bottle-shape over basal 70%; spines blunt, sparsely distributed.

Female genitalia. Undissected: Tergite 8 cuticle polished dark brown/black with black erect fine hairs; sternite 8 dark brown basally, pale brown apically; hypogynial valves pale brown with a few fine hairs; lateral lobe with fine black setae; cerci brown with pale setae; acanthophorite spines black.

Type Material. HOLOTYPE. (here designated), ♂ labelled: "[rectangular white label] USA: California: San Luis Obispo/Co., Oceano dunes @ Pismo State/beach, 1 km S of Oceano,/Ericameria gully, N 35.08746°/W 120.61552°, elev: 12 m,/12 Mar 2014, TA McKnight #546.". My holotype label "HOLOTYPE/ Lasiopogon ♂/ bitumineus McKnight/ des. T.A. McKnight 2017 [red, black-bordered label]" has been attached to this specimen. USNM

PARATYPES (68 designated). **USA: California: San Luis Obispo Co.,** Dune Lakes, 3 mi S of Oceano [35.068 -120.615], 15.ii.1974, J. Doyen, J. Powell (4♂ 5♀ EMEC, 2♂ 1♀ RBCM), 23.ii.1974, J. Powell (6♂ 3♀ EMEC), 20.iii.1974, J. Doyen, J. Powell (2♂ EMEC), 23.ii.1975, J. Powell (1♂ 1♀ RBCM), 24.ii.1975, J. Powell (1♂ EMEC, 1♂ RBCM), 4.iii.1977, J. Doyen (1♀ BEZA); Montaña de Oro State Park, dunes @ Sand Spit trailhead (*Ericameria* zone), 35.30111 -120.87299, 12.iii.2014, T.A. McKnight (5♂ 5♀ [2 pr in cop] TAM); Montaña de Oro State Park, dunes @ Sand Spit trailhead (iceplant zone), 35.30214 -120.87527, 12.iii.2014, T.A. McKnight (3♂ 2♀ [1 pr in cop] TAM); Morro Bay, 2.iii.1973, D.A. Thomas (2♂ 1♀ CAS); Oceano dunes

@ Pismo State beach, 1 km S of Oceano, *Ericameria* gully, 35.08746 -120.61552, 12.iii.2014, T.A. McKnight (7♂ 3♀ [2 pr in cop] TAM); Oso Flaco Lake, 5 mi S of Oceano [35.032 -120.627], 23.iv.1966, J. Powell (1♂ FISH); **Santa Barbara Co.**, Vandenberg AFB, Coast road, back dunes, 34.641129 -120.617618, 14.ii.2016, A.J. Abela (13 specimens [EtOH] TAM); Vandenberg AFB, South Spur Road, 34.737300 -120.619964, 2.ii.2016, A.J. Abela (1♂ [EtOH] TAM).

Type Locality. U.S.A. California, San Luis Obispo Co., Pismo State Beach, 1 km S of Oceano.

Taxonomic Notes. Specimens of this species have occasionally been misidentified as *L. zonatus*, *L. gabrieli,* and *L. drabicola*.

Etymology. Latin for bitumen; adjective; refers to both the black color of this species in contrast to the sympatric pale *L. littoris*, as well as the type locality of Pismo, which is derived from "pismu" meaning bitumen in the language of the indigenous Chumash people.

Distribution (Fig. III.2). Nearctic; coastal dunes in San Luis Obispo County, California.

Phylogenetic Relationships. Member of the *bivittatus* section but with uncertain placement, potentially sister to *L. littoris* or *L. gabrieli*.

Natural History. Habitat: Coastal dunes, especially sandy patches near vegetation in backdune gullies, especially common around mock heather (*Ericameria*) and veldt grass (*Ehrharta calycina*), less often by iceplant (*Carpobrotus*) (Fig. III.6h). Flight dates for museum specimens range from 2 February–23 April; specimens recognizable from photographs on BugGuide.net (#1187437) extend this to 30 January. Preliminary field observations by the first author and A. Abela (pers. comm.) suggest that the flight period for this species begins and peaks a few weeks before the sympatric *L. littoris* emerges in numbers. Prey: one female with *Acreophthiria* (Bombyliidae). In addition, a photograph on BugGuide.net (#1198571) shows a male with Tipulidae prey.

***Lasiopogon bivittatus* Loew**

Lasiopogon bivittatus Loew, 1865-72. *Dipt. Amer. septentrionalis* (II), p. 93.

Daulopogon bivittatus (Loew); Osten Sacken, 1877. *West. Dipt.* p.310. Unnecessary emendation.

Diagnosis. A medium-sized dark species from coastal dunes of central and northern California; mystax black, thoracic tomentum grey with dark dorsocentral stripes, thoracic setae mostly black except light hairs on postpronotal lobe in male; femur basally with white setae and thin grey tomentum, apical 40% black haired and with cuticle polished; tergites with dark brown/black cuticle subshining basally, grey tomentum bands cover apical 30% and lateral margins; lateral bristles on tergite 1 mostly pale, 3–4 black. Epandrium polished dark brown/black, in dorsal view narrow, coming to sharp apex, with moderately concave medial margins, apex straight or gently concave into strong ventral subapical tooth; ovipositor black with light hairs.

Description.

Head. Face with silver-grey tomentum, vertex sparse grey under setae patches, subshining otherwise. Beard and labial hairs white, sometimes tinged yellowish; mystax and all other setae black. Occipital bristles relatively fine and long; those behind the dorsomedial angle of the eye the longest, moderately curved anterolaterally; lateral and ventral bristles shorter, straighter. Frontal setae fine, long, and erect, reach midpoint of F1; orbital setae also fine and long, slanting over eye margin.

Antennae. Black, slightly lighter at base of F1. Setae black; F1 sometimes with a seta. F1 long, spindle shaped, widest at midpoint.

Thorax. Prothorax grey, with white hairs; postpronotal lobes grey, the lateral angle yellowish red, hairs mostly white in male, a few brownish hairs on outside edge. In female, all hairs on postpronotal lobes brown. Scutum tomentum thin, slate grey, sometimes with a brownish tinge especially around perimeter. Dorsocentral stripes dark brown, edged in yellow; acrostichal stripes absent. Notal and acrostichal setae black, widely spaced, long (up to 60% as long as dorsocentrals). Dorsocentral setae fine, black; anteriors 4–5, can be hard to distinguish from surrounding hairs, 3–4 posteriors. Postalars 2–3, with about 4 long surrounding hairs; supra-alars

2–3 with a few short hairs; presuturals 2–3; posthumerals 1. Scutellar tomentum grey/greyish brown; rim inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, abundant (10+ on each side) and mixed with many other long hairs. Hairs on uppermost edge of rim short (half the length of other bristles), point straight up.

Pleural tomentum grey to brownish grey. Katatergite bristles black, 8, with a few fine white hairs about half as long; katepisternal setae fairly long, wavy, white; anepisternal setae 14+, mostly black with a few white hairs ventrally and a patch of short black setae along dorsal edge; anepimeron with 5 fine white setae.

Legs. Base color dark brown/black, chestnut at femur-tibia joint and trochanters. Tomentum on coxae grey, on basal 60–70% of femur sparse grey, elsewhere shining black. No coxal peg. Coxae with long straw/white setae. Main bristles of legs black, hairs on basal 60–70% of femur white, elsewhere black. Dorsolateral bristles on femur are numerous, long, fine, and are almost indistinguishable from the surrounding hairs, at least on the profemur. Setae erect on outside face of femur, reclinate on inside face. At least 10+ dorsolateral bristles on profemur, mesofemur with 3–5, metafemur 8–13, colored as with the shorter hairs. Longest ventral setae are longer than the width of the femur. Tibiae and tarsi have dark, strong bristles typically arranged; hairs brown. Short dense bristles on inside of protibiae yellow. Protibia with longest bristles about 4 times longer than tibial width. Claws dark chestnut over basal 60%, black apically.

Wings. Veins dark brown; membrane hyaline, very pale brown when viewed obliquely. Halter yellow; knob without dark spot.

Abdomen. Male. Tergite cuticle dark brown/black. Very thin brown tomentum on tergite bases, extensively lacking so the dark cuticle shines through, bands of grey tomentum cover apical 30% of each tergite in an even band (tergite 1 is half covered) and extending ventrolaterally to cover lateral margins. Tergite 1 with 2–4 black and 4–6 white/yellow lateral bristles; lateral setae on tergites long, erect, white; on tergites 2–4 setae longer than F1, on tergites 1 and 5–7 as long as scape + pedicel. Dorsal setulae white/brownish white, relatively long. Sternite tomentum grey, hairs white.

Female. Tergite bases have thicker brown tomentum. More black bristles on side of tergite 1, usually between 4–9.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle polished dark brown/black, entirely devoit of tomentum; with dark brown/black hairs, setal brush black. Epandrium elongate, slender, in lateral view the width 40% the length, with dorsal and ventral margins parallel; apex straight or gently concave from dorsoapical corner to sharp subapical ventral tooth. In dorsal view, epandrium moderately concave, tapered; basal sclerite weak.

Phallus paramere sheath dorsally 35% the length of phallus; paramere sheath with sharp ventral subapical tooth; dorsal carina a flat fin curving away apically into shallow sharp point parallel to aedeagal tube, leaving a narrow gap between the apices. Ejaculatory apodeme in lateral view long, slender, straight to slightly bent in basal quarter, dorsal carina narrow basally, wider apically. Subepandrial sclerite U-shaped, central unsclerotized area shaped like a tall bottle over basal 90%; spines parallel-sided, blunt, densely and evenly distributed, apical spines moderately erect.

Female genitalia. Undissected: Hairs white, erect. Tergite and sternite 8 cuticle dark brown/black; hypogynial valves long, black, with a few hairs basally; cerci reddish brown with pale setae; acanthophorite spines black.

Type Material. LECTOTYPE (examined) ♂ labelled: "[rectangular white label with illegible handwritten symbol on back] Cala."; "[rectangular beige label] Loew/ Coll."; "[square red label] Type/ 12804"; "[handwritten rectangular beige label] bivittatus/ m."; "[rectangular white label] Museum of/ Comparative/ Zoology"; "[rectangular white label] MCZ-ENT/ 00012804"; "[handwritten rectangular pink label] Should have a lectotype/ label; will designate at/ a later date. RAC". My lectotype label "LECTOTYPE/ Lasiopogon ♂/ bivittatus Loew/ des. T.A. McKnight 2017 [red, black-bordered label]" has been attached to this specimen.

Other Material Examined (162 specimens). **USA: California:** no loc (1♀ FISH); **Marin Co.,** no loc, v.1964, P.A. Gage (1♀ BEZA); Mill Valley [37.904 -122.534], 24.v.1926, M.C. Van Duzee (1♂ FISH); Pt. Reyes [38.074 -122.976], 30.iii.1956, E.A. Kurtz (1♂ FSCA, 1♂ RBCM),

J.C. Downey (1♂ ESUW, 1♂ FSCA), W.H. Lange (1♂ FISH, 1♂ FSCA), 31.iii.1956, A.M. Barnes (1♂ BPBM, 17♂ 2♀ EMEC, 3♂ RBCM), 7.iv.1956, A.M. Barnes (2♂ BEZA, 4♂ 1♀ [1 pr in cop] EMEC), 7.iv.1957, Menke, Strange (1♀ EMEC), 11.iv.1959, G.I. Stage (1♂ 2♀ EMEC), R.W. Thorp (2♂ 1♀ EMEC), 14.iv.1959, D. Burdick (1♂ 1♀ EMEC); Pt. Reyes beach, north [38.074 -122.976], 13.iv.1976, E.M. Fisher (1♂ 2♀ CSUC, 10♂ 8♀ FISH, 1♂ LACM); Point Reyes beach streams S of N beach parking lot, 38.07444 -122.97589, 14.iii.2014, T.A. McKnight (1♂ 1♀ TAM); Pt. Reyes lighthouse, 1 mi N [38.007 -123.007], 7.iv.1957, A.M. Barnes (7♂ 4♀ EMEC, 1♂ 1♀ RBCM), Pt. Reyes lighthouse, 2 mi N [38.018 -123.002], 7.iv.1956, A.M. Barnes (1♂ CAS); Stinson Beach [37.897 -122.642], 7.iv.1962, J. Doyen (1♂ EMEC); **Monterey Co.,** Carmel [36.556 -121.931], 26.iii.1930, L.S. Slevin (1♂ EMEC); Little Sur Beach [36.332 -121.893], 17.v.1976, L. Bezark (1♂ BEZA); Marina, Coastal Sand Dune Association [36.697 -121.809], 10.v.1971, M.E. Irwin (1♂ 2♀ [1 pr in cop] UCRC); Pacific Grove [36.633 -121.936], 1.iv.1904 (1♂ EMEC), 15.iv.1965, B.A. McKinley (1♂ CAS); **San Francisco Co.**, no loc, 29.iii.1920, A.J. Basinger (2♂ 4♀ EMEC), 2.v.1920, A.J. Basinger (1♂ EMEC); Baker Beach [37.793 -122.484], 18.iii.1977, J. Powell (3♂ 1♀ [1 pr in cop] EMEC); Fort Funston [37.717 -122.504], 16.iv.1960, G.I. Stage, R.R. Snelling (1♀ EMEC), Fort Funston dunes by Battery Davis, 37.71862 -122.50398, 14.iii.2014, T.A. McKnight (1♂ 2♀ TAM); Lake Merced [37.719 -122.489], 9.iv.1916, E.C. Van Dyke (1♂ EMEC, 1♂ OSUC); Lobos Creek [37.791 -122.485], 16.v.1960, J.F. Lawrence (1♀ EMEC), 26.iii.1967, P.H. Arnaud, Jr. (3♂ CAS); Presidio [37.791 -122.485], 3.iv.1954, E.I. Schlinger (2♀ EMEC, 2♂ FSCA, 1♂ 1♀ FISH), W.H. Lange (2♂ FSCA); Presidio, open area back of US Marine Hospital [37.791 -122.485], 31.iii.1968, T.W. Davies (1♂ 1♀ CAS); San Francisco [37.784 -122.444], H. Edwards (1♂ MCZ), 28.iii.1876, Osten Sacken (1♂ 3♀ 1? [1 pr in cop] MCZ), 19.iv.1908, E.C. Van Duzee (1? CAS), 20.iii.1915, C.L. Fox (2♂ 2♀ EMEC), 30.iii.1919, E.P. Van Duzee (1♀ MCZ), 4.iv.1920, A.J. Basinger (2♂ 1♀ EMEC), 22.v.1926, M.C. Van Duzee (1♂ FISH), 25.v.1926, M.C. Van Duzee (1♂ CAS), 3.iii.1957, D. Rentz (1♀ CAS), 1.iii.1960, J.A. Goodwin (2♂ EMEC), 18.iii.1960, G.I. Stage (1♀ CAS), 9.v.1960, P.H. Arnaud, Jr. (1♀ CAS), 28.iii.1961, D.C. Rentz (1♀ CAS), 23.iii.1963, P.H. Arnaud, Jr. (4♂ 1♀ CAS, 1♀ RBCM), 24.iii.1968, H.B. Leech (1♀ CAS); San Francisco beach [37.763 -122.511], 13.iv.1958, A.D. Telford (2♂ FSCA); San Francisco, Quintara Street dunes [37.747 -122.508], 7.iv.1961, R.L. Langston (1♀ FISH); San Francisco, Sunset sand dunes [37.743 -122.508], 1.iv.1960, G.I. State (1♂ USNM); **San**

Mateo Co., Greyhound Rock coast [37.0792 -122.2674], 22.v.1952, P.H. Arnaud, Jr. (1♂ CAS); **Santa Cruz Co.**, Ano Nuevo State Beach [37.129 -122.336], 16.v.1976, L.S. & R.B. Kimsey (1♀ BEZA); Santa Cruz [36.964 -122.009], 5.iv.1961, R. Brown (2♂ CAS); Waddell Creek [37.097 -122.279], 11.iii.1956, D.J. Burdick (1♂ EMEC), Waddell Creek Stanford University lot 6068 sub 4, 20.iii.1930, F. Bianchi (1♂ LACM); **Sonoma Co.**, Bodega Head, UC Davis Bodega Marine Lab, 38.31788 -123.06657, 10.v.1975, R.W. Thorp (1♀ BEZA), 13.iii.2017, C.E. Herbert (4M 1F [1 pr in cop] UCDC), 14.iii.2017, C.E. Herbert (1M [EtOH] UCDC), 15.iii.2017, C.E. Herbert (1M 1F [2 in EtOH] UCDC).

Type Locality. California (no other data). Many species described in Loew's Centuries were based on specimens collected in California by A. Agassiz, but the description and labels for *L. bivittatus* lack the usual annotations for this and leave us at a dead end. However, given the known range for this species and the fact that most insect collectors in antebellum California stopped in San Francisco, we can assume that the specimen was collected from those general environs.

Taxonomic Notes. Back's (1909) comment that "a single female in the Loew collection is probably the type" is incorrect as Loew's original description is for a male and the specimens in the MCZ Loew collection are both male. Alexander (1969) noted that when the Loew collection was returned to America in 1876, type specimens had been isolated and given individual handwritten labels with only the species name; this protocol is apparent for the specimen listed as holotype above. The other fly, evidently donated to Loew from the San Francisco lepidopterist Henry Edwards, has different labels. However, since the description does not list the number of specimens examined and localities in Loew's Centuries were typically not recorded more precisely than states, we cannot preclude the possibility that Loew had both specimens when he wrote the description and they should be considered syntypes.

In all previous publications, the species concept of *L. bivittatus* included *L. canningsi* sp. nov. and *L. tumulicola* sp. nov., closely related allospecies found on beaches to the north. I have chosen to split this complex because specimens along the Pacific coast sort into three discrete groups based on epandrium shape and mitochondrial genome. Of the three, *L. bivittatus* has the

most divergent genome and specimens can be further distinguished by their broader stripes of apical grey tomentum on the tergites.

Etymology. No explanation given in the original description, but evidently from the Latin *bi* = two, *vitta* = ribbon, stripe; thus, two-striped, a reference to the dark dorsocentral stripes on the mesonotum.

Distribution (Fig. III.2). Nearctic; coastal dunes in central California from Bodega Head to Monterey, but with most specimens from the San Francisco bay area. As the first dark-colored species described from western North America, several erroneous records exist in the literature: Coquillett specimens from Los Angeles County (Back 1909, Cole & Wilcox 1938) are actually *L. zonatus*; Cole specimens from Mt. Hood, Oregon (Cole and Lovett 1921) are actually *L. ripicola*; other records from Mt. Hood (Back 1909 and Cole & Wilcox 1938) and Sheridan, Wyoming (Metz and Nonidez 1924) are undoubtedly also misidentifications although voucher specimens have not been located for verification.

Phylogenetic Relationships. Basal member of the *bivittatus* species group, which is basal to the rest of the *bivittatus* section.

Natural History. Habitat: Coastal beaches and dunes. Found perching on bare sand near sparse vegetation in back dune field, also on logs across streams running through beach (similar to Fig. III.6d, III.6e). Flight dates range from 1 March to 25 May, most in late March to mid April. Three females with prey: 1 *Bibio* c.f. *necotus* Hardy (Bibionidae), 2 Muscidae c.f. *Hydrotaea*. The cytology observations of Metz and Nonidez (1924) are misattributed to this species; it does not occur in Wyoming. One specimen has an associated pupal case; this will be described in a forthcoming work.

***Lasiopogon californicus* Cole & Wilcox**

Lasiopogon californicus Cole & Wilcox, 1938. *Entomologica Americana* 43:31–32.

Diagnosis. A medium-sized species from the coastal range of central and northern California; setae of mystax, upper head, and scutum dark brown/black except some white hairs on antennal scape; dorsocentral and acrostichal stripes weakly apparent; tergites with brown tomentum basally, grey tomentum over apical 30–50%, in male basal brown as straight band, in female grey extends forward to divide brown into lateral spots; lateral hairs on tergites 5–7 (4–7 in female) dark brown, other tergites with white lateral hairs. Epandrial halves in dorsal view moderately curved, in lateral view dorsal margin gradually curving ventrally to rounded apicoventral corner; phallus dorsal carina triangular, not extended apically; gonostylus dorsomedially flattened, similar to dumbbell. Ovipositor dark brown/black, hypogynial valves reddish at base, acanthophorite spines black.

Description.

Head. Face yellow-grey, vertex brown. Ventral hairs (on beard, labium, palps) white; mystax and dorsal setae black. Frontal and orbital setae long (reach basal quarter of F1), occellar setae indistinct among other hairs; occipital setae long, relatively straight.

Antennae. Black with faint grey tomentum. Setae on scape white, on pedicel black; no hairs on F1. F1 long, with straight dorsal and slightly curved ventral margins; arista slender.

Thorax. Prothorax grey, with white hairs; postpronotum brown-grey with white hairs medially and black hairs laterally. Scutum tomentum brown; dorsocentral and acrostichal stripes slightly darker. Fine hairs and bristles of scutum black, except a few white short hairs along apical margins. Dorsocentral bristles long and relatively strong, anteriors 3–5; posteriors 4; postalars 2–3, with several finer hairs; supra-alars 2–3; presuturals 2–3; posthumerals 0–1. Scutellar tomentum brown; apical bristles black, 4–8 on each half, with several finer hairs; short vertical hairs on uppermost edge of rim black, about half as long as main bristles.

Pleural tomentum grey-brown. Katatergite setae black, 6–9, with a few fine short white hairs; katepisternal setae white, mid-length; anepisternal setae 4–8, black, with several short fine

black hairs on dorsal margin and a few white hairs in posterioventral corner; anepimeron with 4 fine white setae.

Legs. Cuticle black, with thin grey tomentum except bare at femur joints. No coxal peg. Coxae with white setae. Fine setae white on femur except apically and tibia ventrally; black elsewhere; bristles black. Ventral setae on femur longer than width of femur; dorsolateral bristles fine and difficult to distinguish from surrounding hairs, profemur with 6–11; mesofemur 6–7; metafemur 14–16. Protibia with ventral bristles fine, only 3 times longer than tibial width; dense patch of short yellow bristles on inside of protibia, none on metatibia. Claws chestnut over basal 70%, black apically.

Wings. Veins dark brown; membrane hyaline, but faintly brown when viewed obliquely. Halter knob cream, without spot, stem light brown.

Abdomen. Male. Tergite cuticle dark brown/ black. Brown tomentum over tergite bases; bands of grey tomentum cover apical 30–50% of each tergite, extending anteriorly along lateral margins (segment 1 is fully covered in grey) but not dorsally. Tergite 1 with 2–6 black bristles, 1 white bristle; lateral setae white, on tergites 1–3 as long as halter, on tergite 4 as long as scape + pedicel, on tergites 5–7 mostly black and as long as scape; dorsal setulae black, short. Sternite tomentum grey, hairs white.

Female. As in male, except grey tomentum extends anteriorly along midline to divide brown tomentum into two lateral spots; lateral setae on tergite 4 black; as long as scape + pedicel on tergites 1–3, shorter than scape on tergites 4–7.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown/black; covered in grey tomentum, except polished medially on hypandrium; epandrium with moderately long and erect black hairs, setal brush dark brown. Epandrium elongate, in lateral view the width 47% the length, widest in basal third, with dorsal margin gradually curving ventrally down to rounded apicoventral corner; in dorsal view moderately curved, tapering to apex; basal sclerite strong.

Phallus paramere sheath dorsally 50% the length of phallus; paramere sheath without ventral ornamentation; dorsal carina a triangular fin that does not protrude apically and rejoins paramere sheath well before apex. Ejaculatory apodeme in lateral view long and narrow, gently bent dorsally, sometimes recurved at apex, with narrow dorsal carina. Subepandrial sclerite with triangular central unsclerotized area in basal 47% narrowing to a slender gap in central portion; spines parallel-sided, blunt, densely arranged in basal half, sparse apically.

Female genitalia. Undissected: Tergite and sternite 8 polished dark brown; hypogynial valves orange at base, short; short erect hairs on tergite and sternite 8 white; cerci hairs white; lateral lobe bristles black; acanthophorite spines black.

Type Material. HOLOTYPE (photos examined) ♂ labelled: "[rectangular beige label] StanU Cal/ 12 May 1921";"[rectangular red label] HOLOTYPE/ Lasiopogon/ californicus/ Cole & Wilcox"; "[rectangular white label] California Academy/ of Sciences/ Type No. 6408"; "[rectangular white label] ALLOTYPE IS STORED/ IN THE/ GENERAL COLLECTION". CAS.

ALLOTYPE (examined) ♀ labelled: "[rectangular beige label] StanU Cal/ 20 May 1921";"[rectangular red label] ALLOTYPE/ Lasiopogon/ californicus/ Cole & Wilcox"; "[rectangular white label] Collection of the/ California Academy of Sciences/ San Francisco, Calif". CAS.

PARATYPES: (17 examined): **U.S.A.: CALIFORNIA: Alameda Co.**, Sunol [37.588 -121.8915], 15.v.1922 (1♂ FISH); **Monterey Co.**, Bradley [35.864 -120.809], 23.v.1920, E.P. VanDuzee (1♂ EMEC); **San Mateo Co.**, Stanford University [37.4129 -122.1925], 11.iv.1906, J.M. Aldrich (3♂ 2♀ EMEC, 1♀ FISH), 30.iv.1920, F.R. Cole (1♂ FISH), 5.v.1920 (1♂ FISH), 12.v.1921 (1♀ FISH); **Santa Clara Co.**, Palo Alto [37.442 -122.109], 29.iv.1906, J.M. Aldrich (1♂ 1? EMEC); **Sonoma Co.**, Cloverdale [38.8053 -123.0058], 9.v.1926 (2♂ EMEC, 1♂ 1♀ FISH).

Other Material Examined (91 specimens). **U.S.A.: CALIFORNIA: Alameda Co.**, Niles, 1 mi

NE [37.586 -121.962], 15.iii.1962, J. Doyen (1♂ EMEC); **Contra Costa Co.**, Danville [37.828 -122.031], 17.iv.1952, F.X. Williams (1♀ FISH), 21.iv.1952, F.X. Williams (2♀ FISH), 8.v.1952, F.X. Williams (2♂ CAS, 4♂ 7♀ FISH), 9.v.1952, F.X. Williams (1♂ 1♀ CAS); Danville, San Ramon Creek [37.828 -122.031], 29.iv.1949, F.X. Williams (1♂ 1♀ FISH), 16.vi.1951, F.X. Williams (1♀ FISH), 17.vi.1951, F.X. Williams (2♂ 1♀ [1 pr in cop] FISH); Walnut Creek [37.901 -122.059], 21.iv.1940, C.D. Michener (1♀ FISH), 22.iv.1940, E.S. Ross (1♂ 1♀ CAS, 4♂ 1♀ FISH); **Humboldt Co.**, Richardson Grove, 5 mi N [40.058 -123.785], 12.vi.1959, T.R. Haig (1♂ FISH); **Lake Co.**, Rice Fork Eel River near Bear Creek [39.327 -122.871], 23.iv.1987, Baumann, Stark, Nelson, Wells (1♂ BYU); **Mendocino Co.**, Albion [39.227 -123.764], vii.1965, G. Kessler (1♂ FISH); Hendy Woods State Park, Navarro River, 39.07694 -123.47194, 12.vi.2009, E.M. & J. Fisher (4♂ 2♀ RBCM); Smithe Redwood Grove, Eel River [39.898 -123.752], 18.vi.1979, L.G. Bezark (1♂ 1♀ [pr in cop] BEZA); **Monterey Co.**, no loc, 24.iv.1993, M. Petroelje (1♂ LACM); King City along E side Salinas River [36.206 -121.154], 17.iv.1990, D.W. Webb, M.E. Irwin (3♂ 2♀ INHS); **Napa Co.**, Monticello [38.578 -122.207], 16.iv.1952, E.I. Schlinger (1♂ FISH); **San Luis Obispo Co.**, Paso Robles, Salinas River E bank [35.642 -120.683], 17.iv.1990, D.W. Webb, M.E. Irwin (1♀ INHS); Simmler, 10 mi W [35.387 -120.151], 3.v.1962, R.L. Langston (2♂ 1♀ FISH), 5.v.1962, R.W. Thorp (1♀ FISH); Templeton, Salinas River [35.555 -120.694], 28.v.1991, M.E. Irwin (1♂ INHS); **San Mateo Co.**, Stanford University [37.413 -122.193], 11.iv.1906, J.M. Aldrich (2♂ USNM), 20.v.1910 (1♂ LACM), v.1921 (1♀ LACM); **Solano Co.**, Davis [38.518 -121.770], 4.iv.1951, R.C. Bechtel (1♀ FSCA), 23.iv.1951, A.T. McClay (1♂ CAS, 1♂ FISH), 8.v.1951, R.C. Bechtel (1♂ FISH), 27.vi.1951, E.L. Schlinger (2♀ FISH), J.G. Hall (1♀ FISH), 24.v.1956, J.C. Hall (1♂ FISH), 22.iv.1959, J.R. Powers (1♂ FISH); Winters, Putah Creek @ jct Winters Rd and Putah Creek Rd, 38.5204 -121.9675, 12.v.2012, T.A. McKnight, E.M. Fisher (1♂ [EtOH] TAM); **Stanislaus Co.**, Del Puerto Canyon, Frank Raines Park, 335 m [37.423 -121.382], 29.iv.1973, P.H. Arnaud Jr. (1♂ USNM); **Yolo Co.**, Putah Canyon [38.514 -122.072], 21.iv.1949, H.E. Cott (1♀ FSCA), 13.iv.1950, A.T. McClay (1♂ FSCA), 15.iv.1952, W.J. Wall (1♂ FISH); Putah Creek Canyon, Putah Creek below Monticello Dam, Hwy 128, 38.51389 -122.07194, 24.v.1995, R.A. Cannings, H. Nadel (8♂ 10♀ RBCM).

Type Locality. USA, California, Santa Clara Co., Palo Alto, Stanford University campus.

Taxonomic Notes. Specimens of this species have frequently been confused with *L. drabicola*, *L. zonatus*, and *L. odontotus* sp. nov. Figures and references to *L. californicus* in Cannings (2002) actually depict *L. odontotus* sp. nov.

Etymology. No explanation given in the original description, but evidently refers to California, as the species is endemic to the central portion of the state.

Distribution (Fig. III.3). Nearctic; USA, California; interior lowlands and foothills.

Phylogenetic Relationships. Member of the *bivittatus* section, *drabicolum* group.

Natural History. Habitat: stream sides. Found perching on small stones (~10 cm diameter) 1–5 m from water's flow (Fig. III.8g), labels note "on boulders in rocky creek", "on bare sand", "on sandbar", and "algal mat". Dates collected: 29 March to 27 August. *Myelaphus melas* (Asilidae) was also collected in the same microhabitat at Putah Creek in Winters.

***Lasiopogon canningsi* McKnight sp. nov.**

Diagnosis. A medium-sized dark species from coastal dunes of extreme northern California; mystax black, thoracic tomentum grey with strong dorsocentral stripes, thoracic setae mostly black, postpronotal lobes with dark hairs laterally; femur with thin grey tomentum and white setae except at joint; tergites with dark brown/black cuticle subshining basally, grey tomentum bands cover apical 20% and lateral margins narrowly, not extending dorsally in either sex; lateral bristles on tergite 1 mostly black (4–10). Epandrial halves polished dark brown/black, in dorsal view slightly swollen, coming to stubby apex, moderately concave medial margins, apex bent ventrally with semicircular emargination and a shallow ventral subapical tooth; Ovipositor black; acanthophorite spines black.

Description.

Head. Face with silver-grey tomentum, vertex sparse grey under setae patches, subshining otherwise. Beard and labial hairs white, sometimes tinged yellowish; myxtax and all other setae black. Occipital bristles relatively fine and long; those behind the dorsomedial angle of the eye the longest, moderately curved anterolaterally; lateral and ventral bristles shorter, straighter. Frontal setae fine, long, and erect, reach midpoint of F1; orbital setae also fine and long, slanting over eye margin.

Antennae. Black, slightly lighter at base of F1. Setae black; F1 sometimes with a seta. F1 long, roughly parallel, widest subapically.

Thorax. Prothorax grey, with white hairs; postpronotal lobes grey, the lateral angle yellowish red, hairs mostly dark, with a few whitish hairs on inside corner in both sexes. Scutum tomentum grey/brown. Dorsocentral stripes distinct: dark brown edged in lighter brown; acrostichal stripes faint greyish brown. Notal and acrostichal setae black, widely spaced, long (up to 60% as long as dorsocentrals). Dorsocentral setae fine, black; anteriors 4–5, can be hard to distinguish from surrounding hairs, 4–5 posteriors. Postalars 2–3, with about 4 long surrounding hairs; supra-alars 2–3 with a few short hairs; presuturals 3–4; posthumerals 1. Scutellar tomentum grey/greyish brown; rim inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, abundant (10+ on each side) and mixed with many other long hairs. Hairs on uppermost edge of rim short (half the length of other bristles), point straight up.

Pleural tomentum grey to yellowish grey. Katatergite bristles black, 8–9, with a few fine white hairs about half as long; katepisternal setae fairly long, wavy, white; anepisternal setae 14+, mostly black with a few white hairs ventrally and a patch of short black setae along dorsal edge; anepimeron with 5 fine white setae.

Legs. Base color dark brown/black, chestnut at femur-tibia joint and trochanters. Tomentum on coxae grey, sparse grey on femur, elsewhere shining black. No coxal peg. Coxae with long strawish white setae. Main bristles of legs black; hairs all white on femur and tibia, sometimes a few black on apex of femur; tarsal hairs black, a few white on basitarsus. Setae erect on outside

face of femur, reclinate on inside face. Ventral setae on femur longer than width of femur; dorsolateral bristles on femur are long, fine, and colored to match shorter hairs; 10+ dorsolateral bristles on profemur but indistinguishable from surrounding hairs, mesofemur with 3–8, metafemur 8–14. Protibia with longest bristles about 4 times longer than tibial width; golden patch of short dense bristles on inside of protibia. Claws chestnut over basal 60%, black apically.

Wings. Veins dark brown; membrane hyaline, very pale brown when viewed obliquely. Halter yellow/white; knob without dark spot.

Abdomen. Male. Tergite cuticle dark brown/black; very thin brown tomentum on tergite bases, extensively lacking so the dark cuticle shines through, bands of grey tomentum cover apical 20% of each tergite (segment 1 is half covered), extending ventrolaterally so that the tergite sides are between half and completely covered in grey, but straight across dorsum. About 4–10 black bristles and 2–3 white/yellow bristles on side of tergite 1, abundant long white hairs. Lateral setae on tergites long, erect, white; on tergites 2–4 setae longer than F1, on tergites 5–7 as long as scape + pedicel. Dorsal setulae brown, fine. Sternite tomentum grey, hairs white.

Female. Grey tomentum bands on tergites somewhat wider, covering apical 30%. More black bristles on side of tergite 1, between 6–10.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle shining dark chestnut/black, entirely devoid of tomentum; with dark brown/black hairs, setal brush black. Epandrium moderately elongate, in lateral view the width 50% the length, widest medially, dorsal margin mostly straight but slumping ventrally at apex; apex directed ventrally, with shallow semicircular emargination between dorsoapical corner and broadly rounded ventroapical tooth. In dorsal view, epandrial lobes relatively fat and moderately concave, with stubby apex, close set; basal sclerite prominent.

Phallus paramere sheath dorsally 38% the length of phallus; paramere sheath with sharp ventral subapical tooth; dorsal carina a straight flat fin with shallow sharp point apically parallel to aedeagal tube, leaving a narrow gap between the apices. Ejaculatory apodeme in lateral view long, slender, straight to strongly bent in basal quarter, dorsal carina moderately broad. Subepandrial sclerite U-shaped, central unsclerotized area shaped like a tall bottle over basal

89%; spines parallel-sided, blunt, densely and evenly distributed, apical spines relatively recumbent.

Female genitalia. Undissected: Hairs white, abundant, erect. Tergite and sternite 8 black; lateral lobes chestnut, with long setae mixed brown and white; hypogynial valves long, with short fine hairs medially, otherwise bare; cerci black with yellow setae; acanthophorite spines black.

Type Material. HOLOTYPE (here designated) ♂ labelled: "[rectangular white label] USA; CA; Humboldt Co./ Eureka, S. Jetty Road/ 40 41.9'N 12416.5'W/ 10 MAY 1995/ R.A. Cannings & H. Nadel/ RC95-13"; "Sand dunes with Abronia/ latifolia, Lathyrus littoralis,/ Tanacetum sp./ 12:30 -13:45 PDT"; "[rectangular white label] RBCM". My holotype label "HOLOTYPE/ Lasiopogon ♂/ canningsi McKnight/ des. T.A. McKnight 2017 [red, black-bordered label]" has been attached to this specimen. USNM

PARATYPES (63 specimens designated): **USA: California: Del Norte Co.**, no loc, 10.v.1910, Oldenberg (1♀ USNM); Crescent City [41.747 -124.199], 13.vii.1937, E.C. Van Dyke (1♀ EMEC); Tolowa Dunes State Park N, 41.86972 -124.21222, 5–6.vi.2009, E.M. Fisher (3♂ 2♀ RBCM); **Humboldt Co.**, no loc, 1911, Oldenberg (1♂ USNM), 3.v.1953, W.D. Hawes (1♀ EMEC), 4.v.1953, W.D. Hawes (1♀ EMEC); Arcata, 20 mi N [41.141 -124.145], 27.v.1964, J. Schuh (1♂ WSUC); Clam Beach County Park, 5 mi SE of Trinidad, 40.99350 -124.11619, 15.v.2012, T.A. McKnight (3♂ 1♀ TAM); Clam Beach County Park, N entrance 0.8 km S Hwy 101 exit, 41.00667 -124.11333, 10.v.1995, R.A. Cannings (1♂ 1♀ RBCM); Crannell, 2 mi N [41.029 -124.111], 28.iv.1959, T.R. Haig (1♂ 2♀ FISH); Eureka, S Jetty Road, 40.7005 -124.2731, 10.v.1995, R.A. Cannings, H. Nadel (3♂ 11♀ RBCM); Mad River Beach [40.929 -124.134], 26.vi.1969, W.G. Goodman (1♀ FISH); Samoa dunes [40.764 -124.226], 28.v.1969, C. Slobodchikoff (1♂ EMEC), 25.vi.1969, D. Levin (1♀ LACM); Trinidad State Beach, 41.05807 -124.14933, 15.v.2012, T.A. McKnight (6♂ 3♀ [2 pr in cop] TAM); **Mendocino Co.**, Inglenook Fen, 5 mi N Fort Bragg [39.513 -123.776], 6–7.v.1976, J. Powell (1♀ EMEC); MacKerricher Beach, 3 mi N Fort Bragg [39.490 -123.794], 7.v.1976, J.A. Powell (3♂ 1♀ EMEC); MacKerricher Beach, 5 mi N Fort Bragg [39.512 -123.781], 1–2.v.1977, J. Powell (11♂ 1♀ EMEC); MacKerricher State Park, 39.48737 -123.79421, 10.vi.2009, E.M. Fisher (1♂

[EtOH] RBCM); MacKerricher State Park beach [39.495 -123.794], 16–18.v.1984, L. Varela (1♂ BEZA); **Oregon: Curry Co.,** Crissey Field State Park, beach dunes, 42.0022 -124.2133, 13.v.2015, T.A. McKnight (1♂ 1♀ TAM).

Type Locality. USA: California: Humboldt Co., Eureka, S. Jetty Road, N40°41.9' W124°16.5'.

Taxonomic Notes. Specimens from this new species have usually been identified as *L. bivittatus*, or sometimes misidentified as *L. dimicki*.

Etymology. Named for Dr. Robert A. Cannings, whose work in revising *Lasiopogon* set the stage and assisted the first author's work by sharing knowledge, notes, collections, and gentle encouragement.

Distribution (Fig. III.2). Nearctic; coastal dunes from the California/Oregon border south to Mendocino County.

Phylogenetic Relationships. Member of the *bivittatus* section, *bivittatus* species group; sister to *L. tumulicola* sp. nov.

Natural History. Habitat: Coastal beaches and dunes. Perches on bare sand next to sparse vegetation, such as *Abronia latifolia*, *Lathyrus littoralis*, and *Tanacetum* sp. (Fig. III.6d). Recorded flight dates: 10 May to 10 June.

***Lasiopogon condylophorus* McKnight sp. nov.**

Diagnosis. A medium-sized dark species from subalpine meadows of the Sierra Nevada; with mystax black, thoracic setae dark brown/black (including prothorax), scutal bristles and surrounding hairs abundant and long; ventral hairs on femur and on metacoxae dark brown; thoracic tomentum grey to brown with distinct dorsocentral stripes; tergites basally subshining brown, apical 40–60% covered in straight bands of grey tomentum. Epandrial halves moderately curved over medial margins; phallus dorsal carina comes to a spherically swollen apex parallel to gonopore; gonostylus elongate and extends medially beyond medial flange. Ovipositor dark brown, acanthophorite spines black.

Description.

Head. Face with silvery grey tomentum, vertex brownish-grey. Ventral hairs (on beard, labium, palps) white; mystax and all dorsal setae black, dense. Occipital bristles relatively fine, strongly bent anteriorly; frontal setae reach end of pedicel, orbital and ocellar setae reach basal quarter of F1.

Antennae. Black, with thin grey tomentum. Setae black, abundant, no hairs on F1. F1 relatively short, dorsal and lateral margins straight. Arista of average length.

Thorax. Prothorax grey, with brown and white hairs; postpronotal lobes grey, the lateral angle dark brown, hairs black. Scutum tomentum grey to greyish brown; dorsocentral stripes dark brown; acrostichal stripes absent or faintly brown. All bristles and hairs of scutum black; fine notal hairs long, dorsocentral bristles accompanied by many long hairs; anterior dorsocentrals 5–7, posteriors 4–5; postalars 3–4, with several shorter hairs; supra-alars 2–3, with several shorter hairs; presuturals 2–3; posthumerals 1. Scutellar tomentum thin brown; rim slightly inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, long, 8–12 on each side, with several other long hairs; hairs on uppermost edge of rim half as long as bristles, point straight up.

Pleural tomentum pale brown. Katatergite bristles black, 6–9, with a few fine short brown and white hairs; katepisternal setae of moderate length, white; anepisternal setae all black, 6–8

strong setae with several shorter hairs along dorsal margin and in posterioventral corner; anepimeron with 1 fine white seta.

Legs. Base color dark brown/black except reddish at femur-tibia joint; covered in thin grey tomentum except at femur joints. No coxal peg. Coxae with white setae except brown hairs ventrally on metacoxa. Bristles and hairs of legs all black. All femorae copiously covered in fine hairs; longest ventral hairs equal to femur width; apicolateral bristles do not stand out, profemur with 8+ bristles; mesofemur 5–7; metafemur 10–13. Protibia with ventral bristles 3 times longer than tibial width, dense patch of short yellow-brown hairs along inside apical half of protibia. Claws chestnut over basal 60%, black apically.

Wings. Veins brown; membrane hyaline but pale brown when viewed obliquely. Halter knob cream, without spot, stem brown.

Abdomen. Male and female. Tergite cuticle dark brown/black; thin brown tomentum on tergite bases, grey tomentum in straight bands that cover apical 40–60% of each tergite (tergite 1 is completely covered in grey except mid-dorsally) but do not extend anteriorly along the midline. Tergite 1 with 4–7 lateral black bristles, 0–2 white. Lateral hairs on tergites 1–3 or 4 white, as long as halter, on tergites 4 or 5–7 brown, as long as scape + pedicel; dorsal setuale short, brown. Sternite tomentum grey, hairs white on sternites 1–5, brown on sternites 6–7.

Male genitalia. Epandrium cuticle dark brown, reddish brown on hypandrium/gonocoxite complex, covered in thin grey/brown tomentum; hairs long and black, setal brush dark brown. Epandrium elongate, in lateral view the width 47% the length, widest in basal third, slightly sinuate along ventral margin, gently curved to straight along dorsal margin, apex rounded with ventral subapical tooth. In dorsal view, medial margins of epandrium slightly to moderately curved, curvature starts about 45% from base, basal sclerite prominent.

Phallus paramere sheath dorsally 40% the length of phallus; paramere sheath with long buttress-like ventral flange along basal half; dorsal carina extending parallel to gonopore, with spherical apex. Ejaculatory apodeme in lateral view moderately bent dorsally in basal quarter, dorsal carina narrow basally, moderately broad medially. Subepandrial sclerite with triangular

central unsclerotized area in basal 54%; spines parallel-sided, blunt, densely and evenly distributed.

Female genitalia. Undissected: cuticle dark brown except reddish at base of hypogyinal valves. All setae dark brown/black except short white hairs on cerci; wispy but long hairs on tergite and sternite 8; lateral lobes with long black bristles; acanthophorite spines black.

Type Material. SYNTYPES (here designated) ♂ and ♀ on same pin labelled: "[rectangular white label] CAL. TulareCo./ Seq. Natl. Pk, 2mi/ SSW Little 5 Lakes/ 14-VII-1964"; "[rectangular white label] Arthur A. Lee/ Collector"; "[rectangular white label] Pr. in copulo“; "[rectangular white and pink label] CAS"; “[rectuangular white label] FISH”. My type label “[red and black bordered label] SYNTYPE/ Lasiopogon condylophorus/ des. T.A. McKnight 2017” has been added. USNM.

PARATYPES (2 designated). U.S.A.: CALIFORNIA: Tulare Co., Sequoia National Park, 2 mi SSW Little 5 Lakes [36.483 -118.578], 14.vii.1964, A.A. Lee (1♂ FISH); Sequoia National Park, 9 Lakes Basin [36.563 -118.535], 16.vii.1964, A.A. Lee (1♂ FISH).

Type Locality. U.S.A. California, Tulare Co., Sequoia National Park, 2 mi SSW Little 5 Lakes.

Etymology. From the Greek κόνδυλος, kondylos, meaning condyle, and –phorus, the combining form of ‘bearer of’; noun in apposition; referring to the uniquely swollen rounded knob at the apex of the phallus dorsal carina.

Distribution (Fig. III.3). Nearctic; high southern Sierra Nevada in California.

Phylogenetic Relationships. No samples were found with viable DNA, however, based on genitalia morphology this species is surely a member of the bivittatus section and is likely related to *L. apoecus* sp. nov. and *L. gabrieli*, especially the former.

Natural History. Habitat: unknown, likely rocky ground around high montane lakes and streams. Dates collected: 14 to 16 July.

***Lasiopogon dimicki* Cole & Wilcox**

Lasiopogon dimicki Cole & Wilcox, 1938. *Entomologica Americana* 43:44–46.

Diagnosis.

A medium-sized dark brown species from the beach dunes of Oregon; bristles and hairs of head, antenna, and thorax mostly black, a few ventrolateral hairs of mystax golden-tipped; lateral setae on tergites golden, tergite 1 with 7-9 black bristles; scutum tomentum dark brown, with dark brown dorsocentral stripes; tergites subshining brown basally, apical 40% covered in grey tomentum as straight band in male, but extending anteriorly in female to divide brown into lateral spots. Epandriual halves moderately concave medially, with black hairs; phallus dorsal carina flattened into a disc opposite gonopore. Ovipositor dark brown/black; acanthophorite spines black.

Description.

Head. Face brown-grey, vertex brown. Ventral hairs (on beard, labium, palps) white; mystax black except some golden hairs ventrolaterally, all other setae black. Occipital bristles fine, long and strongly curved anterolaterally behind vertex, lateral bristles short and straight. Frontal setae abundant, long (longest reach midpoint of F1); orbital setae fine, long, gently curving over eye margin; ocellar setae fine, indistinct amidst other hairs.

Antennae. Black, with thin grey tomentum. Setae black, abundant on scape and pedicel, one on F1. F1 long, narrow, straight-edged. Arista long.

Thorax. Prothorax brown, with yellowish-white hairs; postpronotal lobes brown, the lateral angle chestnut, hairs black. Scutum tomentum dark brown; dorsocentral stripes dark brown;

acrostichal stripes indistinct. All setae of scutum black, major bristles with accompanying shorter hairs; anterior dorsocentral bristles 6–8, posterior dorsocentrals 3–5; postalars 4; supra-alars 3; presuturals 3–4; posthumerals 2. Scutellar tomentum brown; rim inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, abundant (9–12 on each half), mixed with other hairs; hairs on uppermost edge of rim half as long as bristles, point straight up, black.

Pleural tomentum grey-brown. Katatergite bristles black, long, 7–10, with a few fine short yellowish-white hairs; katepisternal setae fairly long, yellowish-white; anepisternal bristles 4–6, black, with many short black hairs along dorsal margin and a few yellowish-white hairs in posterioventral corner; anepimeron with 3 fine white setae.

Legs. Base color black, covered in thin grey tomentum except at joints; No coxal peg. Coxae with yellowish-white setae. Bristles of legs black, finer hairs on femur yellow-white basally with some black hairs apicodorsally; fine hairs on tibia white; first tarsomere on pro- and mesolegs with white hairs, otherwise tarsi with black hairs. Ventral hairs on femur dense, longer than femur width; dorsolateral bristles on profemur relatively fine and indistinct basally, 4–7; on other femorae strong, short, mesofemur with 6–13, metafemur with 15–17. Protibia with ventral bristles 3–4 times longer than tibial width; dense patch of short yellow bristles on inside of protibia. Claws dark chestnut over basal 60%, black over apical half.

Wings. Veins brown; membrane hyaline but pale brown when viewed obliquely. Halter knob cream-colored, without spot, stem brown.

Abdomen. Male. Tergite cuticle black; thin subshining brown tomentum on tergite bases; bands of grey tomentum cover apical 40% of each tergite, not extending anteriorly on dorsum. Tergite 1 with 7–9 lateral black bristles, 3–4 gold bristles; lateral setae on tergites yellow-white, as long as halter stem on tergites 1–3, tapering to length of scape+pedicel on posterior segments; dorsal setulae fine, brown. Sternite tomentum grey-brown, hairs yellow-white, long.

Female. Similar to male, but basal tomentum thicker, and grey tomentum extends anteriorly along midline to separate brown tomentum into lateral spots; lateral setae on tergites 4–7 dark brown/black and much shorter (same length as scape); dorsal setulae black, shorter. Sternite hairs short.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle shining black with thin grey tomentum; setal brush and other hairs dark brown. Epandrium elongate, in lateral view the width 48% the length, widest in basal third, with straight dorsal and ventral margins; apex rounded with a shallow ventral subapical tooth. In dorsal view, medial margins of epandrium moderately curved, curvature starts about 32% from base, outer margins suddenly tapered at apex; basal sclerite short.

Phallus paramere sheath dorsally 40% the length of phallus; paramere sheath without ventral ornamentation; dorsal carina divergent from aedeagal tube and protruding just farther in length, apex flattened into a disc. Ejaculatory apodeme in lateral view moderately bent dorsally in basal quarter, sometimes slightly recurved at apex, dorsal carina of moderate width. Subepandrial sclerite with triangular central unsclerotized area in basal 38% narrowing to a parallel-sided gap in central portion; spines parallel-sided, blunt, densely and evenly distributed.

Female genitalia. Undissected: Tergite and sternite 8 dark brown/black, with pale brown erect fine hairs; lateral lobe with long brown bristles; cerci brown with pale setae; acanthophorite spines black.

Type Material. HOLOTYPE (photos examined) ♂ labelled: "[rectangular beige label] Newport/ Ore. V-24 '31"; "[rectangular white label] J. Wilcox/ Coll."; "[rectangular beige label] Lasiopogon/ dimicki/ n.sp./ Male- Type"; "[rectangular salmon label] HOLOTYPE/ Lasiopogon/ dimicki/ Cole & Wilcox"; "[rectangular white label] California Academy/ of Sciences, Type No. 6441"; "[rectangular white label] ALLOTYPE IS STORED/ IN THE/ GENERAL COLLECTION". CAS.

ALLOTYPE (examined) ♀ labelled: "[rectangular beige label] Newport/ Ore. V-3 '31"; "[rectangular white label] J. Wilcox/ Coll."; "[rectangular salmon label] ALLOTYPE/ Lasiopogon/ dimicki/ Cole & Wilcox"; "[rectangular beige label] Lasiopogon/ dimicki/ n.sp./ Female-type" "[rectangular white label] Collection of the California Academy of Sciences San Francisco, Calif". CAS.

PARATYPES (245 inspected): **U.S.A.: OREGON:** no loc, J.E. Davis (1♂ CAS); **Lincoln Co.,** Devil's Lake [44.967 -124.015], 17.v.1931, S.C. Jones (1♀ CAS); Newport [44.659 -124.058], 8.vi.1925, E.P. Van Duzee (1♂ 1♀ EMEC), 10.v.1930, R.E. Dimick (4♂ 1♀ CAS), 11.v.1930, J. Wilcox (1♀ CAS, 1♀ WSUC), 17.v.1930, R.E. Dimick (4♂ 4♀ CAS), 3.v.1931, I. Wilcox (4♂ 4♀ CAS, 1♂ FISH, 1♂ MCZ), J. Wilcox (18♂ 12♀ CAS, 1♂ CNC, 2♂ FISH, 1♂ 1♀ USNM), 24.v.1931, J. Wilcox (3♂ 2♀ CAS), 22.v.1932, J. Wilcox (16♂ 20♀ CAS, 1♂ EMEC, 3♂ FISH, 3♂ 3♀ MCZ, 1♂ 1♀ OSUC, 4♂ 2♀ USNM, 1♂ WSUC), 5.vi.1932, J. Wilcox (2♂ 5♀ CAS, 1♀ USNM), R.E. Dimick (4♂ 5♀ [1 pr in cop] CAS, 1♀ EMEC), 12.v.1935, J. Wilcox (2♂ BEZA, 24♂ 24♀ 1? CAS, 1♀ CNC, 3♂ 2♀ EMEC, 1♂ 4♀ FISH, 1♂ 1♀ RBCM, 1♂ 1♀ UCRC, 2♂ 2♀ USNM), S.E. Crumb (19♂ 5♀ CAS, 1♀ EMEC, 1♂ LACM, 1♂ 1♀ USNM); Waldport [44.433 -124.084], J.E. Davis (3♀ CAS), 7.vi.1925, E.P. Van Duzee (1♂ 2♀ EMEC).

Other Material Examined (29 specimens). **U.S.A.: OREGON: Lincoln Co.,** Agate Beach [44.684 -124.068], 19.vi.1971, R.L. Westcott (1♂ 1♀ FISH, 1♂ LACM); Agate Beach State Park dunes [44.65795 -124.05732], 21.vi.2013, T.A. McKnight (1♂ TAM); Newport [44.659 -124.058], 8.vi.1925, E.C. Van Dyke (1♂ 2? EMEC), 11.v.1930, J. Wilcox (1♀ EMEC), 17.v.1930, R.E. Dimick (1♀ EMEC), 3.v.1931, I. Wilcox (1♂ 1♀ EMEC), J. Wilcox (3♂ 1♀ EMEC, 1♂ RBCM), 22.v.1932, J. Wilcox (1♀ RBCM); Newport, S side Yaquinna River mouth, dunes E of South Jetty Rd [44.601 -124.065], 8.v.1995, R.A. Cannings, H. Nadel (4♂ 4♀ RBCM); Newport, South Beach State Park trailhead, 44.60146 -124.06497, 17.v.2012, T.A. McKnight (1♂ TAM); Waldport [44.433 -124.084], 7.vi.1925, E.P. VanDuzee (2♂ CAS); Waldport, 1 mi N], 16.v.1964, T.F. Marsh (1♂ INHS).

Type Locality. USA, Oregon, Lincoln Co., Newport.

Taxonomic Notes. Some records are actually *L. canningsi* sp. nov.

Etymology. Named for R.E. Dimick, who collected the first specimens of this species seen by Cole and Wilcox (Cole & Wilcox 1938).

Distribution (Fig. III.3). Nearctic; USA, Oregon coast.

Phylogenetic Relationships. Member of the *willametti* group within the *bivittatus* section, likely as sister to *L. willametti*.

Natural History. Habitat: beach dunes. Perches on bare sand adjacent to low, scraggly vegetation, such as *Elymus*, *Lupinus*, *Fragaria* (Fig. III.6c). Dates collected: 3 May to 21 June.

***Lasiopogon drabicolum* Cole**

Lasiopogon drabicolum Cole, 1916. *Psyche* 23:65.
Lasiopogon drabicola Cole; Melander 1923, *Psyche* 30:137. Unnecessary emendation.

Diagnosis. A small to medium dusty grey species from southern and central California; mystax variable but usually partly to completely white; setae on scape and pedicel at least partly white; scutal bristles black, finer hairs white at least medially; scutum tomentum grey to brown with dorsocentral and acrostichal stripes indistinct; tergites with faint patches of brown tomentum basally, but mostly greyish white; lateral setae on tergites white. Male terminalia cuticle reddish to dark brown with sparse hairs; epandrium in dorsal view appears circular, evenly rounded from base to apex; gonostylus in lateral view flattened, longer than tall; phallus with dorsal carina flat, extended apically equidistant to gonopore like a rounded porpise fin. Ovipositor dark brown/black; acanthophorite spines black.

Description.

Head. Face grey, vertex brown-grey; occiput grey. Ventral hairs (on beard, labium, palps) white; occipital setae black; orbital and occelar setae usually black, rarely white; mystax and frontal setae usually predominately white, but variable from completely white to mostly black with some ventral white hairs. Occipital bristles relatively straight, longest and most curved posterior corners of vertex; frontal and orbital setae relatively short, reaching base of F1; occellar setae also relatively short.

Antennae. Dark brown, with thin grey tomentum. Setae mostly white, at most 2 brown bristles dorsally and 1 ventrally on pedicel; no hairs on F1. F1 moderately long, dorsal and ventral margins straight; arista moderately long.

Thorax. Prothorax grey, with white hairs; postpronotal lobes grey, the lateral angle light chestnut, hairs white. Scutum tomentum brown to grey; dorsocentral and acrostichal stripes slightly darker but indistinct. Fine notal setae usually white, sometimes black except anteromedially; bristles always black. Dorsocentral and lateral bristles well developed: anterior dorsocentrals 3–5; posteriors 3–5; postalars 2, with 2–3 fine hairs; supra-alars 2–3; presuturals 2–3; posthumerals 0–1. Scutellar tomentum grey-brown; apical bristles black, 4–9 on each half; shorter hairs pointing straight up white, about 60% the length of apical bristles.

Pleural tomentum greyish brown. Katatergite setae black, 6–8, with a few shorter white hairs, sometimes 1–2 white long bristles; katepisternal setae wispy, white; anepisternal setae 3–4, black, with short white hairs along dorsal margin and a few in ventroposterior corner; anepimeron with 2–3 short fine white hairs.

Legs. Cuticle dark brown/ black, covered in grey tomentum except at femur joints. No coxal peg. Coxae with white setae. Fine hairs of femur and tibia white, on tarsi black; Bristles of femur and tibia white basoventrally, black dorsoapically; black (rarely white) on tarsi. Ventral hairs on femur as long or shorter than femur width; dorsolateral bristles on profemur 5–11, with many finer hairs; on mesofemur 3–5; on metafemur 7–12. Protibia with ventral bristles 2–3 times longer than tibial width; faint patch of short yellow setae on apical half of protibial and brown setae on metatibia. Claws chestnut over basal 60%, apically black.

Wings. Veins brown; membrane hyaline but brown when viewed obliquely. Halter knob cream, without spot, stem light brown.

Abdomen. Male and female. Tergite cuticle dark brown/black. Apical bands of grey tomentum frequently weakly extend anteriorly along midline to divide basal brown tomentum into two lateral spots, but overall pattern weakly apparent and occasionally replaced by straight bands or

totally grey (tergite 1 entirely covered in grey tomentum); lateral margin of tergites broadly grey. Tergite 1 with 0–4 brown and 2–7 white lateral bristles; lateral setae on tergites white, as long as halter on tergites 1–3, as long as scape + pedicel on tergites 4–7 in male, as long as scape only in female; dorsal setulae very fine, white or pale brown in male; black in female. Sternite tomentum grey, hairs white.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle red/dark brown, thin grey tomentum on epandrium, hypandrium mostly bare; hairs mostly black (a few white), moderately long and erect but sparse; setal brush dark brown. Epandrium elongate, in lateral view the width about 50% the length, widest in basal third, dorsal and ventral margins gently sinuate; apex rounded into strong ventral subapical tooth. In dorsal view, epandrium appears circular, evenly rounded from base to apex; medial margins moderately curved, curvature starts about 39% from base; basal sclerite prominent.
Phallus paramere sheath dorsally 55% the length of phallus; paramere sheath without ventral ornamentation; dorsal carina flat, extended apically equal to gonopore like a rounded porpise fin, leaving a broad gap between apices. Ejaculatory apodeme in lateral view strongly bent dorsally in basal quarter, with broad dorsal carina. Subepandrial sclerite with triangular central unsclerotized area in basal 71%; spines parallel-sided, blunt, sparsely but evenly distributed.

Female genitalia. Undissected: tergite 8 cuticle dark brown/black; sternite 8 dark brown/black basally, pale red-brown apically and at bases of hypogynial valves. Setae on segment 8 fine, white; cerci with white hairs; a few short white setae on lateral lobes; acanthophorite spines black.

Variation. Mystax, frontal, orbital, and antennal hair color vary greatly from all white to mostly black in this species, but this variation does not follow a geographic cline and frequently occurs within a single population.

Type Material. HOLOTYPE (examined) ♂ labelled: "[rectangular beige label] Redlands,/ 1913 Cal."; "[rectangular beige label] FRCole/ Coll"; “[rectangular beige label] Lasiopogon/

drabicola/ Cole"; "[rectangular red label] Type No./ 20183/ U.S.N.M."; "[rectangular white label] USNMENT/ 00972437". USNM.

ALLOTYPE. (examined) ♀ labelled: "[rectangular beige label] LaQuinta, Cal./ 3-14"; "[rectangular beige label] FRCole/ Coll"; "[rectangular salmon label] ALLOTYPE/ No./ 20183/ U.S.N.M."; "[rectangular white label] USNMENT/ 01100210". USNM.

Other Material Examined (250 specimens). no loc, D. Martin (1♂ FSCA); **U.S.A.: CALIFORNIA:** Santa Ana Canyon, 11.iii.1934, M.W. Stone (1♀ CAS), Santa Ana Canyon, 21.iii.1934, M.W. Stone (1♂ 1♀ CAS); **Los Angeles Co.**, Artesia [33.865 -118.103], 10.ii.1935, M.W. Stone (1♂ BEZA, 5♂ 4♀ CAS, 1♂ ESUW), 27.iii.1934, M.W. Stone (1♀ BEZA, 13♂ 3♀ CAS, 1♀ ESUW, 1♂ FISH, 2♂ 2♀ USNM); Burbank [34.171 -118.309], 23.iii.1933, C.H. Hicks (1♂ 1♀ WSUC); El Monte [34.066 -118.004], 17.ii.1935, M.W. Stone (16♂ 5♀ CAS, 2♀ UCRC); 18.iii.1933, M.W. Stone (1♂ 2♀ CAS), Sloop & M.W. Stone (1♂ CAS), 2.iii.1934, M.W. Stone (4♂ CAS, 1♂ FISH, 1♂ OSUC, 1♂ UCRC), 31.iii.1933, Sloop & M.W. Stone (5♂ CAS, 1♂ 1♀ MCZ); El Monte, San Gabriel River wash [34.066 -118.004], 2.iii.1934, M.W. Stone (8♂ 8♀ CAS, 1♂ 1♀ CNC, 1♀ OSUC, 2♂ 2♀ USNM); **Napa Co.**, Monticello [38.578 -122.207], 16.iv.1952, E.I. Schlinger (1♂ CAS), R.M. Bohart (1♀ CAS); **Orange Co.**, no loc, 3.iii.1957, R. Swigart (1♂ CAS); Anaheim [33.835 -117.863], 5.iii.1937, J. Wilcox (3♂ 5♀ CAS), M.W. Stone (1♂ CAS); **Riverside Co.**, Mira Loma [33.973 -117.511], 26.iii.1957, J. Wilcox (1♀ CAS); Riverside [33.989 -117.393], 17.iii.1935, A.L. Melander (1♂ 4♀ USNM), 23.iii.1941, Timberlake (2♂ 5♀ UCRC), 6.iv.1941, Timberlake (4♂ 2♀ UCRC); Riverside, Santa Ana River [33.969 -117.426], 11.iv.1964, M.E. Irwin (1♂ UCRC), 12.iii.1944 (1♀ FSCA), C.H. Martin (2♂ 5♀ FSCA), D. Martin (1♀ FSCA), 24.iii.1942 (2♂ 1♀ FSCA), C.H. Martin (3♂ 6♀ FSCA), D. Martin (4♂ FSCA), 24.iii.1969, F.G. Andrews (2♂ 1♀ UCRC); Santa Ana River at Mt. Rubidoux [33.98948 -117.39281], 4.iii.2013, T.A. McKnight (5♂ 4♀ [2 pr in cop] TAM); **San Bernardino Co.**, South Fork [34.169 -116.826], 12.vii.1942, C.H. Martin (2♂ 2♀ FSCA); **San Luis Obispo Co.**, Paso Robles, Salinas River E side [35.642 -120.683], 17.iv.1990, D.W. Webb, M.E. Irwin (1♂ 1♀ INHS); Simmler, 10 mi W [35.387 -120.151], 5.v.1962, R.W. Thorp (2♀ FISH); **Ventura Co.**, Casitas Springs [34.372 -119.309], 20.iv.1979, R.P. Meyer (2♀ BEZA); Moorpark [34.284 -118.856], 22.iv.1941, M.W. Stone (1♂ 3♀ CAS, 1♂ FISH); Ojai

valley [34.439 -119.237], 6.iv.1941, J. Wilcox (1♀ CAS); Piru Creek, NE base Alamo Mtn [34.703 -118.937], 3.v.1959, J. Powell (1♀ FISH); Santa Ana Valley, 6.iv.1941, J. Wilcox (13♂ 9♀ CAS, 1♀ FISH); Sespe River [34.492 -118.945], 6.v.1942, M.W. Stone (3♂ 3♀ CAS); **Yolo Co.**, Davis [38.5177 -121.7696], 17.iv.1952, R.C. Bechtel (1♂ 1♀ CAS), 2.iv.1952, A.T. McClay (2♂ CAS), E.I. Schlinger (2♂ 1♀ CAS), 22.iv.1959, J.R. Powers (1♀ FISH), 27.iv.1951, R.C. Bechtel (1♂ 1♀ FISH), 6.iv.1951, R.C. Bechtel (2♂ CAS, 1♂ FISH, 1♂ 1♀ [pr in cop] FSCA), 7.iv.1956, W.H. Lange (1♂ 1♀ [pr in cop] CAS, 1♂ 1♀ ESUW, 2♂ 3♀ FSCA), 7.v.1961, V.L. Vesterby (1♂ BEZA), 8.iii.1960, F.D. Parker (1♀ CAS); Putah Canyon [38.514 -122.072], 15.iv.1952, S. Miyagawa (1♂ FSCA), 2.iv.1954, R.C. Bechtel (1♂ CAS, 1♂ 1♀ [pr in cop] FSCA), 20.iii.1951, A.T. McClay (1♂ CAS), R.M. Bohart (1♀ CAS, 1♂ FSCA), 24.iii.1951, R.C. Bechtel (1♂ FSCA).

Type Locality. U.S.A., California, San Bernardino Co., Redlands [34.085 -117.166].

Taxonomic Notes. Cole's original description used the spelling "drabicolum", evidently in a case of improper gender matching ('-cola' names are already masculine by default). Subsequent authors have almost universally used the corrected Latinization "drabicola", but since incorrect gender matching is not spelling in the sense of ICZN code, it seems this cannot be corrected (even via the prevailing usage clauses) and must revert to the original spelling.
Several cryptic species in California have historically been identified as this species, including *L. apoecus* sp. nov., *L. esau* sp. nov., and *L. nelsoni* sp. nov.

Etymology. No explanation given in the original description, but since the description mentions that the flies "were collected on wild flowers", it evidently was derived from the Latin "draba" = mustard plant, "cola" = dweller of.

Distribution. (Fig. III.3). Nearctic, U.S.A., southern and central California.

Phylogenetic Relationships. Member of the bivittatus section, *drabicolum* group. Likely closely related to *L. esau* sp. nov. and *L. nelsoni* sp. nov.

Natural History. Habitat: mountain and lowland river banks. Despite Cole's remarks about collecting this species on flowers, we have only encountered it perching on patches of bare sand interspersed with vegetation or rocks along the riverbank <1-20 m from the water (Fig. III.7h). Specimens recorded between 10 February to 12 July, most in March and April. Two males and two females with prey: 3 small Scarabaeidae (c.f. Aphodiinae) and Muscidae c.f. *Phaonia*. Occasionally found flying simultaneously with *L. nelsoni* sp. nov., but perching habit may help distinguish these taxa.

***Lasiopogon esau* McKnight sp. nov.**

Diagnosis. A small to medium dusty grey species from northwestern California; mystax variable but usually mostly black with some white hairs ventrally; setae on scape white, on pedicel black; scutal bristles black, finer hairs black except white along anterior margin; scutum tomentum grey to brown with dorsocentral and acrostichal stripes faint; tergites with brown tomentum basally, grey over apical 40–60%, tomentum along dorsal midline thin and subshining, leaving pattern indistinct; lateral setae on tergites white. Male terminalia cuticle dark brown with hairs long, erect, and dense; epandrium in dorsal view appears tapered, wider at base than apex; gonostylus in lateral view flattened, longer than tall; phallus with dorsal carina flattened, extending apically almost equidistant to gonopore like a squared-off porpise fin. Ovipositor dark brown/black; acanthophorite spines black.

Description.

Head. Face silver-grey, vertex brown-grey. Ventral hairs (beard, labium, palps) white; dorsal setae (frontal, orbital, occellar, occipital) black; mystax usually mostly black, frequently with a few hairs white ventrolaterally, occasionally ventral quarter white, rarely white predominates mystax. Occipital bristles fine, posterior to frons longest and strongly curved anteriorly, lateral bristles short, straight. Frontal setae fine, long (reach midpoint of F1); orbital setae also fine and long, cuving over eye margin; occelar setae indistinct among hairs.

Antennae. Black, with thin grey tomentum. Setae on scape white, on pedicel black; no hairs on F1. F1 short, rectangular. Arista long.

Thorax. Prothorax grey, with white hairs; postpronotal lobes grey, the lateral angle light brown, hairs white. Scutum tomentum grey-brown; dorsocentral stripes faint brown; acrostichal stripes faint grey. Bristles and setae of scutum black except a few short white hairs on anterior margin of scutum; dorsocentral bristles anteriors 5–6; posteriors 3–5; postalars 2–3, with a few short hairs; supra-alars 2, with 1–2 short hairs; presuturals 2–3; posthumerals 0–1. Scutellar tomentum brown; apical bristles black, abundant (10+ on each half), mixed with other long hairs.

Pleural tomentum brownish grey. Katatergite setae black, long, 7–10, with a few short white hairs; katepisternal setae white; aneptisternal setae 6, black, a few black hairs along dorsal margin and 1–2 white hairs in ventroposterior corner; anepimeron with 0–1 fine white hairs.

Legs. Cuticle dark brown/black and covered in thin grey tomentum though bare and reddish-black at femur joints. No coxal peg. Coxae with white setae; fine hairs of femur and tibia white, fine hairs of tarsi black; main bristles black except on basal half of femur. Ventral hairs on femur slightly longer than femur width; dorsoapical bristles on profemur fine, indistinct among other hairs, 8–11; on mesofemur and metafemur stronger, 4–7 and 12–16 respectively. Protibia with ventral bristles 3 times longer than tibial width; very faint patch of pale yellow setae on inside of protibia. Claws chestnut over basal 70%, apically black.

Wings. Veins light brown; membrane hyaline, slightly brown when viewed obliquely. Halter knob cream, without spot, stem light brown.

Abdomen. Male. Tergite cuticle dark brown/black; thin brown tomentum on tergite bases; grey tomentum in bands covering apical 40–60% of each tergite (segment 1 completely covered except basomedially), brown cuticle subshining along midline leaving brown/grey pattern indistinct. Tergite 1 with 1–5 black and 2–5 white lateral bristles; lateral setae white, on tergites 1–3 as long as halter stem, on tergites 4–7 as long as scape + pedicel; dorsal setulae short, brown. Sternite tomentum grey, hairs white.

Female. As in male, except tomentum along dorsal midline thicker; lateral setae on tergites 5–7 black, and no longer than scape.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown, covered in thin grey tomentum except medially on hypandrium; hairs dark brown/black, very long, erect and dense; setal brush dark brown. Epandrium elongate, in lateral view the width about 48% the length, widest in basal third, ventral margins gently sinuate, dorsal margin straight; apex rounded into weak ventral subapical tooth. In dorsal view, epandrium appears tapered, wider at base than apex; medial margins moderately curved, curvature starts about 37% from base; basal sclerite prominent.

Phallus paramere sheath dorsally 54% the length of phallus; paramere sheath with short buttress-like ventral flange basally; dorsal carina flat, extended apically almost equidistant to gonopore like a squared-off porpise fin, leaving a broad gap between apices. Ejaculatory apodeme in lateral view strongly bent dorsally in basal quarter, with broad dorsal carina. Subepandrial sclerite with triangular central unsclerotized area in basal 72%; spines parallel-sided, blunt, sparsely distributed, slightly more densely basomedially and apically.

Female genitalia. Undissected: cuticle dark brown, except pale reddish brown at base of hypogynial valves and usually with sternite 8; tergite and sternite 8 with short white hairs; lateral lobe setae short, black; cerci brown with pale setae; acanthophorite spines black.

Type Material. HOLOTYPE (here designated) ♂ labelled: "[rectangular white label] CALIF: Trinity Co./ Junction City/ V-4-1978/ T. R. Haig coll."; "[rectangular green label] FISH". My type label “[red and black bordered label] HOLOTYPE/ Lasiopogon esau/ des. T.A. McKnight 2017” has been added. USNM.

Other Material Examined (140 specimens). **U.S.A.: CALIFORNIA:** no loc, Baron (2♂ OSUC); **Humboldt Co.**, Fort Seward [40.226 -123.646], 30.v.1935, E.W. Baker (1♀ FISH), 7.vi.1935, E.W. Baker (1♀ FISH); Richardson Grove, 5 mi N [40.058 -123.785], 30.iv.1959, T.R. Haig (1♂ 2♀ FISH); S Fork Eel River, Hwy 254 1.2km N of Miranda, sandbars at forest edge, 40.248 -123.824, 10.v.1995, R.A. Cannings, H. Nadel (3♂ 4♀ RBCM); **Lake Co.**, Rice

Fork Eel River near Bear Creek [39.327 -122.871], 23.iv.1987, Baumann, Stark, Nelson, Wells (7♂ 1♀ BYU); **Mendocino Co.**, Branscomb, 3 mi N, NCCRP [39.691 -123.655], 8.v.1976, M.M. Helena (1♂ EMEC), 21–23.v.1982, C. Besette (1♀ BEZA), 18–21.v.1984, D.J. Sandri (1♂ 2♀ EMEC); Branscomb, 5 mi N, NCCRP [39.719 -123.652], 24.v.1976, J. Powell (1♂ 1♀ [pr in cop] EMEC), 24–25.v.1976, R. Wharton (1♂ 1♀ EMEC); Hopland [38.969 -123.117], D.D. Munroe (2♀ CNC); Russian River near Hopland [38.954 -123.102], 3.iv.1968, J. Powell (3♂ 1♀ EMEC), 4.v.1968, W.J. Turner (1♂ ESUW), 9.v.1970, J.A. Powell (1♂ 1♀ EMEC); **Napa Co.**, Samuel Springs, Lake Berryessa W shore [38.605 -122.311], 29.iii.1956, R.M. Bohart (2♀ CAS); **Sonoma Co.**, Duncan Mills, 2 mi E [38.455 -123.050], 13.v.1960, T.R. Haig (1♀ FISH); Hacienda [38.507 -122.929], 20.v.1961, C. Slobodchikoff (1♂ FISH); Healdsburg [38.623 -122.837], 7.v.1974, G. Pereira (1♀ CAS); **Trinity Co.**, Hayfork, Hayfork Creek near Forest Ave, 40.54509 -123.16681, 24.v.2016, T.A. McKnight (1♀ TAM); Hayfork Ranger Station [40.547 -123.168], 23.v.1973, J. Doyen (1♂ EMEC, 1♀ RBCM), J. Powell (4♂ 3♀ EMEC, 1♂ RBCM); Hayfork, 2300' [40.552 -123.1801], 25.v.1973, S.L. Szerlip (1♂ 1♀ [pr in cop] EMEC); Hayfork, 4 mi S [40.498 -123.174], 18/19.v.1973 (1♀ EMEC); Junction City [40.732 -123.056], 1.v.1976, T.R. Haig (2♂ FISH), 21.iv.1977, T.R. Haig (1♂ FISH), 4.v.1978, T.R. Haig (13♂ 13♀ FISH), 25.v.1983, T.R. Haig (4♂ FISH), 23.iv.1984, T.R. Haig (21♂ 6♀ FISH); Morgan Gulch, 1 mi E Hayfork [40.543 -123.148], 22.v.1973, J. Powell (1♂ 1♀ EMEC, 1♂ 1♀ RBCM); Ruth Dam, 6.5 mi NW [40.439 -123.528], 7.iv.1966, G.R. Noonan (2♂ 2♀ FISH, 1♂ 1♀ LACM); **Yolo Co.**, Cache Creek Canyon, 7.iv.1956, P.M. Marsh (1♀ CAS); Davis [38.518 -121.770], 15.iv.1973, Y.B. Ibrahim (1♂ BEZA); Putah Creek Canyon [38.514 -122.072], 13.iv.1930, R.M. Bohart (1♀ FSCA); Rumsey [38.889 -122.236], 31.iii.1956, E.A. Kurtz (1♂ FISH), 7.iv.1956, E.I. Schlinger (1♂ 1♀ CAS), R.C. Bechtel (1♀ CAS, 1♂ LACM), R.M. Bohart (1♀ FISH), 21.iv.1956, E.A. Kurtz (1♂ FISH), 21.iv.1973, Y.B. Ibrahim (1♂ 1♀ BEZA); Rumsey, 2 mi N [38.911 -122.265], 12.iv.1975, R.W. Thorp (1♂ BEZA).

Type Locality. USA, California, Trinity Co., Junction City.

Taxonomic Notes. Specimens have been previously identified as *L. drabicolum* or *L. californicus*.

Etymology. Named after the Biblical person Esau, who was described as a "hairy man" (Genesis 27:11, KJV) and a "cunning hunter" (Gen 25:27); the name is indeclinable in Latin. The dense, strong bristles on the male genitalia are a distinctive character for this species of predator.

Distribution (Fig. III.3). Nearctic; USA, northwestern California.

Phylogenetic Relationships. Member of the *bivittatus* section, *drabicolum* clade.

Natural History. Habitat: river banks in mid-elevation mountains. Found perching on river sandbars near the forest's edge, sometimes concurrently with *L. zonatus* (Fig. III.7e). Specimens recorded between 29 March to 7 June, most in April and May.

***Lasiopogon gabrieli* Cole & Wilcox**

Lasiopogon gabrieli Cole & Wilcox, 1938. *Entomologica Americana* 43: 49–51.

Diagnosis. A small dark species from southern California and northern Baja California, with mystax black, thoracic tomentum brown to grey with clear dorsocentral stripes, thoracic setae mostly black, bristles long and strong, legs black; tergite tomentum in strong bands of brown and grey. Epandrial halves with very strongly curved medial margins, covered in grey tomentum; ovipositor dark brown; acanthophorite spines black.

Description.

Head. Face and vertex with grey/tan tomentum. Beard and labial setae white; mystax, frontal, and occipital dark brown/black. Occipital bristles moderately long and steadily curved through 90°, those behind the dorsomedial angle of the eye and most curved; lateral and ventral bristles shorter, straighter. Frontal setae fine and short; orbital setae longer.

Antennae. Dark brown/black, base of F1 sometimes lighter. Setae dark brown, sometimes a few

white hairs at the base of scape; F1 never with setae. F1 widest medially, dorsal margin straight, ventral margin rounded; F2+3 long and tapered.

Thorax. Prothorax grey/brown, hairs white; postpronotal lobes grey to brownish grey, lateral angle ferruginous, hairs white. Scutum tomentum steel to brown-grey, with a faint golden tint. Dorsocentral stripes usually dark brown; acrostichal stripes absent. Bristles and setae of the scutum black; notal setae short; anterior dorsocentral bristles 4–7mm, relatively fine; 3–5 posteriors; postalars 2–3, with about 4 shorter hairs; supra-alars 1–3 with 1 or 2 shorter hairs; presuturals 2–3; posthumerals 0–1. Scutellum rim slightly inflated, leaving a faint semicircular seam impressed inside the rim; tomentum thin grey/brown; apical bristles black, abundant (6–8 on each side) and mixed with many other long hairs.
Pleural tomentum grey, brownish on the lower anepisternum. Katatergite bristles black, 6–8, sometimes 1–3 white, with a few weaker hairs; katepisternal setae sparse, moderately long, white; anepisternal setae 5–7, mostly black with 1–3 white ventrally, a patch of short black hairs on dorsal margin of sclerite; anepimeron with a 2–4 fine white setae.

Legs. Base color usually dark brown to black, sometimes reddish at joints of coxa/femur, femur/tibiae, and tarsal bases; tomentum of coxae and rest of legs grey, sparse. No coxal peg. Bristles on legs black, except white dorsolateral bristles in medial half of femur; finer setae and long ventral setae on femur white. Ventral hairs on femur as long as femur width; dorsolateral bristles weak, sparse, 5–7 on profemur; stronger on mesofemur (3–5) and metafemur (5–9). Protibia with longest bristles 2–3 times longer than tibial width. Claws dark brown over basal 60–70%, apically black.

Wings. Veins dark brown; membrane transparent, faint light brown in oblique view. Halter yellow, with no spot.

Abdomen. Base cuticle dark brown/black; subshining brown tomentum over on tergite bases, bands of grey tomentum cover apical 50% of each tergite (tergite 1 completely covered, thin at anterior midline) and extend to tergite base laterally but not along midline except in a few rare

specimens. All tergites with white lateral hairs, longer on tergites 1–3; long black (2–5) and white (1–5) bristles on sides of tergite 1. Sternite tomentum grey, hairs white.

Male genitalia. Epandrium and hypandrium/gonocoxite complex dark brown/chestnut, covered in thin grey tomentum, with long black hairs; setal brush dark brown. Epandrium elongate, in lateral view the width 38% the length, straight along dorsal and ventral margins; apex rounded, with only hint of ventral tooth. In dorsal view, medial margins of epandrium very strongly curved, curvature starts about 30% from base; basal sclerite short but strong.

Phallus paramere sheath dorsally 44% the length of phallus; paramere sheath ventrally with a short, very blunt tooth subapically or without ornamentation; dorsal carina extending parallel to aedeagal tube and ending even or just short of gonopore, apex rounded, separated from gonopore by a gap of even width and depth. Ejaculatory apodeme in lateral view gently bent dorsally in basal quarter, with very narrow dorsal carina. Subepandrial sclerite with triangular central unclerotized area in basal 25% narrowing to parallel-sided gap to midpoint; spines parallel-sided, blunt, densely distributed basally and apically, sparse medially.

Female genitalia. Undissected: Hairs white, abundant, erect. Tergite 8 dark brown/black, posterior margin slightly reddish; sternite 8 dark brown/black; lateral lobe setae strong, black; hypogynial valves with fine hairs concentrated basally and apically; cerci brown/black with pale setae; acanthophorite spines black.

Type Material. HOLOTYPE ♂ (photographs examined) labelled: "[rectangular white label] San Gabriel Wash/ Calif. 2-27-1932/ Chas.H.Martin]"; "[rectangular red label] HOLOTYPE/ Lasiopogon/ gabrieli/ Cole & Wilcox"; "[rectangular white label] California Academy/ of Sciences/ Type No. 6433"; "[rectangular white label] ALLOTYPE IS STORED/ IN THE/ GENERAL COLLECTION". CAS.

ALLOTYPE ♀ (examined) labelled: "[rectangular white label] San Gabriel Wash/ Calif. 2-27-1932/ Chas.H.Martin]"; "[rectangular red label] ALLOTYPE/ Lasiopogon/ gabrieli/ Cole & Wilcox"; "[rectangular white label] Collection of the/ CALIFORNIA ACADEMY/ OF SCIENCES, San/ Francisco, Calif.". CAS.

PARATYPES (24 examined). **USA: California: Los Angeles Co.**, Artesia [33.865 -118.103], 27.iii.1934, M.W. Stone (1♂ CAS), 10.ii.1935, M.W. Stone (1♀ EMEC, 1♀ USNM); Azusa [34.156 -117.919], 1.iii.1925, S.W. Bromley (1♂ USNM); El Monte, San Gabriel River wash [34.066 -118.004], 2.iii.1934, M.W. Stone (1♂ USNM, 1♀ CAS), 31.xii.1934, J. Wilcox (1♂ CAS), 25.i.1935, M.W. Stone (1♂ CAS); Whittier, San Gabriel River wash [34.004 -118.069], 25.ii.1932, C.H. Martin (1? CAS), 27.ii.1932, F.R. Cole (2♀ CAS, 2♂ 5♀ EMEC, 1♀ RBCM); **Riverside Co.**, La Quinta [33.643 -116.319], 28.iii.1923 (1♀ EMEC); Riverside [33.989 -117.393], 27.i.1935, M.W. Stone (1♂ CAS); **San Bernardino Co.**, East Highlands [34.102 -117.103], 25.ii.1923 (1♀ EMEC); **San Diego Co.**, Alpine [32.839 -116.760], 8.iv.1915, M.C. Van Duzee (1♂ 1♀ OSUC).

Other Material Examined (188 specimens). **MEXICO: Baja California Norte:** Sierra Juarez, 2.2 mi SE El Topo [32.235 -115.956], 25.iii.1970, J.A. Gruwell, P.D. Perkins (20♂ 5♀ FISH, 1♂ 1♀ LACM); **USA: California: Los Angeles Co.**, Artesia [33.865 -118.103], 10.ii.1935, M.W. Stone (1♂ EMEC), 8.ii.1936, M.W. Stone (1♂ CAS), 17.ii.1937, J. Wilcox (1♂ 2♀ CAS), M.W. Stone (2♂ 2♀ CAS, 1♀ RBCM); Azusa [34.156 -117.919], 1.ii.1937, J. Wilcox (1♂ CAS), 4.ii.1937, J. Wilcox (1♀ UCRC), 9.ii.1937, J. Wilcox (1♂ BEZA), 12.ii.1937, J. Wilcox (1♂ CAS), 16.ii.1937, J. Wilcox (3♂ 3♀ CAS, 1♀ CNC, 2♂ 2♀ FISH), M.W. Stone (4♂ CAS, 1♂ 1♀ ESUW, 1♂ 1♀ RBCM), 19.ii.1937, H. MacBurney (3♂ 2♀ CAS), J. Wilcox (2♂ 5♀ CAS, 1♂ CNC, 1♀ FISH), M.W. Stone (1♀ BEZA, 6♂ 2♀ CAS, 1♂ FISH, 1♂ UCRC), 21.ii.1937, J. Wilcox (6♂ 7♀ CAS, 1♂ 1♀ FISH, 1♂ LACM, 1♂ 3♀ UCRC), 3.iii.1937, J. Wilcox (1♂ FISH); Duarte [34.139 -117.941], 10.ii.1937, J. Wilcox (5♂ 2♀ CAS, 1♀ RBCM); Long Beach [33.839 -118.203], 13.ii.1957, J. Wilcox (7♂ 3♀ CAS, 1♂ RBCM); San Gabriel Canyon, 16.ii.1930, H. Latta (1♂ EMEC); San Gabriel Mountains, 2.iv.1956, R.H. Crandall (1♀ LACM); Whittier, San Gabriel River wash [34.004 -118.069], 27.ii.1932, C.H. Martin (1♀ EMEC), D. Martin (1♂ 1♀ EMEC); **Orange Co.**, Anaheim [33.835 -117.863], 5.iii.1937, J. Wilcox (2♂ 1♀ CAS); Cypress [33.821 -118.062], 22.ii.1930 (1♀ MCZ); Stanton [33.795 -117.978], 20.ii.1952, A.F. Howland (5♂ 2♀ CAS), J. Wilcox (3♂ 4♀ CAS); **Riverside Co.**, Bautista Canyon, T6S R2E S27 [33.693 -116.844], 22.iv.1997, G.P. Kenney (1♀ UCRC); Dripping Springs, 27.iii.1962, J. Wilcox (4♂ 7♀ CAS, 1♂ 1♀ RBCM), 17.iv.1962, J. Wilcox (2♂ CAS); Prado,

Santa Ana Canyon [33.883 -117.647], 20.ii.1937, J. Wilcox (1♂ CAS); Riverside [33.989 -117.393], 17.iii.1935, A.L. Melander (1♂ USNM); San Jacinto River, Hwy 74, 2 mi E of NF boundary, cattails/sand in wash, 33.72741 -116.80946, 10.iii.2014, T.A. McKnight (1♂ 2♀, TAM); San Jacinto River, Hwy 74, 2 mi E of NF boundary, sagebrush slopes, 33.72265 -116.80581, 10.iii.2014, T.A. McKnight (1♂ 1♀ TAM); **San Bernardino Co.**, 9 mi SE Hesperia, Hwy 173 [34.313 -117.275], 21.iv.1981, E.M. Fisher (1♂ FISH); Colton [34.064 -117.306], F.A. Eddy (1♂ 1♀, [pr in cop] MCZ); Crafton [34.075 -117.095], 28.ii.1946, C.H. Martin (1♀ FSCA); Redlands [34.085 -117.166], 1913, F.R. Cole (1♀ MCZ); Rialto [34.109 -117.334], 7.iii.1942, J. Wilcox (1♂ CAS); **San Diego Co.**, Kitchen Creek, Laguna [33.883 -117.647], 24.iii.1979, D.K. Faulkner (1♀ SDMC); Pala, San Luis Rey River wash jct Bompas Wash, 33.36298 -117.06455, 6.iii.2013, T.A. McKnight (3♂ 2♀, [1 pr in cop] TAM); Rancho Santa Fe [33.013 -117.189], 31.iii.1959, E.I. Schlinger (1♀ UCRC); San Luis Rey [33.239 -117.335], 13.iv.1937, J. Wilcox (2♂ 1♀ CAS); San Luis Rey River, 5 km SE of Pauma Valley city, 33.26048 -116.94488, 6.iii.2013, T.A. McKnight (1♂ TAM).

Type Locality. USA, California, San Gabriel River wash near Whittier.

Etymology. No explanation given in the original description, but evidently refers to the type locality on the San Gabriel River.

Distribution (Fig. III.3). Nearctic; USA, southern California and northern Baja California Norte.

Phylogenetic Relationships. Member of the *bivittatus* section, likely related to *L. apoecus* sp. nov. and *L. condylophorus* sp. nov., based on genitalia morphology. Not closely related to *L. opaculus*, despite note in Cole & Wilcox 1938.

Natural History. Habitat: rivers and streams at low to middle elevations. Usually perches on small stones, sticks, pieces of bark, or low lying cattails above the wash bed; occasionally on bare sand (Fig. III.8h). Known flight dates range from 31 December to 22 April. One female with Tipulidae prey.

***Lasiopogon karli* McKnight sp. nov.**

Diagnosis. A medium-seized pale species from the mountains of New Mexico; mystax and most bristles of head and thorax black, fine hairs of scutum white, anterior dorsocentral bristles hairlike, black, posterior dorsocentrals and lateral bristles of scutum strong, black; scutum tomentum grey with faint brown dorsocentral stripes, tergite tomentum uniform grey. Epandrial halves strongly concave medially, with long sparse black hairs; phallus with broad apex pointed dorsally and ventrally, ventrolateral carina near apex, dorsal carina narrow and pointed apically below ventrolateral carina. Ovipositor dark brown/black; acanthophorite spines black.

Description.

Head. Face and vertex covered in silvery grey tomentum. Ventral hairs (on beard, labium, palps) white; mystax, occelar setae, and most occipital setae black; frontal and orbital setae vary from white to black. Occipital bristles moderately fine and curved anteriorly; no lateral bristles beyond top quarter of the eye, ending well before the beard. Frontal and orbital setae reach apex of pedicel; occelar setae reach midpoint of F1.

Antennae. Black. Setae on scape white, on pedicel mostly black; no hairs on F1. F1 long and narrow. F2+3 slender, of moderate length.

Thorax. Prothorax grey, with white hairs; postpronotal lobes grey, the lateral angle chestnut, hairs white. Scutum tomentum silver to yellowish-grey; dorsocentral stripes mostly absent, sometimes faintly brown; acrostichal stripes slightly darker but not prominent. Scutal bristles black, fine hairs white or black. Dorsocentral bristles fine, anteriors 4–6mm; posteriors 3–5; postalars 2–3; supra-alars 2; presuturals 2–3; posthumerals 0–1, very fine. Scutellar tomentum thin, grey; apical bristles black, fine, 4–5 on each side with a few white hairs; short white vertical hairs half as long as apical bristles along upper rim.

Pleural tomentum yellowish grey. Katatergite setae 6–9, color variable, ranging from mostly white to all black, with several shorter white hairs; katepisternal setae fairly short, white; anepisternal setae 3–4, black, a few very short white hairs along dorsal margin and 2–3 black and white hairs in ventroposterior corner; anepimeron with 0–1 short white hairs.

Legs. Cuticle black with very thin grey tomentum, bare and reddish at joints, sometimes reddish on hind tibia. No coxal peg. Coxae with white setae. Fine hairs of legs all white; main bristles mostly black, except a few white bristles basally on femur and tibia. Ventral hairs on femur as long as femur width; dorsolateral bristles fine, variable from white to black, on profemur 5–7; mesofemur 2–4; metafemur 8–11. Protibia with ventral bristles 2–3 times longer than tibial width; patch of dense short setae on inside of protibia yellow-brown; on metatibia brown. Claws chestnut over basal 60%, apically black.

Wings. Veins dark brown; membrane hyaline. Halter knob cream, without spot, stem brown.

Abdomen. Male. Cuticle dark brown/black, covered in predominantly grey tomentum, basally brown-grey from some angles, apically bright silvery-grey. Tergite 1 with 4–7 white and 0–4 black lateral bristles; lateral setae white, on tergites 1–3 as long as halter stem, on tergites 4–7 as long as scape; dorsal setulae white. Sternite tomentum brownish grey, hairs white.

Female. As in male, except lateral hairs on tergites 4–7 black; ventral hairs on sternites 5–7 black.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle brown/black, covered in grey tomentum except medially on hypandrium and basally on epandrium; most hairs black except white hairs laterally on hypandrium and a few hairs on epandrium; setal brush dark brown. Epandrium elongate, in lateral view the width about 47% the length, longest apically; apex rounded. In dorsal view, medial margins of epandrium strongly concave, curvature starts about 36% from base; basal sclerite prominent.

Phallus paramere sheath dorsally 44% the length of phallus; paramere sheath with broad apex, pointed dorsally and ventrally, ventrolateral carina present near apex, but without ventral flange; dorsal carina relatively narrow, pointed apically below level of ventrolateral carina. Ejaculatory apodeme in lateral view slightly bent dorsally in basal quarter, dorsal carina moderately to very broad. Subepandrial sclerite with triangular central unsclerotized area in basal 39% narrowing to a parallel-sided gap in central portion; spines parallel-sided, blunt, densely and evenly distributed.

Female genitalia. Undissected: Cuticle dark brown/black, polished; with short white hairs; lateral lobe with short black bristles; cerci brown with pale setae; acanthophorite spines black.

Type Material. HOLOTYPE (here designated) ♂ labelled: "[rectangular white label] USA: New Mexico: Grant Co.,/Gila River below Forks campsite,/N 33.1842° W 108.2044°,/elev: 1691 m, 6.v.2015, coll./KB McKnight, TA McKnight #753". My type label "[red and black bordered label] HOLOTYPE/ Lasiopogon karli/ des. T.A. McKnight 2017" has been added. USNM.

PARATYPES (10 specimens designated): **U.S.A.: NEW MEXICO: Catron Co.**, Taylor Creek, 0.5 mi SW of Wall Lake, 33.3501 -108.0831, 5.v.2015, K.B. & T.A. McKnight (1♂ 1♀ TAM); Taylor Creek, below Wall Lake, Gila NF [33.345 -108.089], 28.iv.1994, R. Durfee (3♂ 1♀ CSUC); **Grant Co.**, Gila River below Forks campsite, 33.1842 -108.2044, 6.v.2015, K.B. & T.A. McKnight (2♂ 3♀ [1 pr in cop] TAM).

Type Locality. USA, New Mexico, Grant Co., Gila River below Forks campsite, N 33.1842° W 108.2044°.

Etymology. Named for the first author's father Dr. Karl B McKnight, who provided invaluable mentoring, counsel, and assistance throughout this work, and was the ideal field assistant for collecting expeditions. This species was chosen to bear his name because several geographic features with the McKnight surname (e.g., a mountain, creek, road, and Forest Service cabin) are within a few miles of the original collection localities, and Karl helped me catch specimens on our expedition there.

Distribution (Fig. III.2). Nearctic; USA, New Mexico.

Phylogenetic Relationships. Member of the *opaculus* section, putatively in the *cinereus* species group.

Natural History. Habitat: sandy river banks, found perching on bare sand patches 1–20 m from the water (Fig. III.7g). Dates collected: 29 March to 27 August. The asilid *Stichopogon arenicola* was also flying concurrently at the same sites.

***Lasiopogon littoris* Cole**

Lasiopogon littoris Cole, 1924. *Pan-Pacific Entomologist* 1: 8.

Diagnosis. A very small species from central California beach dunes with uniform dusty grey tomentum and white hairs. Antenna with squat F1 and elongate F2+3; scutum silvery grey, practically without stripes or pattern; all setae on body white and relatively long and dense; abdominal tergites with dense grey tomentum; basal brown patches on tergites inconspicuous. Epandrium long, narrow, with ventral tooth, moderately concave medially; phallus apex broadly flattened, with dorsal corner pointed; dorsal carina a rounded triangular point near midpoint of aedeagal tube. Ovipositor brown; acanthophorite spines black.

Description.

Head. Face and vertex with silver-grey tomentum. Beard, labial, mystax, and all other hairs white. Occipital bristles relatively fine and long; those behind the dorsomedial angle of the eye the longest and usually moderately curved anterolaterally; lateral and ventral bristles shorter, straighter. Frontal setae fine and short; orbital setae longer and more prominent.

Antennae. Brown, F2+3 polished, appear darker than basal segments. Setae on scape and pedicel white; F1 without hairs. F1 short and squat, F2+3 very long, always longer than F1.

Thorax. Prothorax grey, hairs white; postpronotal lobes grey, the lateral angle ferruginous, hairs fine, white. Scutum tomentum densely grey, sometimes faintly gold; dorsocentral stripes practically indiscernible, faintly darker from an angle. All bristles and hairs white, acrostichal and notal hairs fine, at least half as long as dorsocentral bristles; dorsocentral bristles long,

amidst finer hairs, 4-6 anteriors, 4-5 posteriors; postalars 2–3; supra-alars 1–3; presuturals 1–2; posthumerals 0–1. Scutellar tomentum grey; apical scutellar setae dense, indistinguishable from surrounding finer hairs.

Pleural tomentum gold-grey. Katatergite bristles 6–7, often with some finer hairs; katepisternal setae fine, wispy; setae along posterior and dorsal edges of anepisternum fine, 3–5 moderately prominent; anepimeron with 1–2 short wispy hairs.

Legs. Base color black; tomentum grey. No coxal peg. All hairs and bristles white. Ventral hairs on femur shorter or as long as femur width; dorsolateral bristles on profemur sparse (0-4) but mixed with many finer setae; stronger and less crowded on mesofemur (2–4) and metafemur (6–11). Protibia with ventral bristles 3 times longer than tibial width; apicomedial patch of short setae on protibia indistinct, white. Claws dark brown over basal 40%, apically black.

Wings. Veins yellow-brown to brown, usually lighter proximally; membrane tinged brownish in oblique view, frosted in direct view. Halter light brown to white, no spot, stem darker brownish.

Abdomen. Tergite cuticle color black; thin brown tomentum on bases of tergites 2–4 (2–5 in female), grey tomentum covers apical 70–90% of each tergite (tergite 1 completely covered), extending anteriorly along lateral margins and midline to divide brown into indistinct lateral spots, overall color primarily silvery grey. Setae white; lateral setae; lateral bristles on tergite 1 white, fine, often inseparable from surrounding hairs. Dorsal setulae short, white. Stenite tomentum grey, hairs white.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown; covered in grey tomentum; hairs white, setal brush yellowish white. Epandrium elongate, in lateral view the width about 45% the length, widest in basal third, with straight dorsal margin and sinuate ventral margin, apex rounded with broad ventral tooth. In dorsal view, medial margins of epandrium moderately concave, curvature starts 34% from base; basal sclerite strong.

Phallus paramere sheath dorsally 58% the length of phallus; paramere sheath without ventral ornamentation; apex broad and flattened, ventral lip rounded and shallow, dorsal lip coming to a longer sharp point; dorsal carina a rounded triangular point near midpoint of

aedeagal tube, very shallow in specimens from the north. Ejaculatory apodeme in lateral view slightly bent in basal quarter, with broad dorsal carina. Subepandrial sclerite with triangular central unsclerotized area in basal 79%; spines parallel-sided, blunt, sparsely and evenly distributed.

Female genitalia. Undissected: hairs white, erect, abundant. Tergite 8 brown, paler apically; sternite 8 dark brown; hypogynial valves paler with very short hairs; lateral lobes with moderate white bristles; cerci yellowish brown with short white hairs; acanthophorite spines black.

Variation. Specimens from the northern part of the range (Morro Bay) have the phallus dorsal carina triangle much less prominent and form a monophyletic mitochondrial clade (McKnight unpublished data); however, this does not merit splitting this population as a new species.

Type Material. HOLOTYPE ♂ (photos examined) labelled: "[rectangular white label] Pismo Cal/ iv.25.19"; "[rectangular white label] EPVanDuzee/ Collector"; "[rectangular white, black-bordered label] Lasiopogon/ littoris/ Type Cole"; "[rectangular white label] California Academy/ of Sciences/ Type No. 1575". CAS

Other Material Examined (373 specimens). **USA: California: San Luis Obispo Co.**, Atascadero State Beach, dunes 1 km N of Morro Rock, 35.3793 -120.8626, 12.v.1995, R.A. Cannings, H. Nadel (1♂ 2♀ LACM, 9♂ 5♀ RBCM), 9.v.2012, T.A. McKnight (1♂ 1♀ TAM); Dune lakes 3 mi S Oceano [35.068 -120.615], 1.vi.1972, J. Powell (3♂ 2♀ EMEC), 26–27.iv.1973, J. Powell (1♂ EMEC), 27.iv.1973, J. Powell (2♂ EMEC), 6.vi.1973, J. Powell (2♂ EMEC), 2.v.1974, J. Doyen (1♂ 1♀ [1 pr in cop] EMEC), J. Powell (2♂ 3♀ EMEC), 21.v.1976, J. Doyen (7♂ 3♀ EMEC); Dune lakes 7 mi S Oceano [34.977 -120.644], 4–5.vi.1971, J.D. Pinto (1♂ UCRC), 20.v.1972, J.D. Pinto (3♂ 2♀ UCRC); Grover City [35.122 -120.634], 27.iv.1959, E.G. Linsley (1♂ 1♀ EMEC); Morro Bay [35.361 -120.858], 23.vi.1951, S.F. Bailey, R.M. Bohart (2♂ FSCA), 30.iv.1962 (1♂ EMEC), C.A. Toschi (9♂ 3♀ EMEC), J. Powell (1♂ EMEC), J.K. Drew (1♂ 2♀ EMEC), P.D. Hurd (11♂ 3♀ EMEC), R.L. Langston (9♂ 3♀ EMEC, 2♂ 3♀ FISH), R.W. Thorp (25♂ 13♀ EMEC, 1♂ RBCM), Timberlake (5♂ 2♀ UCRC), 2.v.1962, C.A. Toschi (2♂ 4♀ EMEC, 1♂ RBCM), R.W. Thorp (4♂ 4♀ EMEC), 26.vi.1963,

J.C. Hall (1♂ 1♀ UCRC), 26.iv.1968, D. Veirs (1♂ CAS, 2♂ 2♀ EMEC), J. Powell (3♂ 1♀ EMEC), P.A. Opler (1♂ CAS, 14♂ 10♀ EMEC), 26.v.1970, J. Wilcox (14♂ 10♀ CAS), 27.v.1970, J. Wilcox (4♂ 2♀ [1 pr in cop] CAS), 27.v.1981, D.A. Powell (1♂ LACM), 7.vi.1982, J. Wilcox (2♂ 1♀ CAS); Morro Bay, 1 mi N [35.379 -120.863], 26.v.1970, J. Wilcox (1♂ FISH), 5.v.1973, J. Doyen (3♀ EMEC, 1♂ RBCM); Oceano [35.095 -120.621], 24.iv.1951, R.M. Bohart (1♂ FSCA), 9.vii.1964, J. Wilcox (1♂ CAS), 27.v.1970, J. Wilcox (2♂ 2♀ CAS), 29.v.1970, J. Wilcox (1♀ BEZA), 22.vi.1970, J. Wilcox (4♂ CAS), 23.vi.1970, M.W. Stone (3♂ 3♀ CAS), 14.vii.1970, J. Wilcox (1♂ BEZA), 18.vi.1972, P.P. Perkins (1♂ FISH); Oso Flaco Lake [35.032 -120.627], 11.v.1965, J. Powell (2♂ EMEC), 22.vi.1965, M.E. Irwin (2♀ UCRC), 23.iv.1966, A.J. Slater (1♂ EMEC), J. Powell (3♂ EMEC), 12.iv.1967, P.A. Rude (1♂ EMEC), 29.vi.1967, M.E. Irwin (1♂ UCRC), 27.iv.1968, D. Veirs (1♂ EMEC), J. Doyen (1♂ 1♀ EMEC), J. Powell (1♀ BPBM, 3♂ 2♀ EMEC, 1♀ RBCM), J.A. Chemsak (1♀ BPBM, 2♂ EMEC), 1.vi.1972, J.Powell (1♂ EMEC), 16.vi.1991, D.E. Russell (2♂ 2♀ BEZA), 13.v.1995, R.A. Cannings (1♂ CUAC, 3♂ 3♀ RBCM); Oso Flaco Lake Preserve dunes, 35.03316 -120.62664, 12.iii.2014, T.A. McKnight (1♂ TAM); 35.03187 -120.62658, 9.v.2012, T.A McKnight (1♂ 2♀ TAM); 9.iii.2013, T.A McKnight (1♂ TAM); Pismo Beach [35.092 -120.629], v.1976, J. Doyen (1♂ EMEC), 13.v.1956, I. Wilcox, J. Wilcox (4♂ 2♀ CAS, 1♂ EMEC, 1♀ UCRC), 13.v.1956, J. Wilcox (25♂ 22♀ CAS, 1♀ EMEC, 1♂ 1♀ ESUW, 4♂ 3♀ FISH, 1♀ UCRC), 23.iv.1960, J.A. Chemsak (1♀ EMEC); Pismo Beach State Park [35.087 -120.626], 15.vii.1967, M.E. Irwin (1♀ UCRC); Poly Hills [35.302 -120.655], 20.v.1962, E. Anderson (1♀ LACM); **Santa Barbara Co.**, Rancho Guadalupe dunes 1 km S of parking lot, 34.94991 -120.65542, 9.v.2012, T.A Mcknight (3♂ 2♀ TAM); Santa Maria River beach dunes [34.967 -120.649], J. Doyen (2♂ EMEC).

Type Locality. USA; California, Pismo.

Etymology. No explanation given in the original description, but evidently from the Latin *litoralis, littoralis* = littoral, of the seashore.

Distribution. (Fig. III.2). Nearctic; USA, known only from central California coast between Morro Bay and Vandenberg Air Force Base.

Phylogenetic Relationships. Member of the *bivittatus* section, perhaps sister to the *bivittatus* species group or to *L. bitumineus* sp. nov. Cole observed that the antennae (with their short F1 and long F2+3) are suggestive of *Lissoteles* Bezzi (another Stichopogoninae genus, found along the Mexican coast), however, the face and genitalia are typical of *Lasiopogon*.

Natural History. Habitat: upper beaches and beach dunes. Perches directly on bare sand, usually within a meter or two of a patch of vegetation, such as *Ericameria ericoides* and *Carpobrotus edulis* (Fig. III.6g, III.6h). Vouchered specimens range from 9 March to 15 July, however, this species has been observed as early as 14 February at Oso Flaco (A. Abela pers. comm.) One female and one male with tiny Diptera prey: *Tethina* sp. (Canacidae) and *Parathalassius* c.f. *aldrichi* (Dolichopodidae); a photograph on BugGuide.net (#901367) also show a male with Chironomidae prey. Can be extremely abundant on the sides of trails through the dunes; we have encountered hundreds in an hour's walk. Completely sympatric with *L. bitumineus* sp. nov., but *L. littoris* appears to have a later emergence season and frequents dunes closer to the beach.

***Lasiopogon martinensis* Cole and Wilcox**

Lasiopogon martinensis Cole and Wilcox, 1938. *Entomologica Americana* 18:54–55.
Lasiopogon martinorum Cole and Wilcox, Cannings 2002. Unnecessary emendation.

Diagnosis. A medium-large grey species from the Columbia River basin; mystax and most setae of head, thorax, and abdomen black; antennal F1 long, white hairs on scape; dorsocentral bristles fine, other scutal bristles strong, fine hairs of scutum half as long as dorsocentrals; apical scutellar bristles sparse. Thoracic tomentum grey, dorsocentral stripes brown, acrostichal stripes faint dark brown; abdominal tergites basally with subshining brownish grey tomentum; thick grey tomentum over apical 50% of each tergite and along lateral margins. Lateral bristles on abdomen long, dense, white; 5–6 black bristles laterally on tergite 1. Epandrium reddish brown,

covered in thin grey tomentum and black hairs; stout, with width 61% of length, apex broadly rounded; medial margin gently concave in dorsal view. Ovipositor dark brown/black; acanthophorite spines black.

Description.

Head. Tomentum of face silver/white; vertex and occiput thin, brown-grey. Beard, and labial hairs white; mystax and other setae brown/black. Occipital bristles strong, relatively sparse, shorter, somewhat curved apically. Frontal and orbital setae sparse, fine, long (most as long as scape+pedicel).

Antennae. Brown, base of F1 and tip of F2+3 chestnut. Setae on scape white, pedicel with brown bristles and finer white hairs; F1 occasionally with a single brown hair. F1 long, straight, slightly constricted past midpoint.

Thorax. Prothorax grey, hairs white; postpronotal lobes grey to brownish grey, lateral angle ferruginous, hairs mostly black, a few white dorsally. Scutum tomentum grey, more brown around the perimeter; dorsocentral stripes brown, acrostichal stripes dark grey. Bristles and setae of scutum black. Dorsocentrals weak anteriorly, 4–5 in number and some only 2x as long as surrounding setae, more prominent posteriorly, 4–5 in number. Other bristles strong; postalars 3, with 7–8 shorter hairs; supra-alars 3; presuturals 2; sometimes a weak posthumeral. Scutellar tomentum grey, ranging from silvery to brownish; rim strongly inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, 3–4 on each side angled upward, with a similar number of fine black hairs; disc of scutellum with short, fine white hairs.

Pleural tomentum grey. Katatergite bristles 8–10, long, mostly black but a few (1–3) white; several fine white hairs half the length of the primary setae; katepisternal setae abundant, rather long, white; anepisternal setae 5, brown, moderately strong and mixed with other hairs, a patch of short white setulae on dorsal margin of sclerite; anepimeron without setae.

Legs. Base color dark brown, paler on tarsi, ferruginous at joints of coxa/femur and femur/tibiae; tomentum of coxae grey, tomentum on rest of legs sparse grey. No coxal peg. Bristles on legs black, finer setae on femur white, on tibiae white above, brown below, on tarsi black. Ventral

hairs on femur shorter than femur width; dorsolateral bristles strong, 5–6 on profemur, mesofemur 5–6, metafemur 10–12. Protibia with ventral bristles 1.5–2.5 times longer than tibial width; apicomedial patch of short dense setae on protibia faint yellow, on metafemur brown. Claws dark brown over basal 60%, apically black.

Wings. Veins brown; membrane transparent, brownish when viewed obliquely. Halter orange-yellow, knob without spot.

Abdomen. Cuticle black; subshining faintly brownish grey tomentum at tergite bases, thick grey tomentum over apical 50% of each tergite, lateral margins broadly grey, overall appearance grey. Lateral setae on all tergites long, white (black on tergites 4–7 in female); tergite 1 with 5–6 long black bristles; dorsal setulae white (black in female). Sternite tomentum grey, hairs white.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown/chestnut; covered in thin grey tomentum; setae dark brown, long and prominent; setal brush dark brown. Epandrium stout, in lateral view the width about 61% the length, widest medially, apex broadly rounded. In dorsal view, medial margins of epandrium shallowly concave, close set; basal sclerite prominent.

Phallus paramere sheath dorsally 46% the length of phallus; paramere sheath with ventrolateral carina, ventral lip strongly projecting, no ventral flange; apex rounded; dorsal carina broad, coming to point even with aedeagal tube that leaves a narrow, shallow gap between apex and gonopore. Ejaculatory apodeme in lateral view bent dorsally in basal quarter, with broad dorsal carina. Subepandrial sclerite with triangular central unclerotized area in basal 38% narrowing to a parallel sided gap in central portion; spines parallel-sided, blunt, densely distributed except basolaterally.

Female genitalia. Undissected: Hairs white, abundant, erect. Tergite 8 shining brown/black with reddish brown apical band; sternite 8 shining reddish brown, dark brown near apical lobes; hypogynial valves black; lateral lobes with short pale setae. Cerci brown with pale setae; acanthophorite spines black.

Type Material. HOLOTYPE ♂ (photos examined) labelled: "[rectangular white label] Pasco, Wn./ IV.17.1934"; "[rectangular yellow label] Chas. H. Martin/ Col."; "[rectangular salmon label] HOLOTYPE/ Lasiopogon/ martinensis/ Cole & Wilcox"; "[rectangular white label] California Academy/ of Sciences/ Type No. 6505". CAS.

ALLOTYPE ♀ labelled: "[rectangular white label] Pasco, Wn./ IV.17.1934"; "[rectangular yellow label] Dorothy Martin/ Col."; "[rectangular salmon label] ALLOTYPE/ Lasiopogon/ martinensis/ Cole & Wilcox". CAS.

PARATYPES (6 examined). **USA: Washington: Franklin Co.**, Pasco [46.206 -119.037], 17.iv.1934, C.H. Martin (1♀ EMEC, 1♂ ESUW, 3♀ FSCA), D. Martin (1♂ EMEC).

Other Material Examined (9 specimens). **USA: Washington: Benton Co.**, Paterson [45.934 -119.598], 26.iv.1936 (2♂ 2♀ USNM); Richland, Yakima River [46.276 -119.317], 2.v.1946, C.H. Martin (1♂ FISH, 2♂ FSCA); **Franklin Co.**, Pasco [46.206 -119.037], 17.iv.1934, D. Martin (1♀ FSCA); **Whitman Co.**, Wawawai [46.581 -117.297], 15.v.1909, W.M. Mann (1♂ RBCM).

Type Locality. USA, Washington, Pasco. Type locality damaged (TAM).

Taxonomic Notes. Figures and characters coded for *L. martinorum* in Cannings (2002) actually correspond to *L. ripicola*; these species have frequently been mistaken for each other.

Etymology. Named in honor of Charles and Dorothy Martin, whose collecting provided much material for work on robber flies (Cole and Wilcox 1938), including the original specimens of this species. Although the ideal suffix given this etymology would be "–orum" instead of "–ensis", the Latinization is not correctable in accordance with ICZN 32.5.1.

Distribution (Fig. III.2). Nearctic; USA, Washington, Columbia River basin.

Phylogenetic Relationships. No specimens were found with viable DNA, but morphology strongly suggests that this species is a member of the *opaculus* section, *tetragrammus* species group, probably closely related to *L. lavignei* Cannings. Specimens of *L. ripicola* were mistakenly used to code *L. martinorum* in the phylogenetic analysis of Cannings 2002; *L. martinorum* species does not belong in the *bivittatus* group.

Natural History. Habitat: unknown, probably riparian sandbanks in grassland. This species has not been collected since the 1930s despite repeated attempts by the authors to find modern populations in eastern Washington. It is possible that anthropogenic ecological changes in the Columbia River Basin have rendered this species extinct.

***Lasiopogon nelsoni* McKnight sp. nov.**

Diagnosis. A medium to small pale species from southern California; setae of head mostly black, mystax black, usually with a few ventrolateral white hairs, scape and frontal hairs mostly white; bristles and hairs of scutum black; scutal tomentum silvery grey or brown, dorsocentral stripes usually brown, acrostichal stripes usually indistinct; tergites with basal brown tomentum in lateral spots; grey tomentum over apical 50–60% of each tergite and extending anteriorly along midline and lateral margins. Epandrial halves tapered, moderately concave medially; phallus dorsal carina flat, broad, and pointed with a wide, deep gap between apex and aedeagal tube. Ovipositor dark brown, acanthophorite spines black.

Description.

Head. Face and frons silvery-grey. Ventral hairs (on beard, labium, palps) white; orbital, occellar, and occipital setae black; frontal hairs usually white, rarely black; mystax usually mostly black with a few ventral white hairs, rarely all black. Frontal and orbital setae short, with longest only reaching base of F1, or at most bottom quarter. Occipital setae gradually curved, longest reach behind frons.

Antennae. Dark brown, with thin grey tomentum. Setae on scape white, at most one black seta; setae on pedicel mixed white and black; no hairs on F1. F1 spindle-shaped, widest just past midpoint; arista long.

Thorax. Prothorax grey, with white hairs; postpronotal lobes grey, the lateral angle chestnut, hairs all white or mixed with black. Scutum tomentum grey or brown; dorsocentral stripes faintly brown, sometimes indistinct; acrostrichal stripes indistinct. Bristles and fine setae of scutum black, a few short hairs white along anterior margin. Dorsocentral bristles moderately robust, anteriors 3–7; posteriors 4–5; postalars 1–4, with several fine hairs; supra-alars 2–3; presuturals 3; posthumerals 1–2. Scutellar tomentum grey; rim inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, 5–8 on each half, mixed with other hairs; short vertical hairs on uppermost edge of rim white, 60% the length of main bristles.

Pleural tomentum grey or brownish grey. Katatergite setae black, long, 6–8, with a few fine short white hairs; katepisternal setae white, fine; anepisternal setae 5–6, black, a few short white setae along dorsal margin and a few longer white setae in posteroventral corner; anepimeron with 2–5 fine white setae.

Legs. Cuticle dark brown/ black, covered in thin yellow/grey tomentum except at femur joints. No coxal peg; coxae with white setae. Fine hairs of femur, tibia, and first tarsomere white, on tarsi 2–5 black; bristles black except basally on profemur. Ventral hairs on femur as long as femur width; dorsolateral bristles on profemur 6–8; mesofemur 6–7; metafemur 10–15. Protibia with ventral bristles 2 times longer than tibial width; apicomedial dense patch of short setae on protibia yellow, on metatibia dark brown/black. Claws chestnut over basal 60%, black apically.

Wings. Veins dark brown; membrane hyaline but pale brown when viewed obliquely. Halter knob cream, without spot, stem brown.

Abdomen. Cuticle dark brown/black. Thin brown tomentum on tergite bases, greyish brown along midline, dividing the brown tomentum into two lateral spots, pattern sometimes indistinct; grey tomentum covers apical 50–60% of each tergite and lateral margins (tergite 1 covered in

grey tomentum except some brown basomedially. Tergite 1 with 3–6 black and 1–2 white lateral bristles; lateral setae on tergites white, as long as F1 on tergites 1–3, on male as long as scape + pedicel on tergites 4–7, on female only as long as scape; dorsal setulae short, black or white. Sternite tomentum grey, hairs white, black on sternite 7 on female.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown/black; covered in grey tomentum except medially on hypandrium; setae long, erect, black; setal brush dark brown. Epandrium elongate, in lateral view the width about 50% the length, widest in basal third, dorsal margin slightly and ventral margin moderately sinuate, apex rounded with strong ventral tooth. In dorsal view, epandrium appears tapered, wider at base than apex, medial margins of epandrium moderately curved, curvature starts about 42% from base, basal sclerite moderately strong.

Phallus paramere sheath dorsally 46% the length of phallus; paramere sheath with very short ventral flange at base; dorsal carina a flat pointed fin, rejoining aedeagal tube well before gonopore, leaving a wide, deep gap between apices. Ejaculatory apodeme in lateral view gently bent dorsally, with broad dorsal carina. Subepandrial sclerite with triangular central unsclerotized area in basal 26% narrowing to a slender gap for another 44%; spines parallel-sided, blunt, moderately and evenly distributed.

Female genitalia. Undissected: Cuticle of tergite 8 polished dark brown/ black; sternite 8 dark brown or reddish brown, reddish near base of hypogynial valves, which are short and wide. Short fine erect hairs abundant, white; cerci with white hairs, lateral lobes with black bristles; acanthophorite spines black.

Type Material. HOLOTYPE (here designated) ♂ labelled: "[rectangular white label] CALIF: S. Brdo. Co:/ Mojave Riv. Forks/ S. Brdo. Mts 1 mi. S./ 8-V-82 E. Fisher"; "[rectangular white label] Lasiopogon/ drabicola/ Cole/ det. E.M.Fisher"; "[rectangular white label] FISH". My type label "[red and black bordered label] HOLOTYPE/ Lasiopogon nelsoni/ des. T.A. McKnight 2017" has been added. USNM.

Other Material Examined (169 specimens). **U.S.A.: CALIFORNIA: Los Angeles Co.**,

Agoura [34.163 -118.762], 7.iv.1954, W. McDonald (1♂ EMEC); Artesia [33.865 -118.103], 27.iii.1934, M.W. Stone (2♂ CAS, 1♂ 1♀ EMEC, 1♂ FISH); Beverly Glen canyon [34.098 -118.442], 22.iii.1952, B. Tinglof (1♀ EMEC); Big Tujunga River, 4 km NE Sunland, 34.2916 -118.28783, 7.iii.2014, T.A. McKnight (1♂ TAM); Burbank [34.171 -118.309], 23.iii.1933, C.H. Hicks (1♀ WSUC); Claremont [34.129 -117.693] (1♀ OSUC); El Monte [34.066 -118.004], 18.iii.1933, Sloop & M.W. Stone (2♂ CAS), 2.iii.1934, M.W. Stone (1♂ UCRC); Elizabeth Lake canyon [34.667 -118.417] (1♂ 1♀ EMEC); Los Angeles river [34.082 -118.228], 5.iii.1931 (1♂ EMEC); Los Angeles, Griffith Park [34.131 -118.275], 26.v.1933, M.W. Stone (4♂ 1♀ CAS); Los Cerritos [33.83 -118.205], 21.iii.1915, (2♂ OSUC), M.C. Van Duzee (CAS, 2♀ EMEC), 9.iv.1915, M.C. Van Duzee (1♂ EMEC); Malibu Creek [34.098 -118.734], 13.iv.1973 (1♀ LACM); Pallet Creek [34.454 -117.894], 20.iv.1950, C.D. Mac Neill (1♂ 1? FISH); Pico Rivera, Rio Hondo River [33.995 -118.107], 24.v, C.H. Martin (1♂ FSCA); Rio Hondo [34.031 -118.045], 1.iii, D. Martin (1♂ FSCA), 23.iii.1930, C.H. Martin (2♂ FSCA), 31.iii.1930, C.H. Martin (1♂ 1♀ CAS, 1♀ FSCA); Rock Creek Wash jct Valyermo Rd, 4 mi SE of Pearblossom, 34.46369 -117.86425, 8.iii.2014, T.A. McKnight (1♂ 1♀ TAM); San Gabriel Canyon, 9.v.1965 (1♂ FISH), 26.iii.1980, F.G. Andrews (1♂ FISH); San Gabriel River @ RV park, 3.5 mi E of E Fork bridge, 34.23268 -117.79132, 16.iii.2014, T.A. McKnight (1♂ TAM); San Gabriel River, E Fork [34.239 -117.822], 21.v.1962, E. Fisher (1♂ FISH), 27.iv.1962, E. Fisher (1♂ 1♀ EMEC, 2♂ 2♀ FISH, 1♀ LACM), 18.iv.1963, E. Fisher (1♀ ESUW, 1♂ 3♀ FISH, 2♂ 1♀ LACM); Santa Monica Mountains, Tapia Park [34.082 -118.706], 20.iv.1968, E. Fisher (1♂ ESUW, 3♂ 1♀ FISH); Santa Monica Mountains, Topanga Canyon [34.0758 -118.5903], 20.iv.1961, E. Fisher (2♀ FISH), 25.iv.1961, E. Fisher (1♂ 1♀ FISH), 3.v.1962, E. Fisher (1♂ EMEC, 1♂ FISH), 21.v.1965, E. Fisher (1♂ FISH), 26.v.1965 (4♂ 1♀ LACM), 25.iv.1973 (1♂ LACM); Soledad Canyon [34.439 -118.312], 23.iv.1950, W.A. McDonald (1♀ EMEC); Valyermo [34.454 -117.855], 13.v.1944, A.L. Melander (1♀ USNM); Whittier [34.004 -118.069], 25.iii.1930 (2♂ 1♀ CAS, 2♀ FISH); **Monterey Co.**, Andrew Molera State Park, path to campsites 0.5 mi W parking lot, 36.287412 -121.849069, 10.v.2012, T.A. McKnight (2♀ TAM); Jolon, 14 mi W [35.997 -121.381], 2.iv.1959, C.W. O'Brien (5♂ 2♀ FISH); Paloma Creek, 4 mi NE Arroyo Seco, Guard Station 850' [36.272 -121.451], 4.v.1975, S. Szerlip (1♀ EMEC); Pfeiffer Big Sur State Park [36.253 -121.789], 16.vi.1949, P.H. Arnaud, Jr. (1♀ CAS), 20.vi.1949, P.H. Arnaud, Jr. (1♀ CAS); **Riverside Co.**, Dripping Springs [33.455 -116.973],

17.iv.1962, J. Wilcox (4♂ 2♀ CAS), 3.v.1962, J. Wilcox (1♂ CAS); Temecula Canyon, 3 mi NW Rainbow [33.454 -117.173], 24.v.1968, M.E. Irwin (1♂ FISH); Temecula Canyon, Santa Margarita River, 800' [33.454 -117.173], E.I. Schlinger (2♂ 1♀ UCRC); **San Bernardino Co.**, Mojave River Forks, 1 mi S [34.341 -117.261], 8.v.1982, E. Fisher (5♂ 1♀ FISH); Mojave River near Deep Creek [34.346 -117.239], 27.iv.1941, J. Wilcox (1♂ 3♀ CAS); Victorville, 3 mi NW, 12.iv.1964, D.D. Linsdale (1♀ FISH); **San Diego Co.**, Descanso, Sweetwater River, 32.8350 -116.6233, 31.v–6.vi.2002, M.E. Irwin, F.D. Parker (4♂, 3♀ INHS); **San Luis Obispo Co.**, San Simeon Creek, rapids above bridge ~4 mi E of San Simeon, 35.60795 -121.09053, 10.v.2012, T.A. McKnight (3♂ 2♀ [1 pr in cop] TAM); **Santa Barbara Co.**, Los Prietos [34.545 -119.805], 23.vi.1965, G.A. Gorelick (1♂ LACM), J. Powell (1♂ FISH); **Ventura Co.**, Casitas Springs [34.372 -119.309], 20.iv.1979, R.P. Meyer (3♂ BEZA); Foster Park [34.356 -119.311], 17.v.1942, G.F. Toland (1♂ 1♀ CAS), J. Wilcox (1♂ 1♀ CAS), 10.iv.1961, E.M. Fisher (1♀ FISH); Lockwood Creek, 4700', 34.7201 119.022, 4.vii.1998, E. Iverson (2♀ LACM); Lockwood Creek, near Stauffer PO [34.736 -119.054], 7.v.1959, J. Powell (1♂ 2♀ FISH), J.R. Powers (1♂ 1♀ FISH); Ojai Valley [34.439 -119.237], 28.iv.1940, J. Wilcox (9♂ CAS); Piru Creek, Blue Point campground [34.530 -118.757], 7.v.1966, S. & S. Frommer (1♂ UCRC); Piru Creek, NE base Alamo Mtn [34.703 -118.937], 3.v.1959, C.W. O'Brien (1♂ FISH), J. Powell (2♂ 1♀ FISH), J.R. Powers (1♂ 3♀ [1 pr in cop] FISH); Santa Ana Valley, 6.iv.1941, J. Wilcox (2♂ 1♀ CAS, 1♀ FISH); Santa Paula [34.348 -119.053], 15.vi.1957, W.E. Simonds (2♂ 1♀ FISH); Sespe River [34.492 -118.945], 23.iv.1950 (1♀ EMEC), 6.v.1942, M.W. Stone (3♂ 1♀ CAS, 1♂ FISH).

Type Locality. USA, California, Sand Bernardino Co., San Bernardino Mountains, 1 mi S of Mojave River Forks.

Taxonomic Notes. Specimens from this new species have usually been identified as *L. drabicolum.*

Etymology. Named in honor of one of the first author's mentors, Dr. C. Riley Nelson, who also loves desert rivers and sports salt and pepper colored facial hair. The heart-shaped epandria bring

to mind my gratitude and friendship for him.

Distribution (Fig. III.3). Nearctic; USA, California.

Phylogenetic Relationships. Member of the *bivittatus* section, *drabicolum* species group.

Natural History. Habitat: mountain stream banks. Perches on boulders, stones, and sandy patches near running water (Fig. III.8e, III.8f). Dates collected: 1 March to 4 July, most in April and May. Occasionally found at sites simultaneously with *L. drabicolum*, but perching microhabitat may help distinguish these taxa.

***Lasiopogon odontotus* McKnight sp. nov.**

Diagnosis. A medium-sized greyish brown species from the western and southern Sierra Nevada; mystax and most setae of head and thorax black; white hairs on antennal scape; dorsocentral stripes brown on grey scutum; tergites with basal brown tomentum in broad bands or lateral spots, grey over apical 50–60% of each tergite and occasionally along midline. Epandrium moderately curved medially; phallus paramere sheath with prominent sharp ventral subapical tooth and long finger-like apical projection on dorsal carina parallel to aedeagal sheath. Ovipositor dark brown/black; acanthophorite spines black.

Description.

Head. Face and vertex silvery grey. Ventral hairs (on beard, labium, palps) white; mystax and dorsal setae mostly black (a few white hairs occasionally in orbital setae). Occipital bristles fine, gradually curved anteriorly, longest posterior to frons; frontal and orbital setae long (reach basal quarter of F1), dense; ocellar setae indistinct.

Antennae. Dark brown, with thin grey tomentum. Setae on scape usually white (rarely mixed

with black), on pedicel black, no hairs on F1. F1 relatively short, widest at basal third with ventral margin curving but dorsal margin straight; F2+3 long.

Thorax. Prothorax grey, with white hairs; postpronotal lobes grey, the lateral angle yellowish brown, hairs white, rarely dark brown. Scutum tomentum grey; dorsocentral stripes brown, acrostichal stripes faint, rarely leaving a pale medial stripe. Bristles and fine hairs of scutum black, rarely a few short white hairs anteromedially. Anterior dorsocentral bristles 3–6; posteriors 4–5; postalars 2–3, with several shorter hairs; supra-alars 2–3; presuturals 2–3; posthumerals 1. Scutellar tomentum grey; rim slightly inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, abundant (6–9 on each half), mixed with many finer hairs; short vertical hairs on uppermost edge of rim black.

Pleural tomentum grey. Katatergite setae black, long, 6–8, with a few short white hairs; katepisternal setae white, sparse; anepisternal setae 6–7, black, several short black hairs along dorsal margin, a few white hairs in posteroventral corner; anepimeron with 3–5 fine white setae.

Legs. Cuticle dark brown/black, covered in grey tomentum except bare at femur joints. No coxal peg. Coxae with white setae; fine hairs white on femur, tibia, and first tarsomere, black on tarsi 2–5; bristles all black except a few basally on femur. Ventral hairs on femur as long as femur; dorsolateral bristles on profemur 6–7, black, fine amidst long hairs; on mesofemur and metafemur shorter and more robust, 4–6 and 8–13 respectively. Protibia with ventral bristles about 2 times longer than tibial width; apicoventral patch of dense short setae on protibia pale yellow and indistinct, brown on metatibia. Claws chestnut over basal 60%, black apically.

Wings. Veins pale brown; membrane hyaline but pale brown when viewed obliquely. Halter knob cream, without spot, stem light brown.

Abdomen. Male. Tergite cuticle dark brown/black; thin brown tomentum on tergite bases, bands of grey tomentum cover apical 50–60% of each tergite and extend anteriorly along lateral margins, tergites occasionally greyish along midline to divide brown into two lateral spots (especially in specimens from the south); segment 1 is fully covered in grey. Tergite 1 with 3–8

black and 1–3 white lateral bristles; lateral setae on tergites white, on tergites 1–3 as long as halter, on tergites 4–7 as long as F1; dorsal setulae black, short.

Female. As in male, except brown tomentum usually in definite widely spaced spots; lateral hairs on tergites 4–7 black, as long as scape, erect.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown/black; covered in thick grey tomentum except thin medially on hypandrium; setae long, erect, black; setal brush dark brown. Epandrium elongate, in lateral view the width about 47% the length, widest in basal third, dorsal and ventral margins slightly sinuate, apex rounded with shallow ventral tooth. In dorsal view, epandrium appears tapered, wider at base than apex, medial margins of epandrium moderately curved, curvature starts about 41% from base, basal sclerite strong.

Phallus paramere sheath dorsally about 48% the length of phallus; paramere sheath with prominent sharp subapical ventral tooth and weak ventral flange at base; dorsal carina flat, with a long finger-like apical projection parallel to aedeagal sheath, base of projection rejoins aedeagal tube well before gonopore leaving a wide, deep gap between equidistant apices. Ejaculatory apodeme in lateral view moderately to strongly bent dorsally, with broad dorsal carina along entire length. Subepandrial sclerite with triangular central unsclerotized area in basal 32% narrowing to a slender gap for another 40%; spines parallel-sided, blunt, moderately and evenly distributed.

Female genitalia. Undissected: Cuticle of tergite 8 polished dark brown/black; sternite 8 dark brown or reddish brown, especially near base of hypogynial valves, which are short and wide. Short fine erect hairs abundant, white everywhere except occasionally on hypogynial valves; cerci with white hairs, lateral lobes with black bristles; acanthophorite spines black.

Variation. Specimens from the southern Sierra Nevada (e.g., Kern and Tulare counties) tend to have more grey in the tergite tomentum, with the basal brown tomentum divided into spots or even indistinct, instead of the distinct banding seen in specimens from the north (e.g., Sacramento and Yosemite). The phallus dorsal carina in southern specimens is also more constricted, but we consider these differences minor given the comparable variation in tomentum

patterns and phallus morphology in the closely related and similarly distributed species *L. sierra* sp. nov. and *L. anaphlecter* sp. nov.

Type Material. HOLOTYPE (here designated) ♂ labelled: "[rectangular white label] Sacramento River Levee/ Sacramento/ Sac. Co. Calif. IV-29-1970"; "[rectangular beige label] ex open/ ground"; "[rectangular white label] M. Wasbauer/ Collector"; "[rectangular white label] from/ collection of/ Larry G. Bezark"; "[rectangular white label] Lasiopogon/ drabicola/ Cole/ det. R.A. Cannings 1996". My type label "[red and black bordered label] HOLOTYPE/ Lasiopogon odontotus/ des. T.A. McKnight 2017" has been added. USNM.

Other Material Examined (69 specimens). **U.S.A.: CALIFORNIA: El Dorado Co.**, Coloma, Little American River S Fork @ Hwy 43 bridge, 38.8069 -120.9028, 23.v.1993, R.A. Cannings, H. Nadel, E. Fisher (1♂ 1♀ RBCM); **Fresno Co.**, Dinkey Creek at N Fork Kings River [36.906 -119.125], 26.iv.1977, D. Wilder (1♂ FISH); Hume Lake [36.787 -118.901], 2.vi.1963, L.G. Bock (1♂ WSUC); Lost Lake [37.204 -118.945], 16.iii.1961, J. Gordon (1♀ CAS); **Kern Co.**, no loc (1♀ OSUC), H.K. Morrison (1♂ 2♀ FISH); Miracle Springs [35.576 -118.534], 29.iv.1964, C.A. Toschi (3♂ 1♀ FISH); **Mariposa Co.**, Merced River, Indian Flat [37.662 -119.847], 15.v.1963, J. Wilcox (1♂ 1♀ CAS); Merced River, near Yosemite, 28.iv.1984, D. Jamieson (1♂ 1♀ BEZA); Yosemite Valley [37.7236 -119.6254], 16.v.1921, E.C. Van Dyke (1♂ 1♀ FISH), 24.v.1921, E.C. Van Dyke (1♂ FISH), 29.v.1921, E.C. Van Dyke (1♂ FISH), 13.vi.1921, E.C. Van Dyke (1♀ FISH), 3.v.1968, R.E. Fontaine (1♂ BEZA); Yosemite, 3880–4000' [37.724 -119.625], 16.v.1938, R.M. Bohart, (1♀ FSCA), 19.v.1938, J.R. Warren (1♀ FISH), K. Snyder (1♀ FISH), 25.v.1938, F.C. Zabaldano (1♂ 1♀ CSUC); **Sacramento Co.**, Sacramento, 13.v.1950, H.T. Robinson (1♀ CNC), 29.v.1956, W.H. Lange (1♂ FISH), 4.iv.1956, H.R. Moffitt (1♀ FISH), 24.v.1962, M. Wasbauer (1♂ FISH), 6.iv.1964, A.S. Menke (1♂ 1♀ FISH); Sacramento, Sacramento River levee [38.595 -121.509], 31.iii.1966, M.S. Wasbauer, F.G. Andrews (1♂ FISH), 1.iv.1966, M.S. Wasbauer, F.G. Andrews (1♀ FISH), 29.iv.1970, M. Wasbauer (3♂ 3♀ BEZA, 2♂ 3♀ FISH, 2♀ LACM), 15.v.1970, M.S. Wasbauer, F.G. Andrews (1♀ FISH); **Tulare Co.**, Fairview [35.9299 -118.4909], 27.iv.1964, C.A. Toschi (1♀ FISH), P. Rude (1♂ 1♀ [pr in cop] FISH), R.L. Langston (2♀ FISH); Fish Creek, Troy Meadows, 12 mi E of Kennedy Meadows General Store, Sequoia NF, 2464 m [36.070 -118.236],

25.vi.1994, J. Cole (1♀ LACM); Johnsondale [35.972 -118.539], 23.v.1965, E.M. Fisher (6♂ 1♀ FISH); Porterville [36.054 -119.003], 16.iv.1961, E. Ball (2♀ FSCA); S Fork Kern River, 6.vi.1945, C. Henne (1♀ CAS); **Yolo Co.**, Elkhorn Ferry [38.673 -121.625], 12.v.1951, R.C. Bechtel (1♂ 1♀ [pr in cop] FISH); W Sacramento, 11.iv.1961, M.E. Irwin (1♂ BEZA); W Sacramento, 4 mi S, 27.v.1962, M. Wasbauer (1♀ FISH); W Sacramento, River, 26.iii.1988, E.M. Fisher (1♂ FISH).

Type Locality. USA, California, Sacramento County, Sacramento, Sacramento River Levee.

Taxonomic Notes. Specimens from this new species were previously identified as *L. californicus* (see Fig 248k in Cannings 2002) or *L. sierra* sp. nov.

Etymology. From the Greek οδοντωτός, odontotus, meaning toothed; adjective; refers to the prominent teeth around the phallus tip, and obliquely to its close relationship with *L. sierra* sp. nov. and range along the western slopes of the Sierra Nevada.

Distribution (Fig. III.3). Nearctic; California, western and southern slopes of Sierra Nevada.

Phylogenetic Relationships. Member of the *bivittatus* section, *drabicolum* clade, likely closely related to *L. sierra* sp. nov.

Natural History. Habitat: mountain and lowland riverbanks. Perches recorded on open ground or downed cottonwood (*Populus fremontii*) logs (likely similar to 7b). Dates collected range from 16 March to 25 June, with most in April; earlier dates were generally from lower elevations or the southern part of the range.

***Lasiopogon puyallupi* stat. nov.**

Lasiopogon willametti puyallupi Cole & Wilcox, 1938. *Entomologica Americana* 43: 77–79.

Diagnosis. A medium-sized dark species from sandy rivers and beaches of northwestern Washington and British Columbia; all setae black except white hairs of beard, coxae, femur, and tergite sides; thorax tomentum ranges from deep brown to grey with strong dorsocentral stripes; tergites usually with basal brown bands. Epandrial halves moderately concave medially, with black hairs; phallus dorsal carina with protruding apex swollen but slightly dorsoventrally flattened, pointing in an acute angle with the aedeagal tube. Ovipositor dark brown/black, acanthophorite spines black.

Description. Body length ♂ 8.5–11.5mm; ♀ 8.5–12.5mm.

Head. Face with silver-yellow tomentum; vertex with grey-brown tomentum, small bare patches between bristle groups. Mystax, frontal, orbital, ocellar, and occipital setae black, occasionally a few ventral hairs on mystax white; beard and labial hairs white. Occipital bristles long and curved to right angle, longest behind dorsolateral angle; lateral and ventral bristles shorter, straighter. Frontal and orbital setae fine and long; almost as long as ocellar bristles.

Antennae. Black; setae black, F1 never with setae. F1 long, rectangular, F2+3 broadly tapering.

Thorax. Prothorax brown/grey, hairs white; postpronotal lobes grey, lateral angle ferruginous, hairs brown. Scutum tomentum ranges from dark brown to light grey. Dorsocentral stripes dark brown, cuticle subshining; acrostichal stripes slightly darker than base tomentum. All hairs and bristles of scutum black. Dorsocentral bristles fine, mixed with other setae, 7–11 anterior, 3–5 posterior. Postalars 2–3, with a few shorter hairs; supra-alars 2–4; presuturals 3; posthumerals 1–2. Scutellar tomentum grey-brown; rim inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, very abundant (10+ on each side) and mixed with many other long hairs.

Pleural tomentum grey-tan. Katatergite bristles black, 8–10, with a few weaker hairs; katepisternal setae moderately long, white; anepisternal setae black, 6–9 relatively strong and

mixed with other short hairs along posterior margin, a patch of short hairs on dorsal margin of sclerite; anepimeron with 0–2 short wispy setae.

Legs. Base color black except apex of femur ferruginous; tomentum grey. No coxal peg. Bristles black, except basal 60% of femur; finer setae white on femur, black on tibia and tarsi. Ventral setae on femur as long or slightly longer than femur width; dorsolateral bristles mixed with finer hairs, 8–12 on profemur difficult to distinguish from surrounding finer hairs, more prominent on mesofemur (4–8) and metafemur (11–17). Protibia with ventral bristles 2–3 times longer than tibial width; ventromedial patch of dense short setae on protibia pale yellow; dark brown on metatibia. Claws reddish brown over basal 60%, apically black.

Wings. Veins dark brown; membrane faintly brown from microtrichia, darker around crossveins at apex of cells br and bm.. Halter cream, with no spot.

Abdomen. Male. Cuticle dark brown/black; brown tomentum at bases of tergites, bands of grey tomentum cover apical 40% of each tergite as a straight band, extending anteriorly along lateral margins. Dorsal setulae dark brown; lateral setae all white; lateral bristles on first tergite mostly black (4–7), 1–3 straw-colored. Sternite tomentum grey; hairs straw-colored/white.

Female. As in male, but grey tomentum enxtends anteriorly along midline to divide brown into lateral spots, and lateral setae on tergites 4–7 black; sternite hairs more sparse.

Male genitalia. Epandrium and hypandrium/gonocoxite complex black; sparsely covered in thin grey tomentum and black hairs, setal brush dark brown, dense. Epandrium elongate, the width of the haves in lateral view about 50% the length, widest in basal third; apex rounded with ventral tooth. In dorsal view, medial margins of epandrium moderately curved, curvature starts about 30% from base, outer margins gradually tapered; basal sclerite prominent.

Phallus paramere sheath dorsally about 48% the length of phallus; paramere sheath without ventral ornamentation; dorsal carina protruding, with apex swollen but slightly dorsoventrally flattened and pointing in an imaginary acute angle with the aedeagal tube. Ejaculatory apodeme in lateral view relatively straight, with broad dorsal carina along entire length. Subepandrial sclerite with triangular central unsclerotized area in basal 35% narrowing to

a parallel-sided gap in central portion; spines parallel-sided, blunt, densely distributed basally, apically, and along midline, sparse laterally.

Female genitalia. Undissected: Tergite 8 dark brown/black, with erect white hairs; sternite 8 dark brown with short brown hairs; lateral lobe setae strong, black; hypogynial valves with fine hairs concentrated medially. Cerci brown/black with pale setae; acanthophorite spines black.

Type Material. LECTOTYPE (here designated) ♂ labelled: "[rectangular white label] Auburn, Wn./ V-10 1932/ J. Wilcox, Col."; "[rectangular beige label] PARATYPE/ Lasiopogon/ willametti/ Cole & Wilcox"; "[rectangular beige label] FORM/ puyallupi/ Cole & Wilcox"; "[rectangular white label with asterix borders] JOSEPH WILCOX/ COLLECTION – 1981/ Gift to California/ Academy of Sciences". My lectotype label "[red and black bordered label] LECTOTYPE/ Lasiopogon puyallupi/ Cole & Wilcox 1938/ des. T.A. McKnight 2017" has been added. USNM.

PARALECTOTYPES (41 examined): **USA: WASHINGTON: King Co.,** Auburn [47.305 -122.193], 10.v.1932, J. Wilcox (14♂ 1♀ CAS, 2♂ USNM); Enumclaw [47.175 -122.029], 12.v.1932, J. Wilcox (10♂ CAS, 1♂ 1♀ [1 pr in cop] FISH); **Pierce Co.,** Buckley [47.172 -122.039], 14.vi.1932, J. Wilcox (2♂ CAS), 15.vi.1932, J. Wilcox (1♂ CAS); Mt. Rainier, Ipsut Creek Camp [46.9755 -121.828], 26.vi.1932, W.W. Baker (4♂ 1♀ CAS); Sumner [47.203 -122.248], 10.v.1932, J. Wilcox (1♂ CAS), 17.vi.1932, J. Wilcox (1♂ CAS, 1♂ FISH, 1♀ USNM)

Other Material Examined (193 specimens). **CANADA: BRITISH COLUMBIA:** Delta, Deas Island [49.125 -123.062], 26.iii.1983, R.A. Cannings (1♂ 1♀ RBCM), 6.iv.1984, R.A. Cannings (1♀ RBCM), 10.iv.1991, R.A. Cannings & H. Nadel (1♀ RBCM), 20.iv.1991, R.A. Cannings & H. Nadel (8♂ 1♀ RBCM), 12.v.1991, R.A. Cannings (1♂ 2♀ RBCM), 7.v.1997, R.A. Cannings (8♂ 2♀ CUAC); Dewdney, River Road South [49.144 -122.182], 19.v.1991, R.A. Cannings (1♂ RBCM); Fraser River, mouth of Hunter Creek [49.359 -121.575], 4.v.1989, R.A. Cannings (1♀ RBCM); Hope, Coquihalla River [49.383 -121.45], 13.vi.1995, R.A. Cannings (1♂ RBCM); Hope, Hunter Creek, at Highway #1 bridge, under RR bridge [49.358 -121.574], 23.v.1996, S.G.

Cannings (1♂ RBCM); Ladner [49.092 -123.095], 23.iv.1987, S.G. Cannings (2♂ CSUC), 18.v.1991, R.A. Cannings (7♂ 1♀ RBCM), 19.v.1991, R.A. Cannings (1♂ RBCM); Lillooet River, Meager Creek Hotsprings, terrace [50.576 -123.465], 19.vii.1988, C.S. Guppy (1♂ RBCM); Lillooet River, near John Sandy Creek [50.486 -122.944], 9.vi.1981, R.J. Cannings (1♂ RBCM); Meager Creek road, 16.v.1987, C.S. Guppy (1♂ RBCM); Miracle Beach Provincial Park [49.85 -125.094], 28.v.1988, S.G. Cannings (1♂ LACM); Tofino, Chesterman Beach [49.114 -125.893], 27.v.1994, R.A. Cannings (10♂ CSUC); Tofino, Wickaninnish Beach [49.013 -125.675], 16.v.1994, R.A. Cannings (1♂ 2♀ RBCM); Vancouver Island, Brooks Peninsula, Cape Cook Lagoon [50.2 -127.8], 2.viii.1981, R.A. & S.G. Cannings (1♂ 1♀ RBCM), R.A. Cannings (1♂ 6♀ [1 pr in cop] RBCM); Vancouver Island, Comox, Cape Lazo Road [49.68828 -124.87444], 2.v.2006, R.A. Cannings & R.G. Bennett (1♂ 1♀ RBCM). **USA: WASHINGTON: Clallam Co.,** Bogachiel River and Sol Duc River confluence, Hwy 110 jct Mora Rd [47.91311 -124.539], 23.vi.2010, R.A. Cannings (1♂ 1♀ RBCM); Bogachiel River, Highway 101 [47.892 -124.355], 31.v.1995, R.A. Cannings & H. Nadel (3♂ 1♀ RBCM); Forks [47.96 -124.393], 2.vii.1920, E.P. VanDuzee (2♂ 1♀ EMEC), 23.vii.1933, J. Wilcox (1♂ 2♀ CAS); Hoh River Campground, Hoh River [47.85856 -123.93828], 24.vi.2010, R.A. Cannings (1♂ RBCM), 25.vi.2010, R.A. Cannings (1♀ RBCM); Quillayute River County Park, trail to Quillayute River bank [47.91194 -124.58283], 23.vi.2010, R.A. Cannings (1♂ RBCM); **Cowitz Co.,** N Fork Toutle River, 10 mi E of Castle Rock, 1 mi S Hwy 504 jct Tower Rd [46.3477 -122.7053], 14.v.2015, T.A. McKnight (1♂ TAM); **Grays Harbor Co.,** W Fork Satsop River, Middle Satsop Road bridge [47.04472 -123.52361], 30.v.1995, R.A. Cannings & H. Nadel (5♂ 1♀ RBCM); **Jefferson Co.,** Hoh River Campground shore, upstream of Spruce Nature Trail [47.86206 -123.92175], 25.vi.2010, R.A. Cannings (1♂ RBCM); Hoh River Campground, Hoh River shoreline [47.85856 -123.93828], 24.vi.2010, R.A. Cannings (6♂ 1♀ RBCM), 25.vi.2010, R.A. Cannings (1♂ RBCM); Hoh River jct Canyon Creek, Upper Hoh Road [47.81 -124.07], 1.v.1995, R.A. Cannings & H. Nadel (4♂ 1♀ RBCM); Hoh River rainforest, 7.vii.1968, W.W.Wirth (1♂ USNM); Hoh River, Upper Hoh Road, 31.v.1995, R.A. Cannings & H. Nadel (9♂ 4♀ [1 pr in cop] RBCM); Hoh River, Upper Hoh Road 6.2 km E of Olympic NP boundary [47.84272 -123.96406], 24.vi.2010, R.A. Cannings (1♂ RBCM); Port Townsend [48.0825 -122.7622], 8.iv, A. Seaton (1♂ OSUC); Upper Hoh Road 7.9 km E of Olympic NP boundary [47.85214 -123.95128], 22.vi.2010, R.A. Cannings (2♂ RBCM); **King Co.,** Auburn [47.305 -

122.193], 10.v.1932, J. Wilcox (2♂ 6♀ [2 pr in cop] CAS, 2♂ 2♀ [1 pr in cop] EMEC); Enumclaw [47.175 -122.029], 12.v.1932, J. Wilcox (1♂ 1♀ [1 pr in cop] EMEC, 1♂ OSUC); Seattle [47.6064 -122.3308], 15.vii.1901, R.C. Osburn (1♀ OSUC); **Lewis Co.,** Ashford 2.5 mi SE, Nisqually River jct Skate Cr Rd. [46.7439 -121.9796], 17.v.2015, T.A. McKnight (1♂ 1♀ [1 pr in cop] TAM); **Mason Co.,** Fernwood, Skokomish River beach at Skokomish River Road mile 4 [47.31792 -123.20542], 7.vi.2009, J. Miskelly (3♂ RBCM); **Pierce Co.,** Electron, 18.v.1936, J. Wilcox (1♀ CAS); Electron, Puyallup River [47.0019 -122.1951], 6.vi.2009, J. Miskelly (1♂ RBCM), 11.vii.2014, T.A. McKnight (1♀ TAM); Mt. Rainier, Ipsut Creek Camp [46.9755 -121.828], 2.vii.1933, W.W. Baker (2♂ 1♀ CAS), 23.vii.1935, S.E. Crumb (2♂ CAS); N. Puyallup [47.199 -122.263], 8.v.1932, C.H. Martin (1♂ 1♀ [1 pr in cop] FISH); Orting, Puyallup River [47.08523 -122.20823], 4.vi.2009, J Miskelly (2♂ RBCM); Puyallup [47.199 -122.292], 2.v.1933, C.W. Getzendaner (1♂ CAS), 11.v.1933, C.W. Getzendaner (1♀ CAS), 13.v.1934, J. Wilcox (1♀ CAS), 23.iv.1935, W.W. Baker (1♀ CAS), 29.iv.1935, C.W. Getzendaner (1♀ CAS); Roy [47.005 -122.539], 29.iv.1932, R. Latta (2♂ CAS); Sumner [47.203 -122.248], 7.v.1932, C.H. Martin (1♂ ESUW), 8.v.1932, C.H. Martin (1♂ 1♀ FISH, 1♀ ESUW), 10.v.1932, R. Latta (3♂ 2♀ CAS), C.H. Martin (1♀ EMEC), J. Wilcox (1♂ 1♀ [1 pr in cop] FISH, 1♀ OSUC, 1♂ 1♀ RBCM, 1♀ USNM), 11.v.1932, C.H. Martin (1♂ EMEC), 12.v.1932, C.H. Martin (1♂ FISH, 1♂ LACM), 17.v.1932, C.H. Martin (1♂ 1♀ [1 pr in cop] FISH), 20.vi.1932 (1♂ FISH), 3.vi.1933, C.H. Martin (1♂ 1♀ FSCA), 8.v.1936, W.W. Baker (2♂ CAS), 16.v.1940, W.W. Baker (1♂ FSCA); **Skagit Co.,** Edison [48.565 -122.443], 5.vi.1968, (1♀ WSUC); **Thurston Co.,** Olympia, Pioneer Park, Deschutes River [46.99304 -122.88711], 6.vi.2009, J Miskelly (1♀ RBCM); Tumwater, Pioneer Park, Deschutes River [46.994 -122.8881], 15.v.2015, T.A. McKnight (3♂ 2♀ [2 pr in cop] TAM).

Type Locality. U.S.A.: Washington: King Co., Auburn.

Taxonomic Notes. Originally described as a subspecies of *L. willametti*. Original paratypes of *L. willametti* without the "Form puyallupi" labels that nevertheless belong to this taxon are listed in the Other Material Examined section, instead of as paratypes.

Etymology. No explanation given in the original description, but evidently named for the type locality near Puyallup, Washington and the Puyallup River.

Distribution (Fig. III.3). Nearctic; Canada: British Columbia and U.S.A.: Washington.

Phylogenetic Relationships. Member of the *bivittatus* section, *actius* group.

Natural History. Habitat: river banks and beach dunes (Fig. III.7b, likely also similar to III.6b). Perches on bare sand, cobble, fallen logs, or boulders; labels note "upper beach sand", "*Carex*/*Elymus* sand dunes", "river edge sand and cobbles", and "on log under bridge". Dates collected: Mar 26 to Aug 2, most in May. One female recorded as having prey, but it is missing.

***Lasiopogon ripicola* Melander**

Lasiopogon ripicola Melander, 1923. *Psyche* 30: 143–144.

Diagnosis. A medium-large grey species from rivers of the Columbia River basin of Washington and Idaho; setae mostly black, except mystax variable from white to black, short notal setae white, fine hairs on femur white; scutum tomentum greyish, with brown dorsocentral stripes; tergites with basal brown tomentum in lateral spots; apical 40–50% covered in grey tomentum. Epandrial halves slender, moderately curved in dorsal view; phallus dorsal carina protruding far past gonopore, with apex swollen and pointed inward to form an imaginary right angle with the aedeagal tube. Ovipositor dark brown/black, acanthophorite spines black.

Description.

Head. Face yellow-grey, vertex brown to grey. Ventral hairs (beard, labium, palps) white; mystax varies from completely yellowish-white to completely black, or mixed; setae of vertex and occiput black. Occipital bristles relatively straight, curved anterolaterally posterioir to frons;

lateral bristles short. Frontal setae reach apex of pedicel; orbital setae curved over eye margin; occelar setae indistinct amidst frontal setae.

Antennae. Black, F2+3 slightly reddish, with thin grey tomentum. Setae mostly black, a few short white hairs on scape, 1 short hair on F1. F1 moderately long, dorsal and ventral margins slightly bowed in near base; F2+3 long.

Thorax. Prothorax grey, with white hairs; postpronotal lobes brown, the lateral angle chestnut, hairs mixed white and black. Scutum tomentum grey to greyish-brown; dorsocentral stripes brown; acrostichal stripes dark grey. Acrostichal and anterior notal setae white, short, other notal setae black. Dorsocentral setae black; anteriors 3–5; posteriors 4–5; postalars 2–3; supra-alars 1–4; presuturals 2–3; posthumerals 1.Scutellar tomentum grey to greyish-brown; rim inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, abundant (6–13 on each half); short vertical hairs on uppermost edge of rim white.

Pleural tomentum dorsally brownish grey, ventrally grey. Katatergite setae mostly black (3–10), with 1–5 white bristles; katepisternal setae long, white; anepisternal setae 4–6, black, many short black hairs along dorsal margin and several long white hairs in posterioventral corner; anepimeron with 0–1 fine hairs.

Legs. Base color dark brown/black, covered in thin grey tomentum; bare at joints. No coxal peg. Coxae with long white setae; main bristles of legs black, fine hairs white except on tarsi 3–5. Ventral hairs on femur as long or slightly longer than femur width; dorsoapical bristles on profemur fine, indistinguishable from the surrounding hairs, 3–6; bristles on other femorae strong, short, mesofemur with 3–9, metafemur with 9–17. Protibia with ventral bristles about 2 times longer than tibial width; dense apicoventral patch of short setae on protibia yellow, no patch on metatibia. Claws chestnut over basal 70%, black apically.

Wings. Veins dark brown; membrane hyaline. Halter knob cream, without spot, stem dark brown.

Abdomen. Male. Tergite cuticle dark brown/black; thin brown tomentum on tergite bases, grey tomentum covers apical 40–50% of each tergite (80% of tergite 1) and extends anteriorly broadly on lateral margins and along midline to divide the brown into two lateral spots. Tergite 1 with 3–7 black and 1–4 gold lateral bristles; lateral hairs white, long (on tergite 1–3 as long as halter, on tergites 4–7 as long as scape + pedicel); dorsal setulae short, white. Sternite tomentum grey, hairs white.

Female. As in male, except lateral hairs of all tergites no longer than scape + pedicel, dorsal setulae black, lateral hairs on tergites 5–7 rarely black.

Male genitalia. Cuticle dark brown/black, with thin grey tomentum; setal brush dark brown, other hairs dark brown/black on hypandrium/gonocoxite complex and ventrolaterally on epandrium, white dorsomedially on epandrium and on cerci. Epandrium elongate, in lateral view the width about 42% the length, widest in basal third; apex rounded with ventral tooth. In dorsal view, medial margins of epandrium moderately curved at 32% from base, relatively straight apically, outer margins suddenly tapered at apex; basal sclerite present.

Phallus paramere sheath dorsally about 40% the length of phallus; paramere sheath without ventral ornamentation; dorsal carina protruding far past gonopore, with apex swollen but slightly dorsoventrally flattened and pointed inward to form an imaginary right angle with the aedeagal tube. Ejaculatory apodeme in lateral view moderately bent dorsally, with broad dorsal carina along entire length. Subepandrial sclerite with triangular central unsclerotized area in basal 30% narrowing to a parallel-sided gap in central portion; spines parallel-sided, blunt, distributed relatively evenly.

Female genitalia. Undissected: cuticle dark brown/black, with sparse fine white hairs; bristles on lateral lobes white; hypogynial valves long, mostly bare; cerci brown with pale setae (rarely dark brown); acanthophorite spines black.

Variation. Mystax color is unreliable in this species. Specimens from the core of the range (near Pasco, WA) have primarily white mystaces, whereas flies from the periphery (the eastern slopes of the Cascades, the Dalles, or southwestern Idaho) have primarily black mystaces. At the Snake River near the Washington–Idaho border we caught flies of all three phenotypes

(white/black/mixed) on the same beach, with no discernible differences in genitalia morphology or genetic sequencing.

Type Material. HOLOTYPE (examined) ♂ labelled: "[rectangular beige label] Wawawai/ Wash"; "[rectangular red label] TYPE/ Lasiopogon/ ripicola/ Melander"; “[rectangular white and green label] ALMelander/ Collection/ 1961”; “[rectangular beige label] Lasiopogon/ ripicola/ Mel.”; "[rectangular white label] USNMENT/ 00972436". USNM.

ALLOTYPE (examined) ♀ labelled: "[rectangular white label] Wawawai/ 20-v-11Wash"; "[rectangular salmon label] ALLOTYPE/ Lasiopogon/ ripicola/ Melander"; “[rectangular white and green label] ALMelander/ Collection/1961”; “[rectangular white label] USNMENT/ 01100254”. USNM.

PARATYPES (17 examined): **U.S.A.: WASHINGTON: Lincoln Co.**, Wilbur [47.757 -118.705], 5.v.1911, A.L. Melander (1♀ USNM); **Whitman Co.**, Pullman, 4.iv.1909, A.L. Melander (1♀ USNM), 24.iv.1909, A.L. Melander (USNM); Wawawai [46.581 -117.297], A.L. Melander (1♂ 1♀ USNM), 17.iv.1908, A.L. Melander (1♂ USNM), 23.iv.1909, A.L. Melander (1♀ USNM), 24.iv.1909, A.L. Melander (1♀ CNC, 4♂ 2♀ 1? USNM); **Yakima Co.**, N Yakima, 8.v.1903, E. Jenne (1♂ USNM), 19.v.1903, E. Jenne (1♀ USNM).

Other Material Examined (241 specimens). **U.S.A.: IDAHO: Ada Co.**, Boise, Barber Park, 43.56977 -116.13908, 17.iv.2014, T.A. McKnight (1♂ TAM); **Boise Co.**, Horseshoe Bend [43.904 -116.197], 18.v.1933, F.H. Shirck (1♂ 1♀ CAS); Horseshoe Bend, Payette River sandbank, 43.90385 -116.19717, 18.iv.2014, T.A. McKnight (15♂ 7♀ [7 pr in cop] TAM); **Canyon Co.**, Boise River @ Ft Boise Wildlife Area, 3 mi W of Parma, 43.80222 -117.00055, 23.iv.2014, T.A. McKnight (4♂ 3♀ [2 pr in cop] TAM); Boise River jct Hwy 95, 4 mi SE of Parma, 43.74877 -116.91538; 18.iv.2014, T.A. McKnight (6♂ 4♀ [3 pr in cop] TAM); Parma [43.802 -117.001], 13.v.1933, F.H. Shirck (1♂ CAS), 18.v.1933, F.H. Shirck (1♂ CAS); **Latah Co.**, Viola [46.838 -117.026], 27.v.1962, B.F. Finnigan (1♀ WSUC); **Nez Perce Co.**, Lewiston [46.451 -116.819], J.M. Aldrich (2♂ EMEC), 12.v.1901, J.M. Aldrich (1♂ CAS), 3.v.1904, J.M. Aldrich (1♂ 1♀ EMEC), 26.iv.1912, J.M. Aldrich (2♀ EMEC, 1♂ RBCM); Lewiston, 10 mi E

,16.iv.1981, J.B. Johnson (1♀ BEZA); Lewiston, 3 mi S [46.361 -117.060], 5.v.1970, W.F. Barr (1♂ 3♀ ESUW, 1♂ 1♀ RBCM); Spalding [46.451 -116.814], 24.iv.1949, M.T. James (1♂ WSUC); **OREGON: Hood River Co.**, Hood River [45.713 -121.516], 15.v.1917, F.R. Cole (3♂ FISH), 22.v.1917, F.R. Cole (1♂ FISH), 12.vi.1917, F.R. Cole (1♂ FISH), 22.vi.1917, F.R. Cole (1♂ FISH), 24.vi.1917, F.R. Cole (1♂ FISH); **Wasco Co.**, The Dalles [45.604 -121.191], 2.v.1927, H.A. Scullen (1♀ CAS); **WASHINGTON: Asotin Co.**, Snake River, opposite Clarkston, 3.v.1925, A.L. Melander (3♂ USNM); Snake River, sandy bank 1.6 mi S of Asotin, jct Hwy 129, 46.33185 -117.02672, 21.iv.2014, T.A. McKnight (3♂ 2♀ TAM); Snake River, sandy bank 4 mi S of Asotin jct Hwy 129, 46.30365 -117.00379, 21.iv.2014, T.A. McKnight (3♂ 4♀ [2 pr in cop] TAM); **Benton Co.**, Benton City, 6.v.1966, C.W. Sabrosky (1♂ USNM); Hanford Works, wash @640', sagebrush [46.4591 -119.542], 29.iv.1952, R.H. Whittaker (1♀ WSUC); **Chelan Co.**, Cashmere [47.5254 -120.472], 12.v.1935, C.W. Getzendaner (2♂ 1♀ CAS); **Franklin Co.**, Pasco [46.206 -119.037], 23.iv.1933, I. Wilcox (14♂ 5♀ 1? CAS, 2♂ 1♀ FISH, 1♂ 1♀ RBCM, 3♂ USNM), J. Wilcox (1♂ 1♀ BEZA, 37♂ 14♀ 3? CAS, 1♀ CNC, 2♂ 1♀ EMEC, 3♂ 2♀ FISH, 1♂ 1♀ LACM, 4♂ 4♀ MCZ, 4♂ 4♀ OSUC, 4♂ 1♀ RBCM, 1♂ 1♀ UCRC, 3♂ 4♀ USNM), 17.iv.1934, C.H. Martin (1♂ ESUW, 1♀ FISH, 3♂ 3♀ FSCA), D. Martin (1♂ FISH, 2♂ FSCA, 1♂ RBCM); **Garfield Co.**, Wawawai, 14 mi S [46.427 -117.324], 9.v.1958, D.W. Tuff (1♀ WSUC); **Okanogan Co.**, Chewuch River, N of Eight Mile Creek [48.609 -120.163], 23.v.1991, S.G. Cannings (3♂ 2♀ RBCM); **Whitman Co.**, Wawawai [46.581 -117.297], 24.iv.1909, W.M. Mann (1♂ MCZ), 1.v.1909, W.W. Mann (1♀ USNM), 30.iv.1961, M.T. James (1♂ 1♀ RBCM, 3♂ 2♀ WSUC), 4 (1♀ EMEC).

Type Locality. USA, Washington, Wawawai.

Taxonomic Notes. The holotype and allotype are not distinguished in the original text, but instead listed as “types”, i.e., syntypes. However, as a single male and single female, with the male (preferred gender for systematics in this genus) already labelled as “type”, we do not see the necessary ambiguity to justify designating a lectotype. Two specimens from Pullman bear the same paratype labels as the other paratypes and help the whole type series add up to the total noted in the original description; however, as these specimens were not included in the original

text, they therefore do not count as official paratypes. Black-mystaced specimens have frequently been identified as *L. willametti*, and the two species are both recorded from Boise, Idaho.

Etymology. No explanation given in the original description, but evidently from the Latin *ripa* = bank, *cola* = inhabitant of; like many *Lasiopogon* species, this one lives on the banks of rivers.

Distribution (Fig. III.3). Nearctic; USA, eastern Washington, western Idaho, and northeastern Oregon. A specimen with a locality label of "Alberta" has been referenced as this species in the literature (Adisoemarto 1967) and would be a far outlier, but the specimen is no longer confidently identifiable due to dermestid damage.

Phylogenetic Relationships. Member of the *bivittatus* section, basal to the rest of the *willametti* group.

Natural History. Habitat: sandy riverbanks. Perches on bare sand adjacent to low, scraggly vegetation (Fig. III.7a), rarely on boulders or cobble. Dates collected: April 4 to June 24, most in late April. Three males and three females (including a female in a mating pair) with prey: three Muscidae, one Sarcophagidae, one Hydroptilidae, one Brachycentridae.

***Lasiopogon sierra* McKnight sp. nov.**

Diagnosis. A medium-large greyish brown species from the eastern and northern Sierra Nevada; mystax and most setae of head and thorax black; white hairs on antennal scape, pedicel hairs mixed white and black; dorsocentral stripes brown on grey or brown scutum; tergites with basal brown tomentum in broad bands or lateral spots, grey over apical 30–50% of each tergite and occasionally along midline. Epandrium moderately curved medially; phallus paramere sheath with a pointed triangular apical projection on dorsal carina parallel to aedeagal sheath. Ovipositor dark brown/black; acanthophorite spines black.

Description.

Head. Face silvery grey, vertex brown-grey. Ventral hairs (on beard, labium, palps) white; mystax and dorsal setae black (a few hairs along oral margin of mystax rarely white). Occipital bristles fine, gradually curved anteriorly, longest posterior to frons; frontal and orbital setae dense, long (reach basal third of F1) but shorter than ocellar bristles.

Antennae. Dark brown, with thin grey tomentum. Setae on scape all or partially white, on pedicel mixed white and black, no hairs on F1. F1 widest apically with ventral and dorsal margins straight; F2+3 long.

Thorax. Prothorax grey, with white hairs; postpronotal lobes grey, the lateral angle yellowish brown, hairs white, rarely dark brown. Scutum tomentum grey to chocolate brown; dorsocentral stripes brown, acrostichal stripes indistinct. Bristles and fine hairs of scutum black. Anterior dorsocentral bristles 4–5; posteriors 3–5; postalars 1–3, with several shorter hairs; supra-alars 2–3; presuturals 2–3; posthumerals 0–1. Scutellar tomentum grey; rim slightly inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, abundant (5–9 on each half), mixed with many finer hairs; short vertical hairs on uppermost edge of rim black or white.

Pleural tomentum grey to brownish grey. Katatergite setae black, long, 6–10, with a few short white hairs; katepisternal setae white, sparse; anepisternal setae 6–10, black, several short black hairs along dorsal margin, a few white hairs in posteroventral corner; anepimeron with 5–6 fine white setae.

Legs. Cuticle dark brown/black, covered in grey tomentum except bare femur joints. No coxal peg. Coxae with white setae; fine hairs on femur, tibia, and first tarsomere white; hairs black on tarsi 2–5; bristles black except a few at femur base. Ventral hairs on femur as long or slightly longer than femur width; dorsolateral bristles on profemur 8–9, black, fine amidst long hairs; on mesofemur and metafemur shorter and more robust, 3–5 and 10–11 respectively. Protibia with ventral bristles about 2 times longer than tibial width; dense apicoventral patch of short setae on protibia pale yellow, dark brown on metatibia. Claws chestnut over basal half, black apically.

Wings. Veins brown; membrane hyaline but brown when viewed obliquely. Halter knob cream, without spot, stem light brown.

Abdomen. Male. Tergite cuticle dark brown/black; thick brown tomentum on tergite bases, bands of grey tomentum cover apical 30–50% of each tergite and lateral margins, tergites rarely greyish along midline to divide brown into two lateral spots; segment 1 is fully covered in grey. Tergite 1 with 3–8 black and 1–3 white lateral bristles; lateral setae on tergites white, on tergites 1–3 as long as halter, on tergites 4–7 as long as scape + pedicel; dorsal setulae black, short.

Female. As in male, except brown tomentum usually in definite spots widely spaced; lateral hairs on tergites 4–7 black, as long as scape, erect.

Male genitalia. Cuticle dark brown/black, covered in thick grey tomentum but thin medially on hypandrium; setal brush dark brown, setae on epandrium and gonocoxite long, erect, black; cerci with white hairs. Epandrium elongate, in lateral view the width about 43% the length, widest apically; apex rounded with strong ventral tooth. In dorsal view, epandrium appears tapered, wider at base than apex, medial margins of epandrium moderately curved, curvature starts about 42% from base; basal sclerite present.

Phallus paramere sheath dorsally about 43% the length of phallus; paramere sheath with a very short ventral flange at base; dorsal carina flat, with a long and pointed triangular apical projection parallel to aedeagal sheath, leaving a wide, deep gap between equidistant apices. Ejaculatory apodeme in lateral view moderately to strongly bent dorsally, with broad dorsal carina along entire length. Subepandrial sclerite with triangular central unsclerotized area in basal 25% narrowing to a slender gap for another 50%; spines parallel-sided, blunt, moderately and evenly distributed.

Female genitalia. Undissected: Cuticle of tergite 8 polished dark brown/ black; sternite 8 dark brown or reddish brown, especially near base of hypogynial valves, which are short and wide. Short fine erect hairs abundant, white everywhere except occasionally on hypogynial valves; cerci with white hairs, lateral lobes with black bristles; acanthophorite spines black.

Type Material. HOLOTYPE (here designated) ♂ labelled: "[rectangular white label] Verdi Nev./ Washoe Co./ VI-18-1964"; "[rectangular beige label] M. E. Irwin/ Collector"; "[rectangular white label] UCR"; "[rectangular white label] FISH". My type label "[red and black bordered label] HOLOTYPE/ Lasiopogon sierra/ des. T.A. McKnight 2017" has been added. USNM.

Other Material Examined (99 specimens). **U.S.A.: CALIFORNIA: Alpine Co.**, Carson River, 8 mi S Markleeville [38.615 -119.696], 22.vi.1962, J. Powell (1♂ FISH); E Fork Carson River, Hwy 89 [38.676 -119.737], 21.vi.2006, B. Kondratieff, R. Baumann (1♂ 1♀ [pr in cop] CSUC); **Butte Co.**, Oroville [39.508 -121.578], 30.iv.1927, H.H. Keifer (1♂ FISH); **Calaveras Co.**, Camp Wolfboro [38.412 -120.076], 1.vi.1941, T. Aiken (2♂ 1♀ FISH); **El Dorado Co.**, Sand Flat, 5300' [38.763 -120.326], 12.vi.1930, G.W. Clurrey (1♂ UCRC); Silver Fork American River at China Flat campground, 3 mi S of Kyburz, 38.75256 -120.26611, 7.vi.2013, T.A. McKnight (2♂ 2♀ [2 pr in cop] TAM); South Fork American River, 2 mi W of Riverton, 38.76734 -120.48353, 7.vi.2013, T.A. McKnight (1♂ TAM); **Mono Co.**, Lee Vining Creek, Hwy 120 [37.939 -119.123], 22.vi.2006, B. Kondratieff, R. Baumann (1♂ CSUC); Walker [38.521 -119.477], 18.vi.1963, J. Wilcox (1♂ 2♀ FISH); **Nevada Co.**, no loc, 25.viii.1974, D. Castleman (1♂ BEZA); Boca [39.384 -120.092], 17.vi.1964, D.F. Veirs (1♂ RBCM, 1♂ UTST); **Plumas Co.**, Blairsden, Feather River [39.777 -120.619], 16.v.1982, D.L. Wagner (1♀ EMEC), J. Powell (2♂ EMEC), M. Buegler (1♀ EMEC), 21.v.1982, J.A. DeBenedictis (1♂ 1♀ EMEC); Portola [39.809 -120.468], 5.v.1960, M. Wasbauer (1♂ FISH); **Shasta Co.**, Little Cow Creek, Hwy 299 turnoff 4.2 km SW jct Oak Run Road, 40.73917 -122.071, 25.v.1995, R.A. Cannings, H. Nadel (1♂ RBCM), 14.v.2012, T.A. McKnight (2♂ 2♀ TAM); **Sierra Co.**, Hobart Mills, 7 mi N [39.485 -120.238], 30.vi.1965, J. Wilcox (2♂ 2♀ CAS); Independence Lake [39.4308 -120.3282], 25.vi.1974, R.D. Moon (1♂ BEZA); **Solano Co.**, Davis, 27.iv.1951, R.C. Bechtel (1♂ FISH), 22.iv.1959, J.R. Powers (1♂ FISH); Putah Canyon, 13.iv.1950, R.M. Bohart (1♂ FISH); **Trinity Co.**, Carrville, 2400–2500' [41.067 -122.699], 2.1934, G.E. Bohart (1♂ FSCA); Douglas City campground, Trinity River, 7 mi S of Weaverville, 40.64661 -122.95591, 24.v.2016, T.A. McKnight (2♂ TAM); Hayfork, Hayfork Creek near Forest Ave, 40.54509 -123.16681, 24.v.2016, T.A. McKnight (1♂ TAM); Hayfork, Hayfork Creek @ Post Office footbridge, 40.55231 -123.18197, 24.v.2016, T.A. McKnight (1♂ TAM); Hayfork, Wildwood

Rd, 3 mi S jct Hwy 3, 40.52474 -123.08882, 24.v.2016, T.A. McKnight (1♂ TAM); **NEVADA: Washoe Co.**, Mogul, Truckee River @ Mayberry Crossing Park, 39.50262 -119.89737, 13.v.2012, T.A. McKnight (2♂ 1♀ [1 pr in cop] TAM), Patrick, 16.vi.1964, C.R. Kovacic (3♂ FISH), D.F. Veirs (1♀ UTST), F.D. Parker (1♂ FISH), M.E. Irwin (3♀ FISH), R.D. Sharp (2♀ BEZA), R.M. Bohart (3♂ FISH, 1♀ UTST), S.G. Seminoff (1♂ FISH); Reno, 27.vi.1927, E.P. Van Duzee (1♂ FISH), 3.iv.1959, F.D. Parker (1♂ FISH); Verdi, 26.vi.1962, R.L. Westcott (1♂ 1♀ EMEC), R.M. Bohart (1♂ 2♀ FISH), 18.vi.1964, A. Gillogly (2♂ 1♀ FISH), C.N. Slobodchikoff (4♂ 4♀ FISH), D.F. Veirs (1♂ UTST), F.D. Parker (1♂ 1♀ FISH), M.E. Irwin (4♂ 5♀ [1 pr in cop] FISH), P. Richerson (1♂ FISH), R.E. Scott (1♀ FISH), R.M. Bohart (1♂ FISH), S.G. Seminoff (1♂ 1♀ FISH), 27.vi.1966, E.E. Grissell (1♀ BEZA), 14.vii.1967, R.L. Westcott (1♂ FISH); Verdi, Truckee River @ US-40 bridge, Crystal Peak Park, 39.51397 -119.99689, 13.v.2012, T.A. McKnight (3♂ 1♀ TAM).

Type Locality. U.S.A.: California: Washoe Co., Verdi.

Taxonomic Notes. Included in Cannings (2002) as L. *biv-2* sp. nov.

Etymology. Refers to the distribution along the Sierra Nevada; *L. sierra* was a manuscript name of Wilcox.

Distribution (Fig. III.3). Nearctic; eastern and northern slopes of Sierra Nevada.

Phylogenetic Relationships. Member of the *bivittatus* section, *drabicola* clade. Based on morphology, this species is likely sister to *L. odontotus* sp. nov.

Natural History. Habitat: mountain riverbanks. Found perching on both bare sand near the water and on boulders in and along the water's flow (Fig. III.8a, III.8b). Dates collected: April 3 to August 25, most in May and June. One male and one female (part of a mating pair) with prey: Isoptera and Trichoptera c.f. Rhyacophilidae.

***Lasiopogon tumulicola* McKnight sp. nov.**

Diagnosis. A medium-sized dark species from coastal dunes of Oregon and Washington; mystax black, thoracic setae mostly black, postpronotal lobe hairs black; thoracic tomentum grey with strong dorsocentral stripes; femur basally with white setae and thin grey tomentum, apical 40% black haired and cuticle polished; tergites with dark brown/black cuticle subshining basally, grey tomentum bands cover apical 10–30% and lateral margins broadly; lateral bristles on tergite 1 mostly dark (7–8). Epandrium polished dark brown/black, in dorsal view of moderate width, coming to sharp apex, medial margins moderately concave; apex strongly concave from dorsoapical corner to ventral subapical tooth. Ovipositor black; acanthophorite spines black.

Description.

Head. Face with silver-grey tomentum, vertex sparse grey under setae patches, subshining otherwise. Beard and labial hairs white, sometimes tinged yellowish; myxtax and all other setae black. Occipital bristles relatively fine and long; those behind the dorsomedial angle of the eye the longest, moderately curved anterolaterally; lateral and ventral bristles shorter, straighter. Frontal setae fine, long, and erect, reach midpoint of F1; orbital setae also fine and long, slanting over eye margin.

Antennae. Black, slightly lighter at base of F1. Setae black; F1 sometimes with a seta. F1 long, spindle shaped, widest at midpoint.

Thorax. Prothorax grey, with white hairs; postpronotal lobes grey, the lateral angle yellowish red, hairs all brownish hairs. Scutum tomentum slate grey, sometimes with a brownish tinge, especially on sides. Dorsocentral stripes distinct: dark brown, edged in yellow; acrostichal stripes absent. Notal and acrostichal setae black, long (60% as long as bristles); dorsocentral bristles fine, black; anteriors 4–5, can be hard to distinguish from surrounding hairs, 3–4 posteriors. Postalars 2–3, with about 4 long surrounding hairs; supra-alars 2–3 with a few short hairs; presuturals 2–3; posthumerals 1. Scutellar tomentum grey/greyish brown; rim inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, abundant (10+ on each side) and mixed with many other long hairs. Short vertical hairs on uppermost edge of rim black.

Pleural tomentum grey to brownish grey. Katatergite bristles black, 8, with a few short fine white hairs; katepisternal setae fairly long, wavy, white; anepisternal setae 14+, mostly black with a few white hairs ventrally and a patch of short black setae along dorsal edge; anepimeron with 5 fine white setae.

Legs. Cuticle dark brown/black, chestnut at femur-tibia joint and trochanters; tomentum on coxae grey, sparse grey on basal 60–70% of femur, shining black elsewhere. No coxal peg. Coxae with long straw/white setae; bristles of legs black, hairs on basal 60–70% of femur white, elsewhere black. Ventral hairs on femur longer than femur width; lateral hairs erect on outside face, reclinate on inside; dorsolateral bristles long, fine, almost indistinguishable from surrounding hairs, on profemur, at least 10+ dorsolateral bristles on profemur, mesofemur with 3–5, metafemur 8–13, colored as with the shorter hairs. Protibia with ventral bristles 3–4 times longer than tibial width; dense apicoventral patch of short setae on protibia yellow, on metafemur black. Claws chestnut over basal half, black apically.

Wings. Veins dark brown; membrane hyaline, very pale brown when viewed obliquely. Halter yellow/brown; knob without dark spot.

Abdomen. Male. Tergite cuticle dark brown/black. Very thin brown tomentum on tergite bases, extensively lacking so the dark cuticle shines through; bands of grey tomentum cover apical 10–30% of each tergite (segment 1 is half covered), and broadly over lateral margins. Tergite 1 laterally with 7–8 black bristles and 2–3 white/yellow bristles; lateral setae on tergites long, erect, white; on tergites 2–4 setae longer than F1, on tergites 1 and 5–7 as long as scape+pedicel; dorsal setulae brown, fine. Sternite tomentum grey, hairs white.

Female. Tergite bases have thicker brown tomentum; black bristles on side of tergite 1 more abundant (8–11).

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle polished dark chestnut/black, entirely devoid of tomentum; with dark brown/black hairs, setal brush black. Epandrium elongate, moderately slender, in lateral view the width 50% the length, with dorsal and ventral margins parallel; apex strongly concave from dorsoapical corner to sharp subapical

ventral tooth. In dorsal view, epandrium moderately concave, curvature starts about 35% from base, each lobe tapered, wide set; basal sclerite prominent.

Phallus paramere sheath dorsally about 35% the length of phallus; paramere sheath with sharp ventral subapical tooth; dorsal carina a straight flat fin with shallow sharp point apically parallel to gonopore, leaving a narrow gap between the apices. Ejaculatory apodeme in lateral view long, slender, moderately bent in basal quarter, dorsal carina broad. Subepandrial sclerite U-shaped, central unsclerotized area shaped like a tall bottle over basal 87%; spines parallel-sided, blunt, densely and evenly distributed, apical spines relatively erect.

Female genitalia. Undissected: Hairs white, erect. Cuticle dark brown/black, narrow pale band at apex of tergite 8, and sometimes reddish brown at base of sternite 8; hypogynial valves long, black, with a few hairs basally; cerci brown with pale setae; acanthophorite spines black.

Type Material. HOLOTYPE (here designated) ♂ labelled: "[rectangular white label] USA; OR; Lincoln Co./Newport, S. side/Yaquinna R. mouth; Dunes/E. of S. Jetty Road/8 MAY 1995/R.A. Cannings & H. Nadel/RC95-9"; "[rectangular white label] sand dunes with Elymus,/Lupinus, Fragaria/15:40-16:40 PDT". My type label "[red and black bordered label] HOLOTYPE/ Lasiopogon tumulicola/ des. T.A. McKnight 2017" has been added. USNM.

Other Material Examined (91 specimens). **USA: Oregon: Clatsop Co.**, Warrenton [46.155 -123.963], 6.v.1947, J.E. Davis (1♀ FSCA); **Lane Co.**, Baker Beach, dunes behind, 44.0853 -124.1178, 27.vi.2012, J.D. Pinto (1♀ UCRC); Florence 1 km N [43.991 -124.115], 3.vi.1991, M.E. Irwin (1♂ 2♀ INHS); Sutton Creek campground, Sutton Creek near vista point, 6 mi N of Florence, 44.06864 -124.12355, 21.vi.2013, T.A. McKnight (2♂ 1♀ TAM); Taylor dunes by lake [43.864 -124.143], 26.iv.1998 (2♂ 1♀ RBCM); **Lincoln Co.**, Gleneden Beach, NW tip of Salishan Spit, 44.92008 -124.02694, 17.v.2012, T.A. McKnight (1♂ TAM); Hidden Lake, open sandy area 0.2 mi W, 44.456665 -124.08055, J.D. Pinto (3♂ 1♀ UCRC), 4.vi.2011, J.D. Pinto (2♂ UCRC), 23.iv.2012, J.D. Pinto (1♂ 2♀ UCRC); Newport [44.659 -124.058], 8.vi.1925, E.C. Van Dyke (1♂ 1♀ EMEC), 8.vi.1925, E.P. Van Duzee (1♂ 2♀ EMEC), 24.v.1931, J. Wilcox (2♂ CAS), 22.v.1932, J. Wilcox (1♂ 1♀ CAS), 5.vi.1932, J. Wilcox (1♂ EMEC, 1♂ MCZ, 1♂ USNM, 1♂ WSUC), R.E. Dimick (1♀ CAS), 12.v.1935, S.E. Crumb (1♂ 3♀ CAS, 1♀ USNM),

J. Wilcox (1♂ CAS, 1♂ 1♀ FISH, 1♂ RBCM, 1♂ USNM); Newport, S side Yaquinna River mouth, dunes E of S. Jetty Road [44.613 -124.069], 8.v.1995, R.A. Cannings & H. Nadel (2♂ 3♀ RBCM); Newport, South Beach State Park trailhead, 44.60146 -124.06497, 17.v.2012, T.A. McKnight (1♂ TAM); Newport, South Beach State Park, dunes S of Yaquina bay jetty, 44.61238 -124.07021, 21.vi.2013, T.A. McKnight (1♂ TAM); Waldport [44.4333 -124.0836], 5.vi.1925, E.P. Van Duzee (1♀ EMEC), 4.vi.1941, Schuh & Gray (1♀ RBCM), 7.vi.1942, R.E. Rieder (1♀ EMEC, 1♂ FISH, 1♂ 1♀ FSCA, 1♀ RBCM), 22.vi.1975, J. Powell (1♀ EMEC); **Tillamook Co.**, Bayocean Peninsula, paths W of parking lot at S tip, 45.52013 -123.95093, 18.v.2012, T.A. McKnight (4♂ 2♀ [1 pr in cop] TAM); Nehalem Bay, 3 mi S Manzanita [45.6641 -123.9345], 7.vii.1971, J.R. Powers (1♂ 3♀ CAS); Pacific City, Bob Straub State Park, dunes W of parking lot, 45.19247 -123.96828, 18.v.2012, T.A. McKnight (2♂ TAM); **Washington: Grays Harbor Co.**, Westport [46.898 -124.129], 28.v.1933, C.H. Martin (1♂ FSCA); Westport, dunes S of lighthouse [46.898 -124.129], 16.v.1994, R.A. Cannings (2♂ RBCM); **Pacific Co.**, Long Beach [46.353 -124.063], 19.v.1977, V.F. Lee (1♂ CAS); Nahcotta [46.501 -124.059], 28.v.1953, T. Kincaid (1♀ WSUC); Ocean Park [46.490 -124.058], 2.vi.1954 (1♂ RBCM), 17.vi.1956, M.T. James (1♂ WSUC), 18.vi.1956, M.T. James (1♂ WSUC), 20.vi.1956, M. James, H. James (1♂ 1♀ WSUC), 21.vi.1956, M.T. James (2♀ RBCM, 2♂ WSUC), M. James, H. James (4♂ 1♀ WSUC), 28.vi.1956, M.T. & H. James (1♂ RBCM), 30.vi.1957, M.T. James (1♂ WSUC); Seaview, beach dunes at end of 38th Pl, 46.33028 -124.06361, 30.v.1995, R.A. Cannings (1♂ 3♀ RBCM).

Type Locality. U.S.A.: Oregon: Lincoln Co., Newport, S side Yaquinna River mouth, dunes E of South Jetty Road.

Etymology. From the Latin *tumulus*, meaning hillock or mound of earth, and *cola* meaning inhabitant of; masculine noun in apposition; named to reference the dune-perching behaviour of this species, and as a translation of the Cornish surname Knowles ("dweller by the knoll") in honor of the first author's PhD advisor Dr. L. Lacey Knowles.

Distribution (Fig. III.2). Nearctic; coastal dunes in Oregon and southern Washington.

Phylogenetic Relationships. Member of the *bivittatus* section, *bivittatus* species group; sister to *L. canningsi* sp. nov.

Natural History. Habitat: Coastal beaches and dunes. Usually perches on the bare sand next to sparse vegetation, or in paths through the dunes (Fig. III.6a). Once, at Sutton Creek, several dozen individuals were found perching on large logs (1 m diameter) in or next to a slow stream; no individuals were found on the dunes themselves at that site. Frequently co-occurs with *L. actius*, but usually perches on the lee-side of the foredune and in the rest of the backdune field whereas *L. actius* usually perches on the sea-side and top of the foredune. Recorded flight dates: April 23 to July 7, most from late May through June.

***Lasiopogon wilcoxi* McKnight sp. nov.**

Diagnosis. A small dark species from southern California and northern Baja California, with mystax black, thoracic tomentum brown to grey with clear dorsocentral stripes, thoracic setae mostly black with hairlike bristles, legs black. Tergite tomentum reduced: male dorsum completely shining black cuticle with grey tomentum only along lateral edges and at apical posterior corners; female with sparse straight bands of basal brown and apical grey tomentum, cuticle subshining throughout. Epandrial halves with straight medial margins in dorsal view; phallus paramere sheath dorsal carina coming to a shallow and wide apical point. Ovipositor dark brown except pale yellow/red hypogynial valves and sometimes pale sternite 8; acanthophorite spines black.

Description.

Head. Face and vertex with grey-brown tomentum, face lighter than vertex; small shining black triangle directly behind antennae. Mystax, frontal and occipital setae black; beard and labial setae white. Occipital bristles moderately long and curved, those behind the dorsomedial angle of

the eye and most curved; lateral and ventral bristles shorter, straighter. Frontal setae fine and short; orbital setae longer, extend over the edge of the eye.

Antennae. Black, with black setae; F1 never with setae. F1 short, truncate, widest at midpoint, with relatively long arista.

Thorax. Prothorax grey/brown, hairs white; postpronotal lobes whitish grey, lateral angle ferruginous, hairs white. Scutum tomentum steel-grey to brown; dorsocentral stripes dark brown; acrostichal stripes absent, but space between dorsocentral stripes usually somewhat darker than outside stripes. All setae on scutum black; anterior dorsocentral bristles 5–6mm, relatively fine and mixed with finer setae; posteriors 4–5; postalars 2–3, with about 4 shorter hairs; supra-alars 2; presuturals 2–3; posthumerals 0–1. Scutellar tomentum grey, from silvery to brownish; two semi-circular wrinkles on disc inside dorsal edge; apical bristles long, black, abundant (usually 8–10 on each side) and mixed with many other long hairs.
Pleural tomentum brown/grey. Katatergite bristles black, 6–8 with a few shorter white hairs; katepisternal setae sparse, moderately long, white; anepisternal setae black, 5–8 moderately strong and with several short black hairs on dorsal margin of sclerite; anepimeron without hairs.

Legs. Base color black; tomentum uniform faint grey over all but trochanter and base of femur, which are shining black. No coxal peg. Bristles on legs black, finer setae mostly black, except long erect white hairs on basal 2/3 of femur. Ventral hairs on femur longer than femur width; dorsolateral bristles faint, inconspicuous among surrounding finer hairs, 5–6 on profemur; longer on mesofemur (3–5) and metafemur (8–12). Protibia with ventral bristles about 3 times longer than tibial width; dense apicoventral patch of short setae on protibia yellow. Claws reddish brown basally, apically black.

Wings. Veins dark brown; membrane transparent, faintly brown, tint stronger when viewed obliquely. Halter pale yellow, with slight brownish tinge but not spot; stem dark brown.

Abdomen. Male. Cuticle dark brown/black, tergites (except tergite 1) bare and shining dorsally with pale grey-brown tomentum along lateral edges and lateral corners of posterior edges; tergite

1 with light grey tomentum covering all but narrow anterior dorsal edge. Tergites 1–4 with abundant erect fine white lateral setae; tergites 5–7 with mostly short recumbent black setae; dorsal setuale black. Lateral bristles on first tergite 6–7, mostly black (2–6). Sternite tomentum grey, hairs white.

Female. Grey tomentum bands cover apical 30–50% of each tergite, basal tomentum bands brown; all tomentum thin, with brown/black cuticle shining through, especially medially.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown/chestnut; epandrium covered in thin grey tomentum except polished along inside dorsal margin and at base, hypandrium complex bare; terminalia with short white hairs, setal brush dark brown. Epandrium elongate, in lateral view the width about 40% the length, widest apically, with dorsal and ventral margins straight for basal half, then curving ventrally to rounded apex. In dorsal view, medial margins straight and parallel; basal sclerite present but weak medially.

Phallus paramere sheath dorsally about 55% the length of phallus; paramere sheath without ventral ornamentation; dorsal carina comes to a shallow, wide, and rounded apical point widely separated from the aedeagal tube. Ejaculatory apodeme in lateral view gently bent dorsally in basal third and slightly recurved apically, with moderately broad dorsal carina. Subepandrial sclerite with triangular central unsclerotized area in basal 58%, relatively narrow; spines sparsely distributed, parallel-sided and blunt only at apex of sclerite, sharply tapered elsewhere.

Female genitalia. Undissected: Hairs white, abundant, erect. Tergite 8 dark brown/black, occasionally with a pale brown apical ring; sternite 8 usually dark brown/black, sometimes paler apically; lateral lobe setae weak; hypogynial valves pale brown/tan with fine hairs. Cerci brown/black with pale setae; acanthophorite spines black.

Type Material. HOLOTYPE (here designated) ♂ labelled: "[rectangular white label] CALIF., River./ Co. 8 mi. E./ Sunnymead"; "[rectangular white label] E. M. Fisher/ coll. III-17-66"; "[rectangular white label] FISH". My type label “[red and black bordered label] HOLOTYPE/ Lasiopogon wilcoxi/ des. T.A. McKnight 2017” has been added. USNM.

PARATYPES (129 specimens designated): No loc, M.C. Van Duzee (1♂ EMEC); **MEXICO: Baja California Norte:** 7 mi S Tecate, [32.501 -116.598], 25.iii.1968, E.M. Fisher (3♂ 4♀ FISH); **USA: California: Los Angeles Co.,** Bouquet Canyon, [34.526 -118.442], 22.iii.1941, J. Wilcox (6♂ 7♀ CAS), 23.iii.1941, J. Wilcox (1♂ 1♀ BEZA, 1♀ FISH, 1♂ 1♀ RBCM, 1♂ 1♀ UCRC); Mint Canyon Forest Camp, [34.4378 -118.4320], 10.v.1941, J. Wilcox (1♀ CAS); Mt. Wilson, Opids Camp, [34.255 -118.095], 14.v.1937, J. Wilcox (7♂ 2♀ CAS, 1♂ RBCM); San Dimas Canyon, [34.163 -117.769], 27.iii.1941, J. Wilcox (1♂ CAS); Santa Monica Mts, 14.iii.1953, A. Ebeling (1♀ EMEC); Santa Monica Mts, Calabasas Highlands, [34.127 -118.641], 2.iii.1972, E.M. Fisher (1♂ 1♀ ESUW, 7♂ 3♀ FISH); Santa Monica Mts, Cold Creek at Stunt Rd, [34.095 -118.649], 20.iv.1974, P.A. de Moraes (1♂ 1♀ FISH); Sierra Madre, [34.178 -118.041], 17.iii.1941, J. Wilcox (1♀ CAS); Soledad Canyon, 4 mi W Soledad Forest Station, [34.439 -118.312], 27.iii.1978, E.M. Fisher (2♂ 3♀ FISH); Upper Stone Canyon, [34.1244 -118.4550], 22.iv.1954, W. McDonald (1♂ FSCA); **Orange Co.,** Black Star Canyon [33.769 -117.682], 20.iii.1967, R.J. Hamton (1♀ FISH); **Riverside Co:** Banning, 4000', [34.008 -116.907], 14.v.1953, J. Wilcox (2♂ 1♀ CAS); 5 mi E Hemet, [33.762 -116.883], 18.iv.1962, E.M. Fisher (1♂ 1♀ FISH); Idyllwild, [33.7430 -116.7130], 28.v.1979, J.W.B. (1♂ SDMC); 7 mi E Sunnymead, [33.985 -117.107], 9.v.1964, P.A. Rauch, (1♀ UCRC), M.E. Irwin (1♂ UCRC); 8 mi E Sunnymead, [33.9416 -117.0340], 12.iv.1958, E.I. Schlinger (1♂ FSCA), 24.iii.1962, E.I. Schlinger (2♂ RBCM, 4♂ UCRC), 18.iii.1964, M.W. Stone (1♂ 1♀ CAS), 17.iii.1966, E.M. Fisher (5♂ 3♀ FISH), 7.iii.1967, J. Wilcox (4♂ CAS, 1♀ ESUW), 9.iv.1971, E.M. Fisher (5♂ 2♀ FISH); Little San Gorgonio Creek at Potrero Blvd bridge, 2 mi NW of Beaumont, 33.9411 -117.0156, 9.iii.2014, T.A. McKnight (1♂ [EtOH] TAM); Noble Creek at Bogart County Park, 5 mi N Beaumont, 33.9974 -116.9528, 10.iii.2014, T.A. McKnight (1♂ 1♀ TAM); Noble Creek at Elm Ave, 1 mi NW of Beaumont, 33.9459 -116.9821, 9.iii.2014, T.A. McKnight (1♂ [EtOH] TAM); 6 mi N Temecula, 15.iii.1963, J. Powell (1♂ RBCM); **San Bernardino Co:** Cajon Pass, summit, [34.3290 -117.4490], 6.v.1956, J. Wilcox (2♂ CAS); Lake Gregory, [34.2420 -117.2770], 31.v.1964, M.W. Stone (4♂ 2♀ CAS, 1♂ 2♀ FISH); 1 mi S Mojave River Forks, [34.3410 -117.2610], 8.v.1982, E.M. Fisher (1♀ FISH); Sheep Creek Canyon, [34.3570 -117.6130], J.C. and E.M. Hall (1♂ 1♀ FISH), 1.v.1946, A.L. Melander (1♂ USNM); **San Diego Co:** 4.5 mi W Ranchita, Hwy S-22, near Warner Springs, [33.2180 -116.5880], 22.iv.1979, E.M. Fisher (2♂ FISH); **Ventura Co:** Moorpark, [34.2760 -118.8770],

22.iv.1941, M.W. Stone (3♂ 2♀ CAS); Sespe Wildlife Area nr. Dough Flat, [34.5230 -118.8940], 15.v.1971, UCR Field Entomology (1♂ UCRC); Tapo Canyon, Santa Susana, [34.3070 -118.7210], 3.v.1964, M.E. Irwin (1♂ UCRC).

Type Locality. U.S.A.: California: Riverside Co., 8 miles E of Sunnymead.

Taxonomic Notes. This species was included in Cannings 2002 as "*L. biv-3* sp. nov."

Etymology. Named for Joseph Wilcox, well known student of the Asilidae who revised the Nearctic *Lasiopogon* in the 1930s and collected thousands of specimens of this genus during his career.

Distribution (Fig. III.3). Nearctic; USA, foothills of southern California and northern Baja California.

Phylogenetic Relationships. Member of the *bivittatus* section, sister species to *L. zonatus*, likely in a position basal to the *drabicolum* group.

Natural History. Habitat: mid-elevation sandy river banks. Caught perching on bare sand adjacent to willows in dry washes (Fig. III.7f). Dates collected: March 2 to May 31, with most in late March and early April.

***Lasiopogon willametti* Cole & Wilcox**

Lasiopogon willametti Cole & Wilcox, 1938. *Entomologica Americana* 43: 77–79.

Diagnosis. A medium-sized dark brown species from sandy rivers in Oregon and northern California; all setae black except white hairs of beard, coxae, femur apex, and tergite sides; thorax tomentum brown, dorsocentral and acrostichal stripes dark brown but indistinct at an angle; tergites with brown tomentum in basal spots, apical grey bands broad. Epandrial halves moderately concave medially; phallus dorsal carina apex dorsoventrally flattened into disc. Ovipositor dark brown/black, acanthophorite spines black.

Description.

Head. Face and vertex brown. Ventral hairs (beard, labium, palps) white; mystax and all dorsal setae black. Occipital bristles fine, longest posterior of frons, moderately curved anterolaterally, lateral bristles reduced to short fine hairs. Frontal setae moderate, reach to end of scape; orbital setae gently curving over eye margin; occelar setae fine, short, indistinct amidst other hairs.

Antennae. Black, with thin grey tomentum. Setae black, no hairs on F1. F1 relatively long, straight edged; F2+3 long, narrow.

Thorax. Prothorax brown, with white hairs; postpronotal lobes brown, the lateral angle chestnut, hairs mixed white and black. Scutum tomentum brown, rarely grey. Dorsocentral stripes darker brown, indistinct when viewed from an angle; acrostichal stripes dark brown. All setae of scutum black, dorsocentral bristles fine, indistinct anterior of suture; lateral bristles strong. Anterior dorsocentrals 3–8; posterior dorsocentrals 5; postalars 2–4; supra-alars 2–3; presuturals 2–3; posthumerals 0–2. Scutellar tomentum brown; rim inflated, leaving a semi-circular line impressed inside the dorsal edge; apical bristles black, moderately fine, 8–10 on each half, mixed with other hairs. A few short hairs pointing straight up on uppermost edge of rim.

Pleural tomentum brown dorsally (rarely grey), grey ventrally. Katatergite bristles black, long, 8–9, with a few fine short white hairs; katepisternal setae white, fairly long, abundant; anepisternal bristles 7–8, black, with several short black hairs along dorsal margin and a few white hairs in posterioventral corner; anepimeron with 1–4 fine white setae.

Legs. Base color dark brown/black, covered in yellowish-grey tomentum; bare at joints. No coxal peg. Coxae with white setae; bristles of femur, tibia, and tarsi black; fine hairs white on basal 70% of femur, apically black. Ventral hairs on femur longer than femur width; dorsolateral bristles on profemur indistinct amidst abundant fine long hairs, mesofemur with 6–8 bristles, metafemur with 12–14. Protibia with ventral bristles 3 times longer than tibial width; dense apicoventral patch of short setae on protibia pale yellow, indistinct; on metatibia dark brown. Claws chestnut over basal 60%, black apically.

Wings. Veins brown; membrane hyaline, but very pale brown when viewed obliquely. Halter knob cream, without spot, stem brown.

Abdomen. Cuticle dark brown/black; thick brown tomentum on tergite bases divided into lateral spots by medial grey tomentum, bands of grey tomentum cover apical 50% of each tergite and extending anteriorly laterally and along midline. Tergite 1 with 4–5 lateral black bristles, 1–3 golden bristles; lateral setae on tergites 1–3 white and as long as halter, on tergites 4–7 in male white and as long as scape + pedicel, in female black and shorter than scape; dorsal setulae short, black. Sternite tomentum grey, hairs white.

Male genitalia. Cuticle black, covered in brown-grey tomentum except at base of epandrium and of hypandrium/gonocoxite complex; with long black hairs; white hairs on cerci; setal brush dark brown. Epandrium elongate, in lateral view the width about 50% the length, widest in basal third, with dorsal and ventral margins straight, apex rounded to short ventral subapical tooth. In dorsal view, medial margins of epandrium moderately curved, curvature starts about 40% from base, outer margins suddenly tapered at apex; basal sclerite prominent.

Phallus paramere sheath dorsally about 45% the length of phallus; paramere sheath without ventral ornamentation; dorsal carina broad, rounded, protruding just farther than aedeagal tube and with apex dorsoventrally flattened into disc, leaving a narrow semicircular gap between apices. Ejaculatory apodeme in lateral view moderately bent dorsally in basal third, sometimes slightly recurved at apex, with dorsal carina of fairly even width. Subepandrial sclerite with triangular central unsclerotized area in basal 31%, gradually narrowing to a parallel-

sided gap along midline; spines parallel-sided, blunt, sparsely arranged in lateral midsection, dense elsewhere.

Female genitalia. Undissected: Tergite and sternite 8 dark brown/black, with white erect fine hairs; lateral lobe with 3–5 strong black setae. Cerci brown with pale setae; acanthophorite spines black.

Type Material. HOLOTYPE (photos examined) ♂ labelled: "[rectangular beige label] Kiger'sIsland/ Ore. IV-19 '30"; "[rectangular white label] J. Wilcox/ Coll."; "[rectangular salmon label] HOLOTYPE/ Lasiopogon/ willametti/ Cole & Wilcox"; "[rectangular beige label] Lasiopogon/ willamettei/ ♂ Type n.sp."; "[rectangular white label] California Academy/ of Sciences/ Type No. 6443". CAS.

ALLOTYPE (examined) ♀ labelled: "[rectangular beige label] Kiger'sIsland/ Ore. IV-8 '30"; "[rectangular white label] J. Wilcox/ Coll."; "[rectangular salmon label] ALLOTYPE/ Lasiopogon/ willametti/ Cole & Wilcox"; "[rectangular beige label] Lasiopogon/ willamettei/ ♀ Type n.sp.". CAS.

PARATYPES (106 examined): **U.S.A.: Oregon: Benton Co.,** Corvallis [44.57 -123.256], 8.v.1929, V.T. Shattuck (1♂ CAS), 10.v.1930, J. Wilcox (2♂ CAS), 27.v.1930, R.E. Dimick (1♂ 1♀ CAS), 2.v.1931, J. Wilcox (1♂ 1♀ CAS), 15.v.1931, J. Wilcox (2♀ CAS); Kiger Island [44.527 -123.238], 8.iv.1930, J. Wilcox (1♂ 2♀ CAS, 2♂ 1♀ EMEC, 1♀ OSUC, 1♀ UCRC, 1♂ 1♀ USNM), R.E. Dimick (1♂ MCZ), 12.iv.1930, J. Wilcox (4♂ 6♀ CAS, 1♂ FISH, 1♀ MCZ, 1♂ UCRC, 1♀ USNM), 16.iv.1930, J. Wilcox (2♂ 2♀ CAS, 1♀ CNC, 1♀ WSUC), R.E. Dimick (3♂ 1♀ CAS), 19.iv.1930, J. Wilcox (8♂ 5♀ CAS, 2♂ 2♀ FISH, 1♀ LACM, 1♀ MCZ, 1♀ RBCM, 1♂ 1♀ UCRC, 2♂ 1♀ 1? USNM), R.E. Dimick (3♂ 1♀ CAS, 1♂ FISH, 2♂ 2♀ MCZ, 1♂ OSUC, 1♂ USNM), 3.v.1930, J. Wilcox (2♂ CAS), 23.v.1930, J. Wilcox (1♀ USNM), 27.v.1930, J. Wilcox (1♂ 1♀ CAS, 1♂ USNM, 1♂ WSUC), 16.iv.1931, R.E. Dimick (1♀ CAS), 3.v.1931, J. Wilcox (1♀ CAS, 1♂ USNM); **Linn Co.,** Albany [44.639 -123.112], 15.v.1931, J. Wilcox (2♂ 1♀ CAS); Crabtree [44.637 -122.928], 15.v.1931, J. Wilcox (2♂ 5♀ CAS); Lebanon

[44.5377 -122.8888], 27.v.1931, J. Wilcox (1♂ 2♀ CAS); **Yamhill Co.,** Wheatland [45.091 -123.046], 10.v.1931, J. Wilcox (1♂ CAS).

Other Material Examined (71 specimens): **U.S.A.: California: Del Norte Co.,** Jedediah Smith Redwoods SP, Howland Hill Rd nr Cedar Creek bridge [41.7893 -124.0779], 13.v.2015, T.A. McKnight (1♂ TAM); **Humboldt Co.,** 4.v.1911, Oldenberg (2♀ USNM), 6.v.1911, Oldenberg (1♀ USNM); Bair's Ranch, Redwood Creek [40.964 -123.842], 11.vi.1903, H.S. Barber (1♀ EMEC); **Oregon: Benton Co.,** Corvallis (1♂ EMEC), 8.vii.1897 (1♀ EMEC), 9.vi.1897 (1♂ EMEC), 3.v.1916 (1♂ EMEC), 14.iv.1930, J. Wilcox (1♀ EMEC), 27.v.1930, R.E. Dimick (1♂ USNM), 2.v.1931, J. Wilcox (1♂ 1♀ USNM), 30.iv.1956, W.J. Hogg (2♀ RBCM); Corvallis, 1 mi S [44.553 -123.255], 6.v.1969, E.M. Fisher (1♂ 3♀ FISH); Corvallis, Willamette Park [44.547 -123.243], 31.v.1964, R.J. Lavigne (4♂ 7♀ ESUW); Corvallis, Willamette Park, Mary's River, 9.vi.1964, R.J. Lavigne (3♂ 2♀ [2 pr in cop] ESUW); Corvallis, Willamette River sandbars at Kendall Natural Area [44.547493 -123.243111], 19.v.2012, T.A. McKnight (2♂ 1♀ TAM); Kiger Island, 8.iv.1930, J. Wilcox (1♂ EMEC), 10.iv.1930, R.E. Dimick (1♀ EMEC), 12.iv.1930, J. Wilcox (1♂ EMEC), 19.iv.1930, I. Wilcox (1♂ EMEC), J. Wilcox (1♂ 1♀ RBCM, 2♂ 1♀ EMEC), R.E. Dimick (1♂ 1♀ EMEC); Kiger Island NE corner, Willamette River, 3 mi SE Corvallis [44.526814 -123.238091], 19.v.2012, T.A. McKnight (3♂ 1♀ TAM); Mary's River, 3 mi W Philomath [44.542 -123.4], 26.iv.1956, E.R. Turner (1♂ FSCA), 26.iv.1957, E.R. Turner (1♀ FSCA); **Lane Co.,** Oakridge, 2 mi NW [43.758 -122.523], 22.v.1953, J.D. Lartin (1♂ EMEC); **Linn Co.,** Crabtree [44.637 -122.928], 15.v.31, J. Wilcox (1♀ FISH); Crabtree Creek @ Hwy 226 bridge 8 mi N of Lebanon [44.65479 -122.85185], 19.v.2012, T.A. McKnight (3♂ 3♀ TAM); **Marion Co.,** Willamette Mission State Park, Willamette River sandbars, 4 mi W of Waconda [45.082128 -123.061812], 18.v.2012, T.A. McKnight (5♂ 2♀ [1 pr in cop] TAM); **Polk Co.,** W Salem, Willamette River bank [44.931 -123.07], 30.iv.1980, R.L. Westcott (1♂ 3♀ RBCM).

Type Locality. U.S.A.: Oregon: Benton Co., Kiger Island.

Taxonomic Notes. On the basis of DNA evidence and genitalia morphology, this concept of *L. willametti* is more strictly circumscribed than previous usage, excluding dark-mystaced

specimens of *L. ripicola* and the northern subspecies of *L. willametti* now called *L. puyallupi* stat. nov.

Etymology. No explanation given in the original description, but evidently named for the type locality on the Willamette river.

Distribution (Fig. III.3). Nearctic; central Oregon, with some populations extending into extreme northern California and southwestern Idaho.

Phylogenetic Relationships. Member of *bivittatus* section, *willametti* group, likely as sister to *L. dimicki*.

Natural History. Habitat: sandy riversides. Usually found perching on patches of open dry sand above the water (Fig. III.7c), often near willow (*Salix*). Dates collected range from April 8 to July 8, with most in April and May. One female with prey: Limoniidae.

***Lasiopogon zonatus* Cole & Wilcox**

Lasiopogon zonatus Cole & Wilcox, 1938. *Entomologica Americana* 43:80–82.

Diagnosis. A small brown species from California, Oregon, and Idaho; mystax black; thoracic tomentum brown to grey with dark dorsocentral stripes; thoracic setae mostly black, bristles often hairlike; tergite tomentum in clear bands of basal brown and apical grey. Epandrium with straight medial margins; phallus paramere sheath dorsal carina coming to a slender apical finger parallel to aedeagal tube. Ovipositor dark brown over basal 80% of tergite 8, otherwise pale brown.

Description.

Head. Face and vertex with golden brown to silvery grey tomentum, lighter around mystax perimeter; small shining black triangle directly behind antennae. Mystax, frontal and occipital setae black; beard and labial setae white. Occipital bristles fine, moderately long and curved, those behind the dorsomedial angle of the eye and most curved; lateral and ventral bristles shorter, straighter. Frontal setae fine, longer than scape + pedicel; orbital setae longer, slanted over the edge of the eye.

Antennae. Black; scape with some to many white setae; pedicel with all black setae; F1 never with setae. F1 long, widest at midpoint, with relatively long arista.

Thorax. Prothorax grey/brown, hairs white; postpronotal lobes whitish grey, lateral angle ferruginous, hairs white, sometimes a few black. Scutum tomentum steel-grey to brown; dorsocentral stripes dark brown; acrostichal stripes indistinct. All setae on scutum black; anterior dorsocentral bristles 4–6 mm, relatively fine and mixed with finer setae; posteriors 3–5; postalars 2–4, with 2–4 shorter hairs; supra-alars 2–4; presuturals 2–4; posthumerals 0–2. Scutellar tomentum grey, from silvery to brownish; two semi-circular wrinkles on disc inside dorsal edge; apical bristles long, black, abundant (usually 12+ on each side) and mixed with many other long hairs.

Pleural tomentum brown/grey. Katatergite bristles black, 6–9 with a few shorter white hairs; katepisternal setae sparse, moderately long, white; anepisternal setae black, 5–8 moderately strong and with several short black hairs on dorsal margin of sclerite; anepimeron with 0-2 short fine hairs.

Legs. Base color brown/black; tomentum uniform faint grey/brown over all but trochanter and base of femur, which are shining brown. No coxal peg. Bristles on legs black, finer setae mostly black, except white setae on coxae and usually along base of femur (variable: white hairs cover all to none of the femur base but usually about half, more prevalent in female). Ventral hairs on femur longer than femur width; dorsolateral bristles weak, on profemur 5–6 inconspicuous among abundant and dense surrounding fine hairs; bristles relatively longer on mesofemur (3–5) and metafemur (8–12). Protibia with ventral bristles 3–4 times longer than tibial width; dense

apicoventral patch of short setae on protibia pale yellow, on metatibia brown. Claws reddish brown basally, apically black.

Wings. Veins brown; membrane transparent, faintly brown, tint stronger when viewed obliquely. Halter pale yellow; stem dark brown.

Abdomen. Male. Cuticle dark brown/black; tergites (except tergite 1) with dense brown tomentum basally, grey tomentum in straight band covering apical 25% of each tergite and extending broadly along lateral edges; tergite 1 with light grey tomentum covering all but narrow anterior dorsal edge. All tergites with white lateral hairs, in male long, abundant, and erect on all tergites; in female lateral hairs short and sparse on tergites 5–7; first tergite with 6–11 lateral bristles, mostly black (2–7); dorsal setuale black. Sternite tomentum grey, hairs long, white.

Male genitalia. Epandrium and hypandrium/gonocoxite complex cuticle dark brown/chestnut, covered in thin grey tomentum except polished along inside dorsal margin of epandrium and medially on gonocoxite; terminalia covered in white hairs, setal brush dark brown. Epandrium elongate, in lateral view the width about 40% the length, widest basally, with dorsal and ventral margins straight for basal half, then curving ventrally to rounded apex. In dorsal view, medial margins of epandrium straight and parallel; basal sclerite strong.

Phallus paramere sheath dorsally about 50% the length of phallus; paramere sheath without ventral ornamentation; dorsal carina coming to a slender apical finger parallel to aedeagal tube. Ejaculatory apodeme in lateral view moderately bent dorsally in basal third, gently recurved at apex, with moderately narrow dorsal carina. Subepandrial sclerite with triangular central unsclerotized area in basal 65%; spines sparsely distributed, parallel-sided and blunt only over apical 20%, sharply tapered elsewhere.

Female genitalia. Undissected: Hairs white, abundant, erect. Tergite 8 dark brown/black, narrowly yellow at apex. Sternite 8 light brown, paler medially and apically, with abundant long, fine hairs; lateral lobe setae weak. Hypogynial valves pale yellow with abundant fine hairs. Cerci brown/black with pale setae; acanthophorite spines black.

Variation. There is considerable variation in setation and tergite color across the range, but we find no significant differences in genitalia morphology. Specimens from the Oregon/Idaho border are predominantly covered in faint grey tomentum with indistinct thoracic stripes; specimens from the southeastern Sierra Nevada in Mono Co., California have dense, dark setae.

Type Material. HOLOTYPE (photos examined) ♂ labelled: "[rectangular beige label, right wing attached] Santa Ana/ Canyon"; "[rectangular beige label] Orange Co./ Cal 4-33"; "[rectangular beige label] M.W.Stone,/ Coll."; "[rectangular salmon label] HOLOTYPE/ Lasiopogon/ zonatus/ Cole & Wilcox"; "[rectangular white label] California Academy/ of Sciences/ Type No. 6437"; "[rectangular white label] ALLOTYPE IS STORED/ IN THE/ GENERAL COLLECTION". CAS.

ALLOTYPE (examined) ♀ labelled: "[rectangular beige label] Santa Ana"; "[rectangular beige label] Orange Co./ Cal 1-IV-33"; labelling uncertain .."[rectangular white label] K. Sloop/ Coll."; "[rectangular salmon label] ALLOTYPE/ Lasiopogon/ zonatus/ Cole & Wilcox". CAS.

PARATYPES. (48 examined). **USA: California: Los Angeles Co.**, no loc, Coquillett (2♂ 1♀ 1? EMEC); Artesia [33.865 -118.103], 27.iii.1934, M.W. Stone (1♂ CAS); **Orange Co.**, Santa Ana Canyon [33.872 -117.702], iv.1933, M.W. Stone (1♂ 1♀ CAS, 1♂ EMEC), 1.iv.1933, K. Sloop, M.W. Stone (6♂ CAS, 1♀ EMEC, 1♂ 1♀ FISH, 1♂ 2♀ OSUC), 11.iii.1934, M.W. Stone (2♂ CAS), 21.iii.1934, M.W. Stone (7♂ 4♀ CAS, 1♂ 1♀ CNC, 1♂ 1♀ EMEC, 1♂ ESUW, 1♂ FISH, 1♂ OSUC, 1♂ 1♀ UCRC, 3♂ 2♀ USNM); **Sonoma Co.**, Santa Rosa [38.437 -122.713], 4.v.1925 (1♀ USNM).

Other Material Examined (187 specimens). **USA: California:** no loc, Baron (1♀ OSUC); **Contra Costa Co.**, Danville [37.828 -122.031], 17.iv.1952, F.X. Williams (1♂ FISH), 8.v.1952, F.X. Williams (1♀ FISH); **Fresno Co.**, Coalinga [36.152 -120.354], 10.v.1938, A.J. Basinger (1♀ CAS), 1.v.1941, J. Wilcox (3♂ CAS, 1♂ RBCM); **Kern Co.**, no loc, H.K. Morrison (1♂ EMEC); Kern River Preserve, 1.5 mi W Weldon [35.672 -118.315], 21.iv.1983, J.D. Pinto, R.K. Velten (1♀ RBCM); Welden, 16 mi S [35.485 -118.205], 26.iv.1964, W. Turner (1♀ BEZA, 1♂ EMEC); **Los Angeles Co.**, no loc, Coquillett (2♂ EMEC, 1♀ FISH); Los Cerritos [33.830 -

118.205], 21.1915, M.C. Van Duzee (1♂ EMEC); Sierra Madre [37.091 -118.046], 17.v.1941, J. Wilcox (1♀ FISH); **Madera Co.**, San Joaquin Experimental Range [37.091 -119.733], 17.iv.1953, J.D. Lattin (1♂ FISH); **Marin Co.**, Hicks Valley, Arroyo Sausal W of Point Reyes–Petaluma Road [38.157 -122.716], 14.iv.1984, P.H. Arnaud, Jr. (7♂ CAS, 1♂ RBCM), 12.iv.1987, P.H. Arnaud Jr. (5♂ 1♀ CAS, 1♂ RBCM); San Antonio Creek, San Antonio Rd 4.5 mi S of Petaluma, 38.17899 -122.62826, 15.iii.2014, T.A. McKnight (2♂ 1♀ TAM); **Mendocino Co.**, Russian River near Hopland [38.954 -123.102], 9.v.1970, J.A. Powell (1♂ 1♀ EMEC); **Mono Co.**, Owens River at Benton's Crossing [37.699 -118.764], 28.vi.1970, J.M. Sheppard, L.J. Sheppard (4♂ 2♀ FISH); **Monterey Co.**, Carmel Valley [36.484 -121.743], 14.iv.1962, R. Schetter (1♀ FISH); King City along E side Salinas River [36.206 -121.154], 17.iv.1990, D.W. Webb, M.E. Irwin (1♂ 1♀ INHS); **Napa Co.**, Markley Canyon, Lake Berryessa [38.491 -122.126], 19.iv.1978, E.M. Fisher (1♀ FISH); Pleasant Valley [38.471 -122.032], 2.v.1970, R.F. Lagier (1♀ WSUC); **Orange Co.**, Santa Ana River [33.872 -117.702], 19.iv.1927, B. Crow (1♂ EMEC); **Riverside Co.**, La Quinta [33.643 -116.319], 28.iii.1923 (1♂ 1♀ EMEC); Riverside [33.989 -117.393], 10.iv.1944, A.L. Melander (1♂ 1♀ USNM); Riverside, Santa Ana River [33.989 -117.393], 12.iii.1944 (1♂ FSCA); **San Benito Co.**, S Hernandez [36.377 -120.816], 22.iv.1957, A.M. Barnes (1♂ EMEC, 1♂ 1♀ FISH); San Benito River, 36.379 -120.902, 1.vi.1998, F.D. Parker (5♂ 6♀ LACM); **San Bernardino Co.**, Adelanto, 4 mi NE [34.629 -117.353], 9.iv.1973, E.M. Fisher (1♀ FISH); Jenks Lake [34.164 -116.882], 18.vii.1946 (1♀ FSCA); Mojave River at Deep Creek [34.343 -117.233], 27.iv.1941, J. Wilcox (1♂ CAS); **San Luis Obispo Co.**, Templeton, Salinas River [35.555 -120.694], 28.v.1991, M.E. Irwin (1♂ INHS); **Shasta Co.**, Redding, 14 mi NE [40.668 -122.156], 6.iv.1959, M.T. James, LaMar (1♂ 2♀ WSUC); Redding, 9 mi NE [40.639 -122.241], 7.iv.1959, M.T. James (1♀ WSUC); Summit City [40.669 -122.392], 7.iv.1959, M.T. James (2♂ 2♀ WSUC), J.F. Howell (1♂ 1♀ RBCM); **Sierra Co.**, Lincoln Creek campground [39.621 -120.525], 16.vi.1975, F.G. Andrews (1♀ FISH); Webber Lake [39.476 -120.417], 24.vii.1876, Osten Sacken (1♀ MCZ), 4.vii.1965, P.H. Arnaud Jr. (4♂ 1♀ CAS, 1♂ FISH, 1♂ RBCM); **Solano Co.**, Cold Canyon, 14.4 km W Winters, near Monticello Dam [38.513 -122.098], 11.v.1969, P.H. Arnaud Jr. (1♂ 1♀ CAS); Dozier, near Dixon [38.283 -121.818], 3.iv.1971, R.W. Thorp (1♂ BEZA); **Sonoma Co.**, Sonoma [38.299 -122.483], 2.iv.1961, D.W. Cavagnaro (1♂ 1♀ BEZA); **Trinity Co.**, Junction City [40.732 -123.056], 21.iv.1977, T.R. Haig (1♂ FISH), 4.v.1978, T.R. Haig (3♂ 2♀ FISH), 17.v.1978, T.R.

Haig (1♂ FISH), 23.iv.1984, T.R. Haig (2♂ 2♀ FISH); **Ventura Co.**, Casitas Springs [34.372 -119.309], 20.iv.1979, R.P. Meyer (1♀ BEZA); Lockwood Creek, near Stauffer P.O. [34.736 -119.054], 5.v.1959, C.W. O'Brien (2♂ 1♀ EMEC, 1♂ 1♀ RBCM), G.I. Stage (1♂ EMEC, 2♀ FISH), J.R. Powell (1♂ EMEC), 7.v.1959, J.R. Powell (1♂ 1♀ BEZA, 1♂ 1♀ BPBM); Wheeler Springs [34.513 -119.274], 16.v.1942, M.W. Stone (1♂ CAS); **Yolo Co.**, Davis [38.518 -121.769], 4.iv.1951, R.G. Bechtel (1♂ FSCA), 20.iv.1951, H.F. Robinson (1♀ LACM), 23.iv.1951, J.C. Downey (1♂ LACM), 27.iv.1951, R.G. Bechtel (1♂ CNC, 1♀ FISH), 2.iv.1952, E.I. Schlinger (2♂ CAS), 23.iv.1952, E.I. Schlinger (1♂ CAS), 12.iii.1956, F.D. Parker (1♂ FSCA), 8.iv.1956, J.C. Downey (1♂ FISH), 24.v.1956, J.C. Downey (1♂ LACM), 22.iv.1959, J.R. Powers (1♂ BEZA, 2♂ EMEC), 7.iv.1961, M.E. Irwin (1♂ BEZA); Putah Canyon [38.514 -122.072], 5.v.1967, R.F. Denno (1♂ BEZA); **Idaho: Canyon Co.**, Parma [43.802 -117.000], 13.v.1933, F.H. Schirck (1♀ CAS); **Oregon: Baker Co.**, Burnt River 2 mi N of Huntington, 44.36724 -117.28899, 1.v.2014, T.A. McKnight (1♀ [EtOH] TAM); Jett, Burnt River [44.426 -117.312], 3.v.1946, C.H. Martin (3♂ FSCA, 1♂ RBCM); **Lake Co.**, Chandler Wayside State Park, Crooked Creek at Hwy 395, 8.5 km S jct Hwy 31 [42.4115 -120.2905], 27.v.1995, R.A. Cannings, H. Nadel (10♂ 12♀ 1? RBCM); **Malheur Co.**, Adrian, Owyhee River [43.781 -117.060], 3.v.1946, C.H. Martin (2♂ FISH, 10♂ 1♀ FSCA, 2♀ RBCM); Ontario [44.040 -116.962], 16.v.1946, C.H. Martin (1♀ FISH, 1♂ 1♀ FSCA); **Washington: Benton Co.**, Richland, Yakima River [46.276 -119.317], 2.v.1946, C.H. Martin (1♂ RBCM).

Type Locality. U.S.A.: California: Orange Co., Santa Ana Canyon.

Etymology. No explanation given in the original description, but evidently named for the "zonate appearance of the abdomen", i.e., the straight bands of light and dark tergite tomentum.

Distribution (Fig. III.3). Nearctic; U.S.A.: California, Oregon, western Idaho.

Phylogenetic Relationships. Member of the *bivittatus* section, sister to *L. wilcoxi* sp. nov., likely in a position basal to the *drabicolum* group.

Natural History. Habitat: sandy stream banks in semiarid areas. Caught perching on bare dry sand 1–10 m from the flowing water (Fig. III.7e), or an open dry flood wash through willows. Dates collected: March 11 to July 24, with most in April or May.

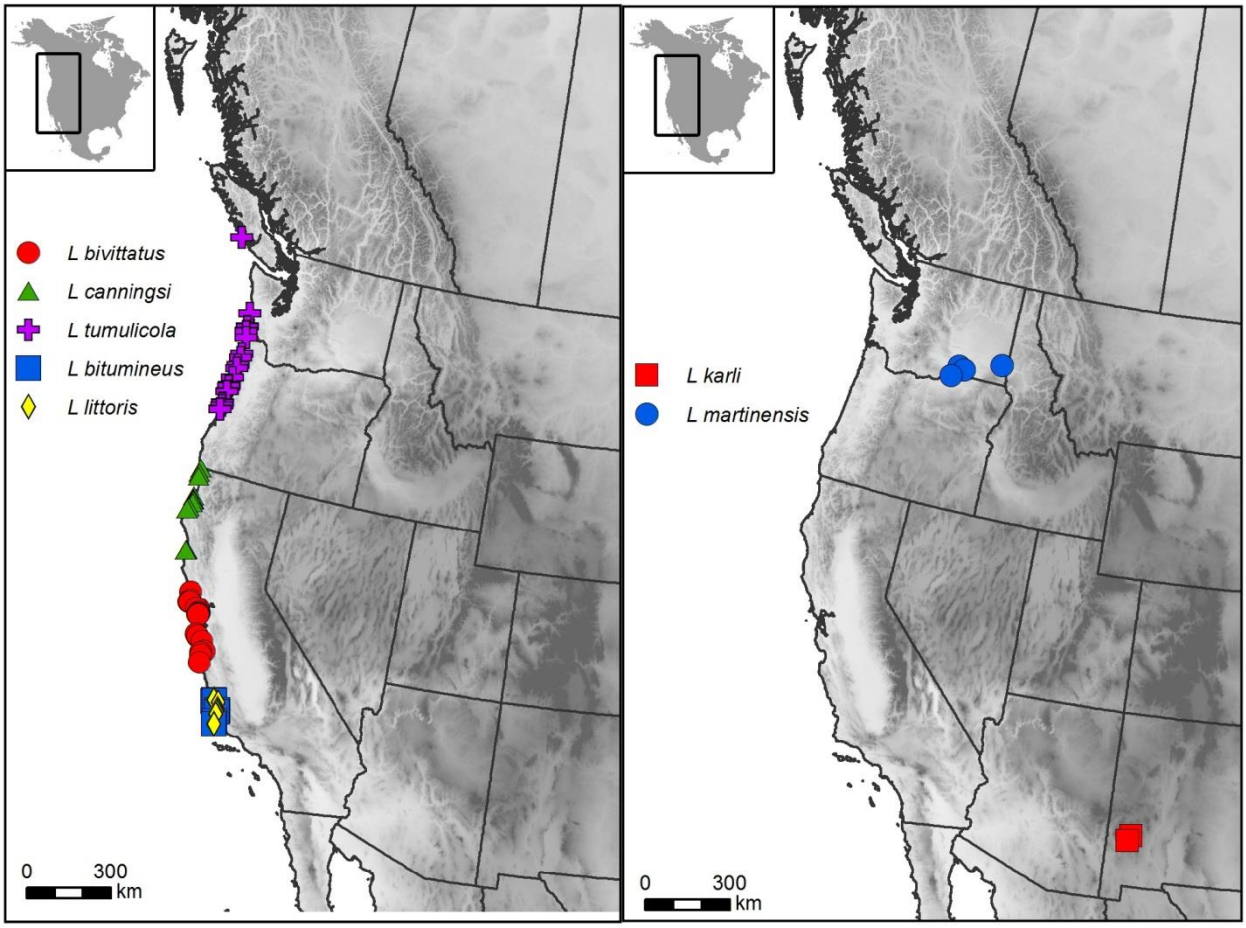


Fig. III.2. Distribution maps of georeferenced records (1 of 2).

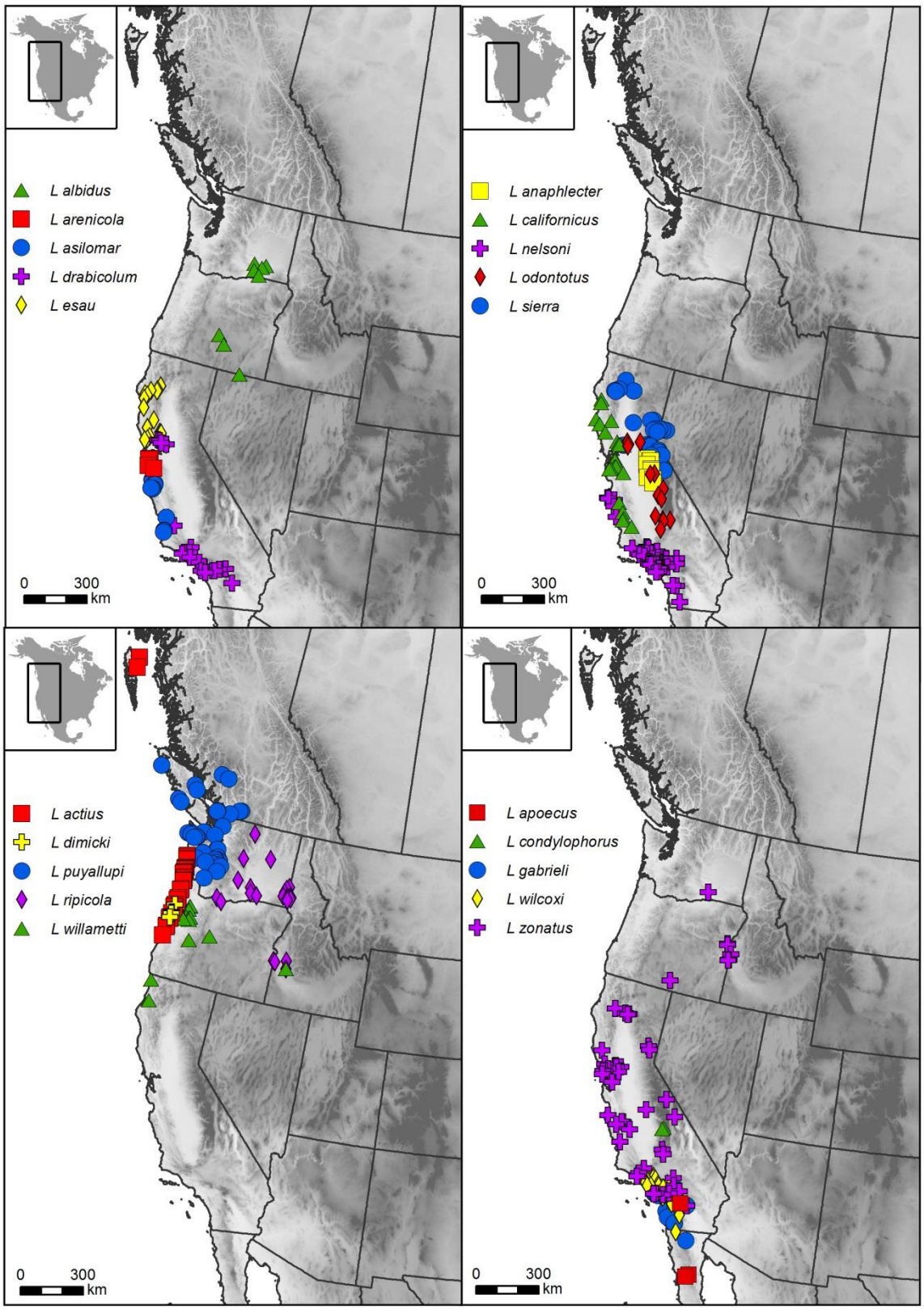


Fig.III.3. Distribution maps of georeferenced records (2 of 2).

Phylogeny

The molecular species tree (Fig. III.4) and morphological cladogram (see Fig. 251 in Cannings 2002) have notable similarities and also differences. Taxa that constitute defined species groups (see the checklist in Cannings 2002) are relievingly consistent across both methods, but the backbone relationships between species groups and the precise arrangement of sister taxa within each species group are not always in concordance. However, positions of topological discord or poor clade support are usually echoed in both trees, and are reasonable given the limitations of specimen sampling, loci sequenced, and characters analyzed.

The most fundamental difference between the molecular and morphological *Lasiopogon* species trees is a shift in the backbone roughly analogous to moving the root in the morphological tree (Fig. 251 in Cannings 2002) from node "A" to "B". In the morphological analysis, the clades formed by node "A" had acknowledged weak and generally homoplastic support, whereas the clade formed at "B" was strongly supported by many unique synapomorphies. Nevertheless, morphological parsimony supported "A". The molecular tree instead went with "B", with high posterior probabilities and robustness across priors and parameters suggesting that the species groups should be grouped as (*bivittatus* + *opaculus*) and (*cinctus* + *montanus* + ((*aldrichii* + *canus*) + (*testaceus* + *fumipennis*))), with the *terricola* group in an undetermined basal position. The *bivittatus* + *opaculus* clade is characterized by long and slender epandria, compact gonocoxites, U-shaped subepandrial sclerite, and strong setae on the female sternite 9 lateral lobes. The other clade has blunt, broad, and frequently ornamented epandria, elongate gonocoxites, heart-shaped subepandrial sclerite, and no strong setae on the female sternite 9 lateral lobes.

As mentioned above, the posterior distribution of trees did not converge on a single position for the *terricola* group, instead usually alternating between positioning it basally to all other *Lasiopogon* or basally to the new *cinctus* clade. This gives some credence to the idea of subgenus *Alexiopogon* Curran, which was originally proposed for the "abberant" *L. terricola*, but given the morphological similarity between the other species in this group and "normal" *Lasiopogon*, we are not elevating this taxon. Our molecular species tree does not show *L. trivittatus* grouping with the *terricola* group (as indicated in the 2002 checklist), but this is best considered unresolved since DNA was only available from one locus and did not strongly support any position.

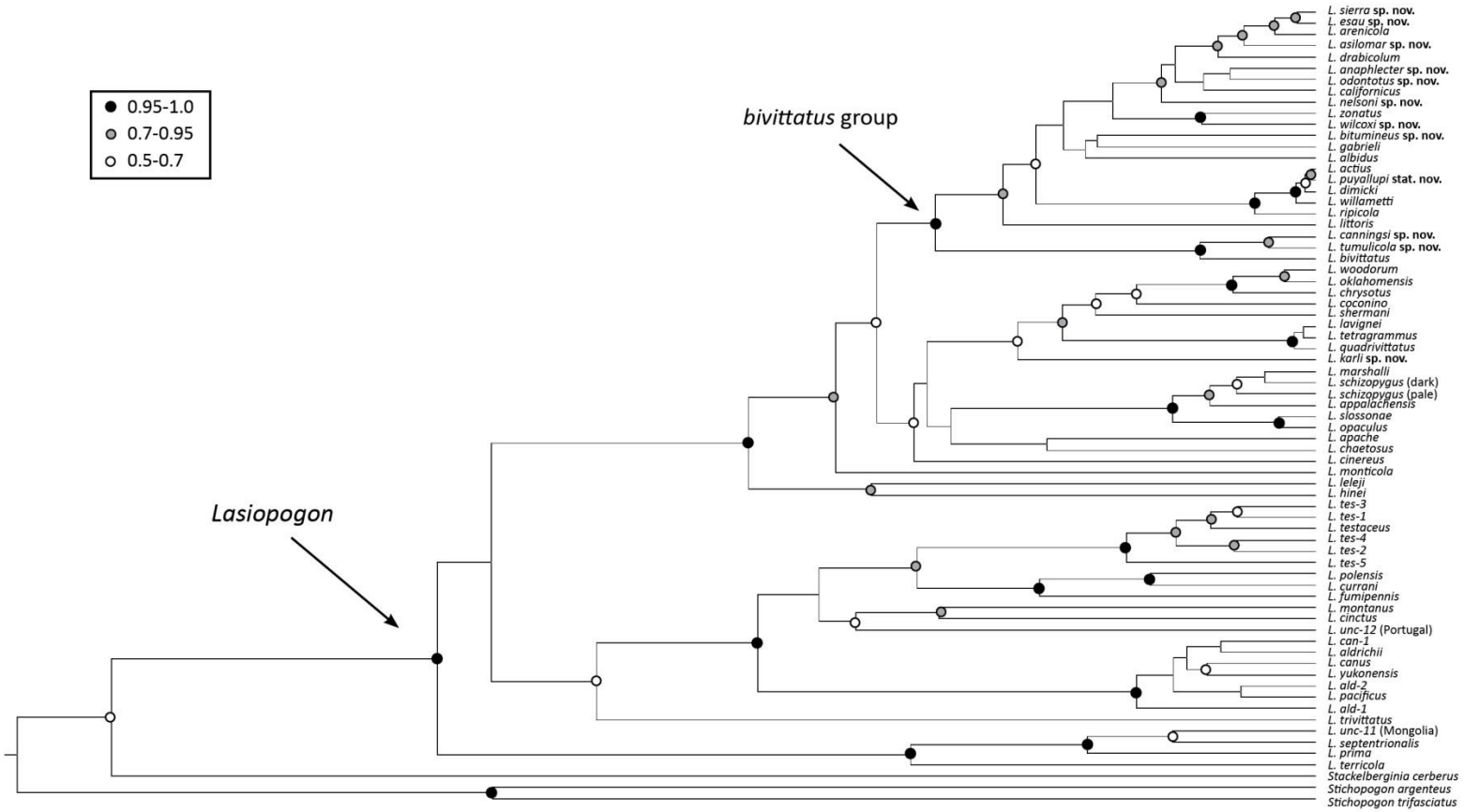


Fig. III.4. Species tree for the genus Lasiopogon, estimated as the Bayesian maximum clade credibility tree in STARBEAST2, with four partitions for one mitochondrial locus (COI) and three nuclear protein coding loci (wingless, PEPCK, AATS). Node shading indicates posterior probability levels. New taxa not described in this publication are designated with abbreviations following Cannings 2002.

The *fumipennis* and *testaceus* groups were strongly supported as monophyletic and as sister groups to each other. Similarities in their genitalia (such as the ferruginous cuticle) and behavioral ecology (these species are frequently found perching on logs and boulders, not necessarily near water) also support this relationship. Except for some overlap in the northern Sierra Nevada, they have relatively complementary distributions across the continent.

The *canus* and *aldrichii* groups did not converge to reliable monophyletic positions in the species tree, but we believe this is likely the result of introgression or incomplete lineage sorting at the mitochondrial barcode and not flawed taxonomy. The nuclear loci and genitalia morphology both support reciprocal monophyly, and species from the two groups with unexpected affinities in the full molecular species tree are geographically adjacent (*L. canus–L. yukonensis*, *L. can-1–L. aldrichii*).

The three representative species from Europe allied together; but more taxa need to be sampled to resolve relationships within and among these groups.

The *opaculus* group and *tetragrammus* group were each strongly supported, and clustered together with each other (i.e., the *opaculus* section). The *cinereus* group, weakly supported in the morphological tree, was not recovered as a monophyletic group; these species instead appeared as poorly supported singletons near the base of the *opaculus* and *tetragrammus* groups. The *hinei* group was strongly supported (based on two taxa), but not nested inside the *opaculus* section as indicated in the morphological tree. Instead, the *hinei* and *monticola* groups were strongly supported as basal to the whole *bivittatus* + *opaculus* clade.

There is strong support for a monophyletic *bivittatus* group. As a "*bivittatus* section" with diversity comparable to its sister the *opaculus* section, some subgroups were consistently recovered and are noted to help direct future work: the *bivittatus* species group (*L. bivittatus*, *L. canningsi* sp. nov., *L. tumulicola* sp. nov.) are an allopatric species complex basal to the rest of the section; the *actius* species group (*L. actius*, *L. dimicki*, *L. puyallupi* stat. nov., *L. ripicola*, *L. willametti*) have likely only recently diverged from each other, given their genetic and morphological similarity; the *drabicolum* species group (*L. anaphlecter* sp. nov., *L. asilomar* sp. nov., *L. arenicola*, *L. californicus*, *L. drabicolum*, *L. esau* sp. nov., *L. nelsoni* sp. nov., *L. odontotus* sp. nov., *L. sierra* sp. nov.) is well supported as a group but had poor consistency of internal relationships; and *L. wilcoxi* sp. nov. and *L. zonatus* are clearly sister taxa.

Evaluating where the molecular and morphological trees failed to match casts light on problems of scale for phylogenetic analyses. Coding morphological characters for cladistic analysis suffers from the Goldilocks principle: deep relationships struggle to find homologous characters that aren't homoplasious, while shallow relationships struggle to find homologous chararcters that nevertheless differentiate closely related taxa. Morphology-based analysis therefore excels at intermediate levels where consistent and equivalent morphological syndromes can be characterized. Molecular analysis has a similar balancing act between finding loci with enough variable sites but not too much nucleotide saturation, but with two significant advantages from the perspective of information theory: it is comparatively easy to amass a large number of independent characters (SNPs, loci), and analysis is more removed from interpretation, leaving less room for individual opinion to bias results (e.g., for morphology one must decide what structures on a phallus are homologous in order to code them, but with DNA sequences uncertainty in whether SNPs are derived or ancestral is effectively integrated out in the nucleotide transition model). Future revisionary work in asilids would benefit from using morphological and molecular data in conjunction.

I**dentification keys**

The tabular image-based key (Fig. III.8) has been arranged to help identify and distinguish the taxa revised in this study, with similar species arranged into a matrix for each two-page spread. Future publications will expand this to include other species groups, but in the meantime we provide the following updated couplets for the dichotomous key to western Nearctic *Lasiopogon* (Cannings 2002) to integrate these taxa with the broader fauna (figure numbers refer to the original publication):

3a Metacoxal peg stout and rounded apically; facial gibbosity mostly absent; mystax reduced to a few rows of setae above oral margin; anepisternal and coxal setae long, stout, and white, the anepisternal setae about twice as long as the antennae; leg bristles white (species active in autumn; Nevada plateau) … ***Stackelberginia cerberus* McKnight**

17a Large species (usually at least 11 mm); phallus apex with dorsal carina much longer than aedeagal tube; apex of dorsal carina expanded and oval in dorsal or ventral view (stream margins in the Columbia Basin of eastern Washington and Idaho) … ***L. ripicola*** **Cole and Wilcox (part)**

17b Small to medium-sized species (to 10 mm long, but most 7–9 mm); coloration variable but usually dusty grey; apex of phallus with dorsal carina and aedeagal tube about equal in length; apex of dorsal carina linear, not expanded and oval in dorsal or ventral view … 77

22a Trochanters and joints of tarsi and tibiae brown/black; lateral abdominal setae long and dense, those on abdominal segment 2 about the same length as those on segment 1 … 78

24a Trochanters and joints of tarsi and tibiae brown/black; lateral abdominal setae long and dense, those on abdominal segment 2 about the same length as those on segment 1; sternite 8 mostly black/dark brown … 78

30a Epandrium clothed in long, strong setae, at least some as long as the lateral width of epandrium; no basal umbo; in dorsal view medial margins concave in apical half, the convex basal margins rather widely separated (figures 33, 49); apex of epandrium halves without small flange; basal epandriual sclerite present; phallus as in figures 35 and 51 … 79

39b Apicoventral angle of epandrium rounded or sharp, but not protruding posteriorly as a strong tubercle … 41

41a Epandrium in lateral view hardly wider at apex than at base, apicoventral corner blunt (figure 245e), apicomedial tooth short and rounded; phallus aedeagal tube slightly bent ventrally to form an obtuse angle; scutum grey, the brown tomentum more-or-less restricted to the dorsocentral and medial stripes; antennal F1 significantly fatter at midpoint than basally or apically (mountain habitats from southern British Columbia and Alberta south to Colorado and Utah) … ***L. aldrichii*** **Melander* (part)**

41b Epandrium in lateral view wider at apex than at base, apicoventral corner a sharp angle, apicomedial tooth also sharp and prominent; phallus aedeagal tube strongly bent ventrally to

form a right angle; scutum grey or brown, if grey, then antennal F1 not noticeably fatter at midpoint … 80

43b Epandrium in lateral view with width about 0.6 times the length; katatergite setae black; lateral setae on tergites long, the longest on tergite 3 more than 0.5 times the length of the tergite (stream sides in eastern Washington and Idaho) … ***L. martinensis*** **Cole and Wilcox**

45a Epandrium shining black, without tomentum; aedeagal tube with sharp ventral subapical spine; antennae with F1 long and narrow; tergites basally with black shining cuticle; moderately large species (ocean beach dunes from California to British Columbia) … 81

46a Small species, scutal and pleural bristles extremely long and prominent; antennae with F1 short; tergites basally with brown tomentum; epandrium apex gently curving out; ventral margin of phallus without spine; sternite 8 and hypogynial valves pale tan (beaches and dunes of the California central coast) … ***L. bitumineus*** **McKnight sp. nov.**

46b Not as above 47

47a Some setae on basal segments of antennae white … 48

47b Setae on basal segments of antennae brown/black … 51

48a Epandrium in dorsal view with medial margins concave in apical half; subepandrial sclerite with thick heavy spines over all … 49

48b Epandrium in dorsal view with medial margins more-or-less straight; subepandrial sclerite with thin tapered spines basally and medially (stream sides from southeastern Washington south to Southern California) … ***L. zonatus*** **Cole and Wilcox**

49a Epandrium in dorsal view with medial margins strongly concave … 83

49b Epandrium in dorsal view with medial margins moderately concave … 84

51a Epandrium in dorsal view with medial margins straight; dorsum of tergites shining brown/black, the apical band of grey tomentum dorsolateral and lateral only; subepandrial

sclerite with thin tapered spines basally (southern California, northern Baja California) … ***L. wilcoxi* McKnight sp. nov.**

51b Epandrium in dorsal view with medial margins moderately concave in apical half (cf. figures 205, 245i); tergites with apical band of grey tomentum continuing over dorsum; subepandrial sclerite with thick heavy spines over all … 52

52a Phallus with ventral margin of paramere sheath abruptly expanded into a buttress-like carina midway between gonopore and base of ventral processes; short appressed setae on dorsum of metafemur brown/black, at least in apical half … 89

52b Phallus with ventral margin of paramere sheath straight; short appressed setae on dorsum of metafemur white apically (except in some *L. puyallupi* stat. nov.) … 53

53a Longer hairs of abdomen mostly white; usually 5–6 dark bristles basolaterally on tergite 1 … 91

60a Short, appressed hairs on dorsum of metafemur black/brown, at least in apical half; tergite tomentum pattern usually vague, the basal brown patches weak to absent … 61

60b Short, appressed hairs on dorsum of metafemur white; tergite tomentum pattern usually definite, the basal brown patches more-or-less clearly defined (except in *L. martinensis*, *L. karli* sp. nov., and *L. drabicolum*) … 62

61b Sternite 8 dark brown/black; apical lobes of sternite 8 with bristles; moderately large species (length usually greater than 12 mm) … 93

63a Long lateral setae on abdominal segments 1–3 white; 3–7 black bristles laterally on tergite 1 … 94

64a Tomentum largely pale silver-grey, the dorsocentral stripes and the basal brown patches on the abdominal tergites pale and often obscure … 98

65a Setae ventrally on abdominal segments 6–7 white; mystax usually with significant portion white (sometimes all black); small to medium-sized species, usually less than 9 mm long … 100

65b Setae ventrally on abdominal segments 6–7 primarily brown/black; mystax dark, or only a few ventrolateral setae pale; larger species, usually more than 9 mm long … 101

68a Hypogynial valves and lateral lobes of sternite 8 ferruginous; lateral lobes of sternite 8 either without long bristles or with bristles pale; scutum normally with medial stripe, but sometimes obscure (absent in *L. wilcoxi* sp. nov. and *L. bitumineus* sp. nov.) … 69

69a Smaller flies; lateral lobes of sternite 8 with fine yellow bristles; scutum without medial stripe; hypogynial valves blunt and do not extend farther than acanthophorite spines (southern California) … 102

69b Larger flies; lateral lobes of sternite 8 without long bristles; scutum with medial stripe (sometimes faint); hypogynial valves tapered and reach beyond acanthophorite spines … 70

71b Venter of metafemora with fine setae mostly gold/brown; setae on venter of abdominal sternite 7 golden or gold mixed with brown/black; usually considerable brown tomentum laterally and posteriorly on scutum, suffused with the grey basal tomentum; scutellus with brown tomentum. … ***L. pacificus*** **Cole and Wilcox*, *L. ald-1* sp. nov.*, *L. ald-2* sp. nov.***
(Females of these species cannot be distinguished with confidence at this time. *L. pacificus* lives in southwestern British Columbia and south along the coastal lowlands to northern Oregon; *L. ald-1* sp. nov. inhabits coastal streams in northern California, *L. ald-2* sp. nov. inhabits mountain streams east of the Cascade Range in Washington and Oregon.)

72a Short fine hairs on dorsum of metafemora brown/black … 103

75a r-m crossvein at, or distal to, middle of discal cell; setae on ventrolateral margins of abdominal tergite 1–7 white; setae on abdominal sternite 7 white/yellow … 81

77a Epandrium profusely covered in long erect hairs, in dorsal view wider at base than apex; fine notal setae lateral of dorsocentral stripes dark; fine hairs on antennae mixed black and white (stream margins in northwestern California) … ***L. esau*** **McKnight sp. nov.**

77b Epandrium with only a few short indistinct hairs, in dorsal view evenly rounded from base to apex; fine notal setae lateral of dorsocentral stripes white; fine hairs on antennae predominantly white (stream margins of southern and central California) … ***L. drabicolum*** **Cole (part)**

78a Tergite tomentum in both sexes with apical grey extending anteriorly along midline, dividing brown tomentum into basolateral spots. Epandrium with medial curvature beginning at 35% the length from base; apical 20% bare of tomentum, with squared apicoventral corner (beaches and dunes of the San Francisco peninsula) … ***L. arenicola*** **(Osten Sacken)**

78b Tergite tomentum in both sexes with dark and light in relatively straight bands, basal brown tomentum thin, subshining. Epandrium with medial curvature beginning at 25% the length from base; apical 30% bare of tomentum, with slightly toothed apicoventral corner (beaches and dunes of California's central coast) … ***L. asilomar*** **McKnight sp. nov.**

79a Anterior dorsocentral bristles fine, hairlike; short notal hairs white, abundant; tergites entirely covered in silvery grey tomentum; dorsocentral stripes very faint brown, acrostichal stripes absent; scutal and pleural tomentum uniform silvery grey (mountain stream margins in southwestern New Mexico) … ***L. karli*** **McKnight sp. nov. (part)**

79b Anterior dorsocentral bristles very robust and prominent; short notal hairs black, sparse; tergites with small anterolateral patches of brown tomentum; scutal and pleural tomentum yellowish grey to brown … 31

80a Scutum usually with much brown tomentum laterally and posteriorly; antennal F1 significantly fatter at midpoint than basally or apically (ocean beaches, coastal streams, and trails from southwestern British Columbia to Oregon) … ***L. pacificus*** **Cole and Wilcox* (part)**

80b Scutum tomentum grey, with brown tomentum more-or-less restricted to the dorsocentral and medial stripes; antennal F1 not noticeably fatter at midpoint (mountain habitats of the Cascade Range and eastern Oregon) … ***L. ald-2*** **sp. nov.***

81a Grey tomentum covers apical 40% of each tergite; epandrium apex straight; postpronotal lobe with mostly white hairs in male; lateral setae on tergite 1 mostly white (only 3–4 black); apical 40% of femur black-haired and bare (beaches and dunes around San Francisco and the California central coast) … ***L. bivittatus* Loew**

81b Grey tomentum covers apical 10–20% of each tergite; epandrium apex with semicircular emargination; postpronotal lobe with predominantly dark hairs in male; lateral setae on tergite 1 mostly black (4–10); femur variable … 82

82a Epandrium apex with small semicircular emargination and rounded apicoventral corner; femur with white hairs and grey tomentum over all except joints (beaches and dunes of far northern California coast) … ***L. canningsi* McKnight sp. nov.**

82b Epandrium apex strongly concave with sharp apicoventral corner; apical 40% of femur black-haired and bare (beaches and dunes from Oregon to Vancouver Island) … ***L. tumulicola* McKnight sp. nov.**

83a Small species; scutum color dark brown; tergites with dark brown tomentum basally; antennae with flagellum short (F2+3/F1 about 0.65); dorsocentral bristles prominent (mountain stream margins of Southern California and northern Mexico) … ***L. gabrieli* Cole and Wilcox**

83b Moderately large species; scutum and tergites covered in dusty grey tomentum; antennae with flagellum long; anterior dorsocentral bristles very fine, hairlike (mountain stream margins in southwestern New Mexico) … ***L. karli* McKnight sp. nov. (part)**

84a Lateral hairs on tergites 5–7 dark brown; epandrium in lateral view with dorsal margin gradually curving ventrally, apicoventral corner rounded; gonostylus dorsomedially flattened, creating a dumbbell-shaped appearance; phallus dorsal carina triangular, not protruding apically (stream margins in the coastal range and valleys of central and northern California) … ***L. californicus* Cole and Wilcox**

84b Lateral hairs on all tergites white; epandrium in lateral view with dorsal margin straight, apicoventral corner pointed; gonostylus with dorsal and medial flanges developed; phallus dorsal carina pointed apically, leaving a curved gap between its apex and the gonopore … 85

85a Lateral bristles on tergite 1 mostly white (2–7 white, 0–5 black); gonostylus in lateral view flattened, much longer than tall … 86

85b Lateral bristles on tergite 1 mostly black (1–3 white, 3–8 black); gonostylus in lateral view semicircularly rounded … 87

86a Hairs on antennal pedicel mostly white (no more than 3 dark brown); frontal hairs all to partially white; epandrium with only a few short indistinct hairs, in dorsal view evenly rounded from base to apex (stream margins of southern and central California) … ***L. drabicolum*** **Cole (part)**

86b Hairs on antennal pedicel black; frontal hairs black; epandrium profusely covered in long erect hairs, in dorsal view wider at base than at apex (stream margins in northwestern California) … ***L. esau*** **McKnight sp. nov. (part)**

87a Frontal hairs mostly white, usually only reach base of F1; phallus dorsal carina with rounded apical point usually not narrowed into a finger; dorsocentral stripes faint or indistinct; grey tomentum on abdominal tergites usually extending anteriorly along midline to divide basal brown tomentum into lateral spots or pattern indistinct (stream margins of southern and central California) … ***L. nelsoni*** **McKnight sp. nov.**

87b Frontal hairs black, reach basal third of F1; phallus dorsal carina extends apically as a tapered finger parallel to gonopore; dorsocentral stripes brown; grey tomentum on abdominal tergites usually a straight apical band, occasionally faintly extending anteriorly along midline to divide basal brown into lateral spots … 88

88a Phallus with sharp apicoventral tooth; grey tomentum over apical 50–60% of abdominal tergites (stream margins along the western slopes of the Sierra Nevada in California) … ***L. odontotus*** **McKnight sp. nov.**

88b Phallus without apicoventral tooth; grey tomentum over apical 30–50% of abdominal tergites (stream margins along the eastern and northern slopes of the Sierra Nevada in California) … ***L. sierra*** **McKnight sp. nov.**

89a Acrostrichal stripes brown; katatergite with 8–10 black bristles; dorsal carina on phallus slender, gently curved, and much longer than gonopore (central Sierra Nevada) … ***L. anaphlecter*** **McKnight sp. nov.**

89b Acrostichal stripes indistinct; katatergite with 6–9 black bristles; dorsal carina on phallus spherically swollen and no longer than gonopore … 90

90a Prothorax with white hairs; lateral hairs on all tergites white; femur with fine basoventral hairs white; metacoxae with white hairs anteroventrally; epandrium in dorsal view moderately concave; gonostylus compact (mountains of Baja California and southern California) … ***L. apoecus*** **McKnight sp. nov.**

90b Prothorax with brown hairs; lateral hairs on tergites 5–7 dark brown; femur with fine basoventral hairs dark brown; metacoxae with dark brown hairs anteroventrally; epandrium in dorsal view less concave; gonostylus elongate, extending medially beyond medial flange (Sierra Nevada of central California) … ***L. condylophorus*** **McKnight sp. nov.**

91a Phallus with apex of dorsal carina broad and completely flattened into a disc; acrostichal stripes usually present; face tomentum brown; mystax all black/brown (hillside rivers in Oregon, northern California, and western Idaho) … ***L. willametti*** **Cole and Wilcox**

91b Phallus with apex of dorsal carina broad but only slightly compressed from hemispherical; acrostichal stripes indistinct; face tomentum silver or yellow-grey; mystax frequently with a few white hairs in ventrolateral corners … 92

92a Fine hairs on profemur white apically; tergites with apical grey tomentum usually extending along midline to divide basal brown tomentum into lateral spots; scutum tomentum grey, with short notal hairs; imaginary angle formed by phallus dorsal carina apex and gonopore close to perpendicular (riversides in eastern Washington and western Idaho) … ***L. ripicola*** **Melander (part)**

92b Fine hairs on profemur black over apical 30%; tergites with apical grey tomentum usually in straight bands; scutum tomentum brown or grey, with longer notal hairs; imaginary angle formed by phallus dorsal carina apex and gonopore acute (rivers and ocean beaches in British Columbia and western Washington) … ***L. puyallupi*** **Cole and Wilcox stat. nov.**

93a Short notal setae and lateral setae on abdominal tergites 3–6 sparse, minute (less than half the length of antennal scape) and black; dorsum of protibia with fine hairs much shorter than bristles (mountains and plateaus of central Arizona and western New Mexico) … ***L. coconino*** **Cannings**

93b Short notal setae and lateral setae on abdominal tergite 3–6 longer (at least as long as antennal scape), white on tergite 3; dorsum of protibia with fine hairs as long as bristles (mountains of Baja California and southern California) … ***L. apoecus*** **McKnight sp. nov.**

94a Dorsocentral bristles very long and robust; antennal F2+3 long; hypogynial valves pale brown; abdominal tergites with brown basal spots faint, usually assimilated into a broad band (beaches and dunes of the California central coast) … ***L. bitumineus*** **McKnight sp. nov. (part)**

94b Dorsocentral bristles fine and of normal length; antennal F2+3 of normal length; hypogynial valves black … 95

95a Many erect black setae on sternites 5–7; acrostichal stripes dark brown (central Sierra Nevada) … ***L. anaphlecter*** **McKnight sp. nov.**

95b Setae on sternites 5–7 white, no more than 1 black; acrostichal stripes variable, but fainter than dorsocentral stripes (Cascade Range, Columbia Basin, and ocean beaches of British Columbia to Oregon) … 96

96a Acrostichal stripes usually present; face tomentum brown; mystax all black/brown (hillside rivers in Oregon, northern California, and western Idaho) … ***L. willamettі*** **Cole and Wilcox**

96b Acrostichal stripes indistinct; face tomentum silver or yellow-grey; mystax frequently with a few white hairs in ventrolateral corners … 97

97a Fine ventral hairs on profemur all white, or black only over apical 10%; scutum tomentum grey, with short notal hairs (riversides in eastern Washington and western Idaho) … ***L. ripicola*** **Melander (part)**

97b Fine ventral hairs on profemur black over apical 30%; scutum tomentum brown or grey, with longer notal hairs (rivers and ocean beaches in British Columbia and western Washington) … ***L. puyallupi*** **Cole and Wilcox stat. nov.**

98a Mystax usually with significant portion white; antennal pedicel usually with some white setae; anepimeron with 2–3 fine white hairs (stream margins of southern and central California) … ***L. drabicolum*** **Cole (part)**

98b Mystax all dark; antennal pedicel with dark setae; anepimeron without hairs … 99

99a Frontal setae and fine hairs on notum and postpronotal lobes brown/black (stream sides in eastern Washington and Idaho) … ***L. martinensis*** **Cole and Wilcox**

99b Frontal setae and fine hairs on notum and postpronotal lobes white (stream sides in southwestern New Mexico) … ***L. karli*** **McKnight sp. nov.**

100a Fine notal hairs white, at least between dorsocentral stripes; antennal scape with some white setae; mystax usually significantly white (sometimes mostly brown); frontal hairs usually white (stream margins of southern and central California) … ***L. drabicolum*** **Cole (part)**

100b Fine notal hairs brown; antennal scape with brown setae; mystax mostly dark with a few white hairs ventrolaterally, rarely with significant white portions or all black; frontal hairs dark (stream margins in northwestern California) … ***L. esau*** **McKnight sp. nov.**

101a Long ventral hairs over basal 40% of mesotibia white; frontal hairs frequently partially white; antennal F1 shorter, widest at midpoint (stream margins of southern and central California) … ***L. nelsoni*** **McKnight sp. nov.**

101b Long ventral hairs at base of mesotibia black; frontal hairs black; if tibial hairs white, then antennal F1 is long, slender, and of even width … ***L. californicus*** **Cole and Wilcox,** ***L. odontotus*** **McKnight sp. nov.,** ***L. sierra*** **McKnight sp. nov.**

(Females of these species cannot be distinguished with confidence at this time. The antennal F1 in *L. odontotus* sp. nov. is usually relatively short and plump (widest at midpoint or in basal half); whereas in *L. californicus* it is long and straight-edged, and in *L. sierra* sp. nov. intermediate, but with a longer F2+3. *L. californicus* inhabits streams of the Costal Ranges in

central and northern California, *L. odontotus* sp. nov. inhabits streams on the southern and west slopes of the Sierra Nevada in California, and *L. sierra* sp. nov. inhabits streams in the northern and eastern slopes of the Sierra Nevada in California.)

102a Dorsocentral bristles fine and of normal length; antennal F2+3 of normal length; abdominal tergites with apical grey tomentum emarginated dorsocentrally, the black shining cuticle and dark brown tomentum reaching or almost reaching, the posterior margin of the tergite (southern California, northern Baja California) … ***L. wilcoxi* McKnight sp. nov.**

102b Dorsocentral bristles very long and robust; antennal F2+3 long; abdominal tergites with broad band of apical grey tomentum even medially, or even extending anteriorly (beaches and dunes of the California central coast) … ***L. bitumineus* McKnight sp. nov. (part)**

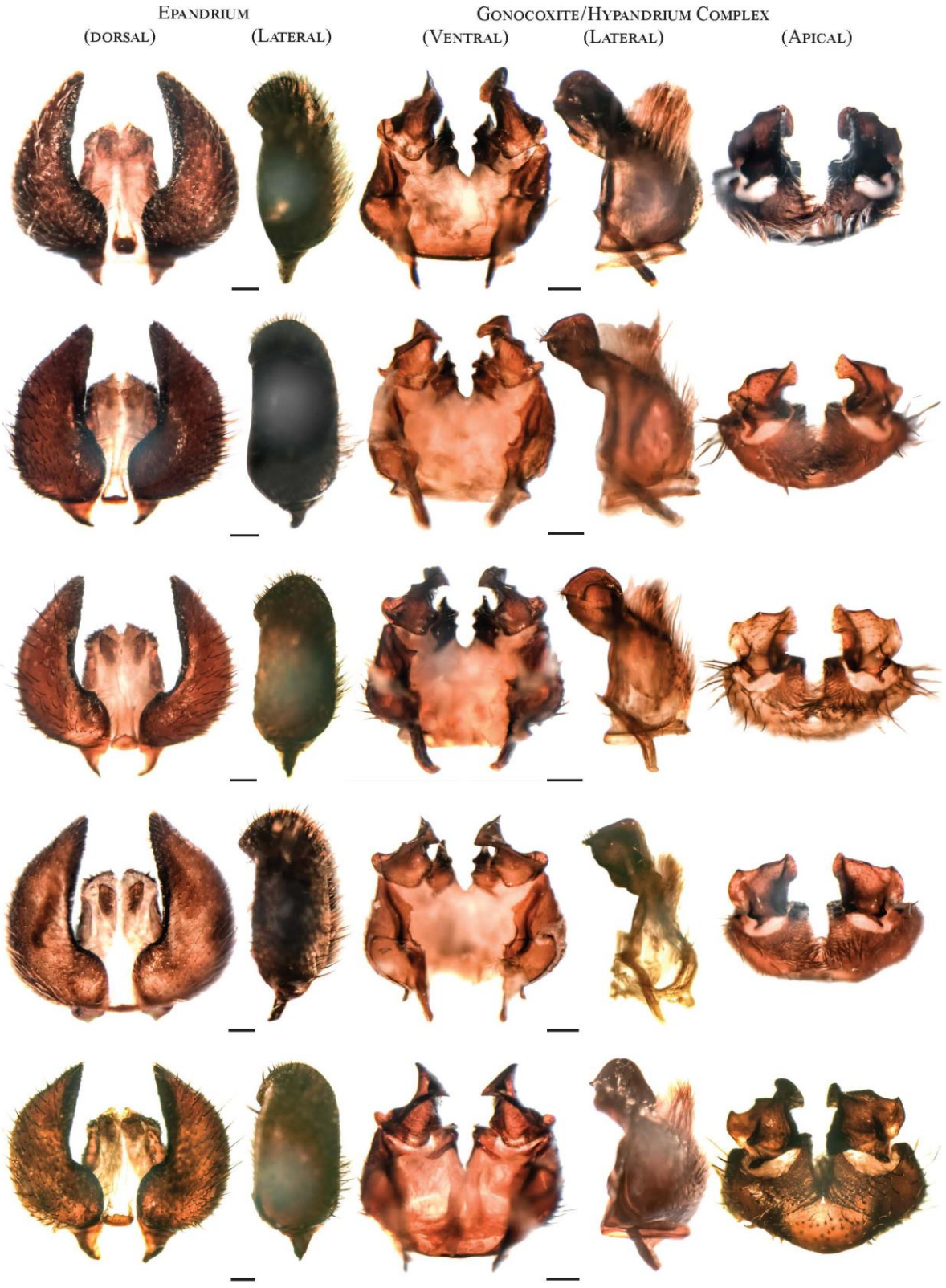
103a Anteroventral hairs on metacoxa white; hairs on antepronotum white; 3–5 strong bristles on each half of scutellum (mountains of southern British Columbia south to California and Utah) … ***L. monticola* Melander**

103b Anteroventral hairs on metacoxa brown/black; hairs on antepronotum brown dorsally; 8+ strong bristles on each half of scutellum (Sierra Nevada of central California) … ***L. condylophorus* McKnight sp. nov.**

Fig. III.5 Tabular key for Lasiopogon species included in this publication, showing details of tergite tomentum, setation, and internal male genitalia

Species	Abdominal Tergites ♂ (dorsal) ♀	Important Setae	Phallus (Lateral)	Subepandrial Sclerite (Ventral)
Lasiopogon actius Melander 1923		Mystax white. Scutal bristles black except white (rarely black) dorsocentrals, fine hairs white. Femur with fine hairs white. Scape setae yellow.		
Lasiopogon dimicki Cole & Wilcox 1938		Mystax black, some setae gold-tipped. Scutal setae black, abundant. Femur with fine hairs golden. Scape setae black.		
Lasiopogon puyallupi Cole & Wilcox 1938 **stat. nov.**		Mystax black. Scutal setae black. Femur covered with fine white hairs basally, apical 40% of femur with black hairs instead. Scape setae black.		
Lasiopogon ripicola Melander 1923		Mystax yellow-white, black, or mixed. Scutal bristles black, fine hairs usually pale medially and dark laterally. Femur with fine hairs all white. Scape setae white and black.		
Lasiopogon willametti Cole & Wilcox 1938		Mystax black. Scutal setae black, abundant. Femur covered with fine white hairs basally, apical 30% of femur with black hairs instead. Scape setae black.		

0.2 MM


Epandrium
(dorsal)
(Lateral)
Gonocoxite/Hypandrium Complex
(Ventral)
(Lateral)
(Apical)

Species	Abdominal Tergites ♂ (dorsal) ♀	Important Setae	Phallus (Lateral)	Subepandrial Sclerite (Ventral)
Lasiopogon albidus Cole & Wilcox 1938		Mystax white. Scutal setae white to golden. Scape setae yellow.		
Lasiopogon arenicola (Osten Sacken 1877)		Mystax white. Scutal setae white to golden. Scape setae white.		
Lasiopogon asilomar McKnight **sp. nov.**		Mystax white. Scutal setae white to golden. Scape setae white.		
Lasiopogon drabicolum Cole 1916		Mystax mainly white, rarely mainly black. Scutal bristles black, fine hairs white. Scape setae white.		
Lasiopogon esau McKnight **sp. nov.**		Mystax mainly black with white hairs ventrally. Scutal setae black. Scape setae white.		

0.2 MM


Epandrium
(dorsal)
(Lateral)
Gonocoxite/Hypandrium Complex
(Ventral)
(Lateral)
(Apical)

Species	Abdominal Tergites ♂ (dorsal) ♀	Important Setae	Phallus (Lateral)	Subepandrial Sclerite (Ventral)
Lasiopogon anaphlecter McKnight **sp. nov.**		Mystax black. Scutal setae black. Scape setae black.		
Lasiopogon californicus Cole & Wilcox 1938		Mystax black. Scutal setae black. Scape setae white.		
Lasiopogon nelsoni McKnight **sp. nov.**		Mystax black with a few white hairs ventrally. Scutal setae black. Scape setae white.		
Lasiopogon odontotus McKnight **sp. nov.**		Mystax black, rarely with some white hairs ventrally. Scutal setae black. Scape setae white.		
Lasiopogon sierra McKnight **sp. nov.**		Mystax black, rarely with a few white hairs ventrally. Scutal setae black. Scape setae white.		

0.2 MM


Epandrium
(dorsal)
(Lateral)
Gonocoxite/Hypandrium Complex
(Ventral)
(Lateral)
(Apical)

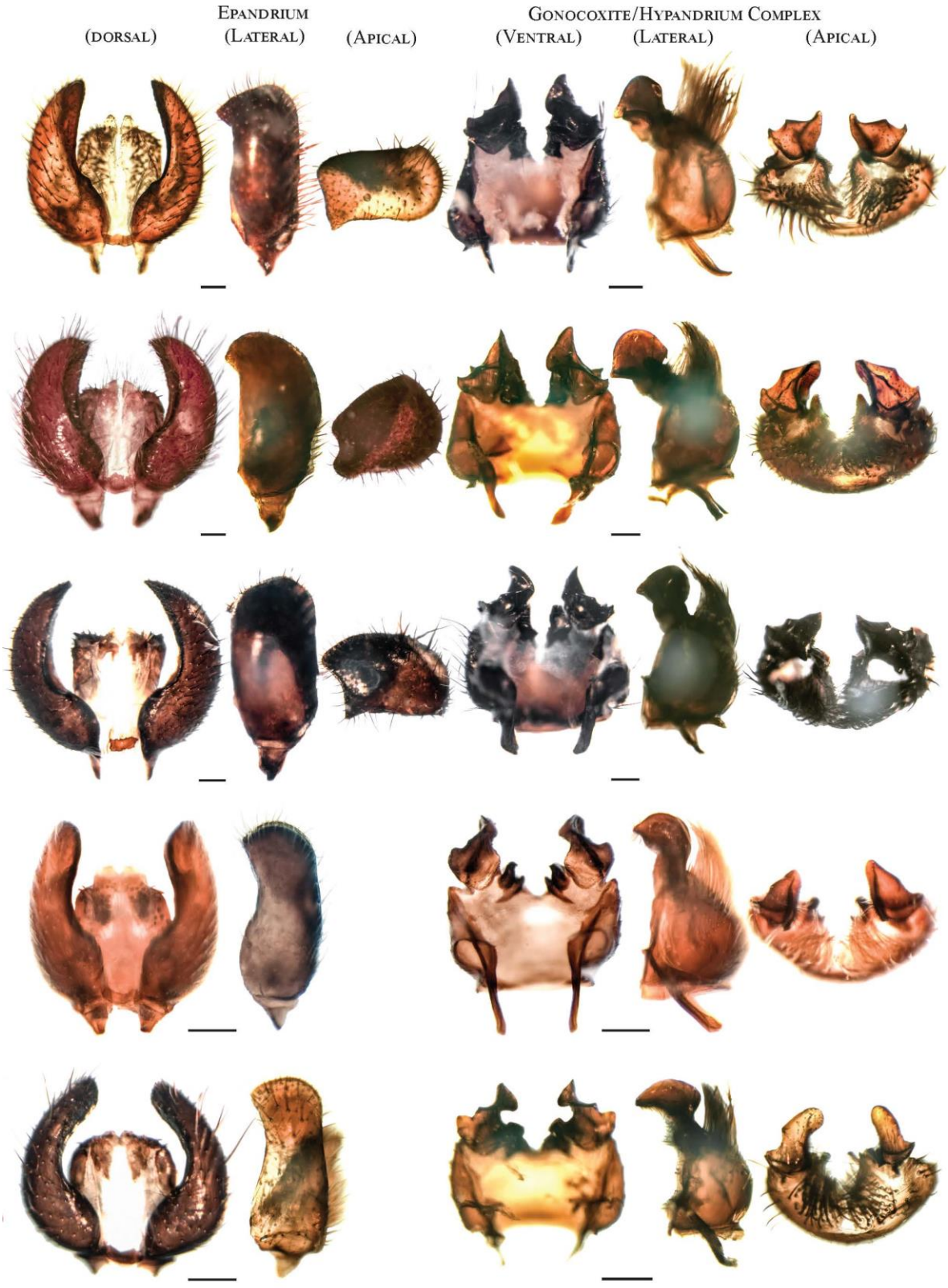
Species	Abdominal Tergites ♂ (dorsal) ♀	Important Setae	Phallus (Lateral)	Subepandrial Sclerite (Ventral)
Lasiopogon apoecus McKnight **sp. nov.**		Mystax black. Scutal setae black. Scape setae black.		
Lasiopogon condylophorus McKnight **sp. nov.**		Mystax black. Scutal setae black, hairs abundant. Scape setae black.		
Lasiopogon gabrieli Cole & Wilcox 1938		Mystax black. Scutal setae black. Scape setae black, rarely a few white hairs.		
Lasiopogon wilcoxi McKnight **sp. nov.**		Mystax black. Scutal setae black. Scape setae black.		
Lasiopogon zonatus Cole & Wilcox 1938		Mystax black. Scutal setae black. Scape setae mixed white and black.		

0.2 MM

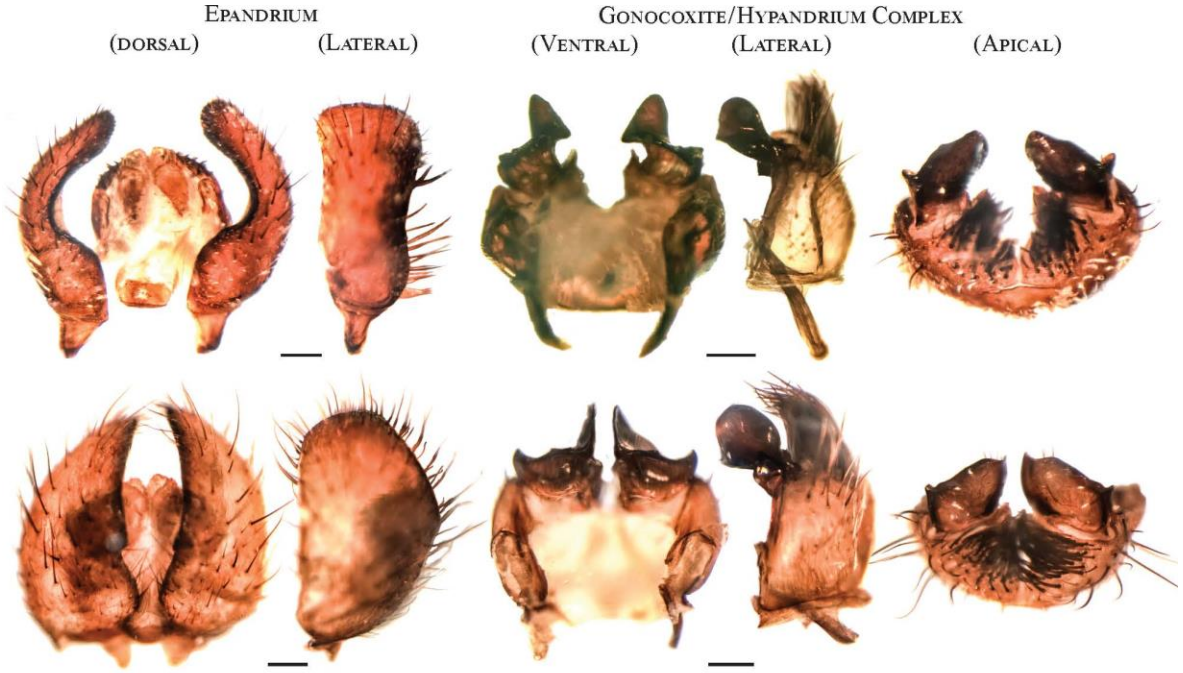

Epandrium
(dorsal)
(Lateral)
Gonocoxite/Hypandrium Complex
(Ventral)
(Lateral)
(Apical)

Species	Abdominal Tergites ♂ (dorsal) ♀	Important Setae	Phallus (Lateral)	Subepandrial Sclerite (Ventral)
Lasiopogon bivittatus Loew 1866		Mystax black. Scutal setae black, some white hairs on ppnl in male. Femur covered with fine white hairs basally, apical 40% of femur with black hairs instead. Scape setae black.		
Lasiopogon canningsi McKnight **sp. nov.**		Mystax black. Scutal setae black, lateral hairs on ppnl black. Femur with white hairs over all but tibial joint. Scape setae black.		
Lasiopogon tumilicola McKnight **sp. nov.**		Mystax black. Scutal setae black. Femur covered with fine white hairs basally, apical 40% of femur with black hairs instead. Scape setae black.		
Lasiopogon littoris Cole 1924		Mystax white. Scutal setae white. Scape setae white.		
Lasiopogon bitumineus McKnight **sp. nov.**		Mystax black. Scutal setae black, bristles very long and prominent. Scape setae black.		

0.2 MM


Epandrium
(dorsal)
(Lateral)
(Apical)
Gonocoxite/Hypandrium Complex
(Ventral)
(Lateral)
(Apical)

Species	Abdominal Tergites ♂ (dorsal) ♀	Important Setae	Phallus (Lateral)	Subepandrial Sclerite (Ventral)
Lasiopogon karli McKnight **sp. nov.**		Mystax black. Scutal bristles black, fine hairs white or black. Scape setae white and black.		
Lasiopogon martinensis Cole & Wilcox 1938		Mystax black. Scutal setae black, anterior dorsocentral bristles fine but relatively long; fine hairs semi-erect. Scape setae white.	 0.2 MM	


Epandrium
(dorsal)
(Lateral)
Gonocoxite/Hypandrium Complex
(Ventral)
(Lateral)
(Apical)

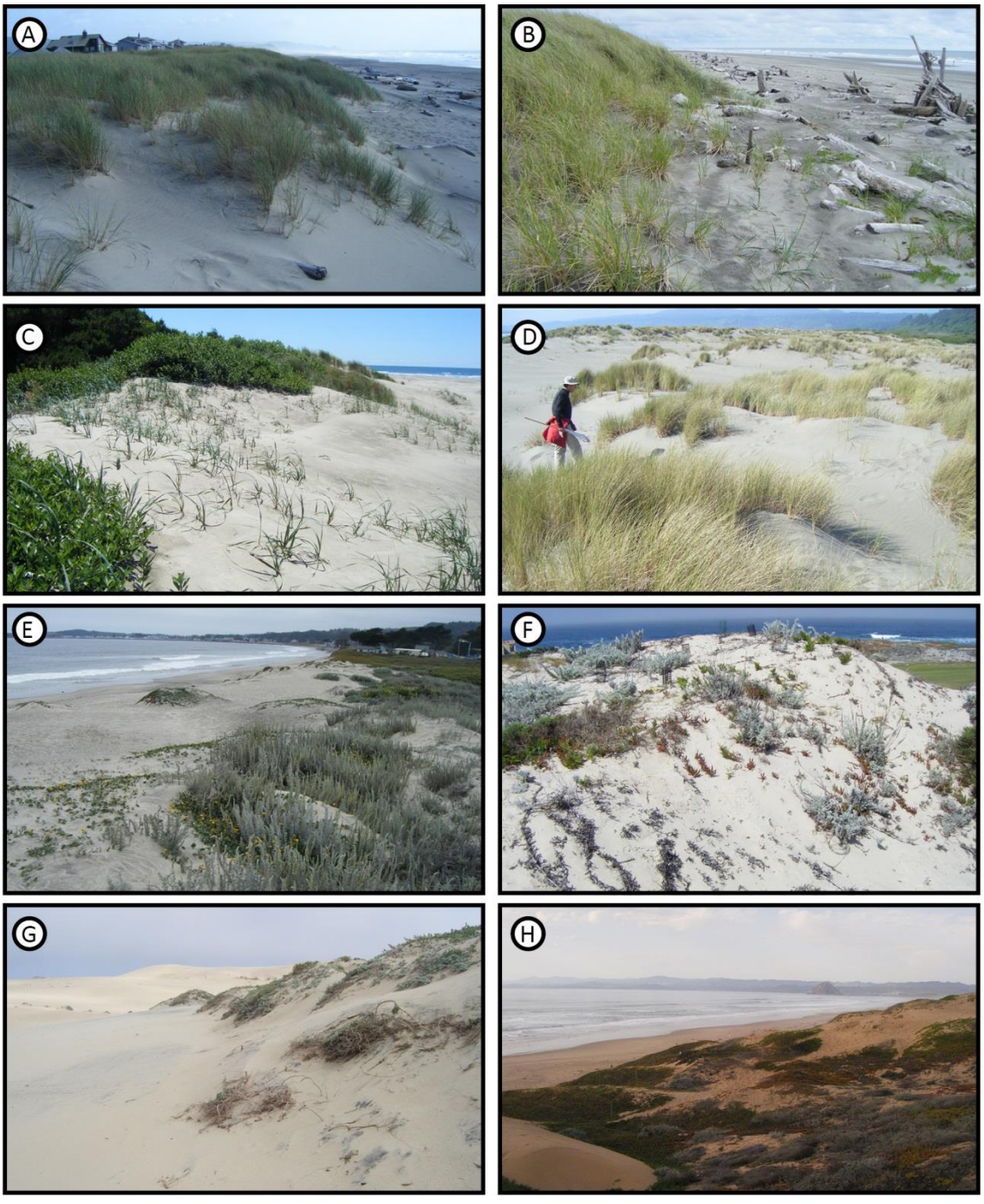

A
B
C
D
E
F
G
H

Fig. III.6. Habitats for coastal sand-perching Lasiopogon species in this revision.
A) U.S.A.: Oregon: Lincoln Co., Gleneden Beach, NW tip of Salishan Spit, N 44.9201° W 124.0269°, 17.v.2012 (L. actius on foredune, L. tumulicola sp. nov. in backdunes)
B) U.S.A.: Washington: Gray's Harbor Co., Westhaven State Park, dunes 2 mi NW of Westport, N 46.9024° W 124.1284°, 20.vi.2013 (L. actius)
C) U.S.A.: Oregon: Lincoln Co., Newport, Agate Beach State Park dunes, N 44.6580° W 124.0573°, 21.vi.2013 (L. dimicki)
D) U.S.A.: California: Humbolt Co., Clam Beach County Park ~5 mi SE of Trinidad, N 40.9935° W 124.1162°, 15.v.2012 (L. canningsi sp. nov.)
E) U.S.A.: California: San Mateo Co., Half Moon Bay State Beach, N 37.4800° W 122.4510°, 5.vi.2013 (L. arenicola)
F) U.S.A.: California: Monterey Co., Pacific Grove golf course, dunes in SW corner, N 36.6330° W 121.9362°, 11.v.2012 (L. asilomar sp. nov.)
G) U.S.A.: California: Santa Barbara Co., Rancho Guadalupe Dunes 1 mi S of parking lot, N 34.9499° W 120.6554°, 9.v.2012 (L. littoris)
H) U.S.A.: California: San Luis Obispo Co., Montaña de Oro State Park, dunes @ Sand Spit trailhead, N 35.3021° W 120.8753°, 12.iii.2014 (L. bitumineus sp. nov., L. littoris weeks later)

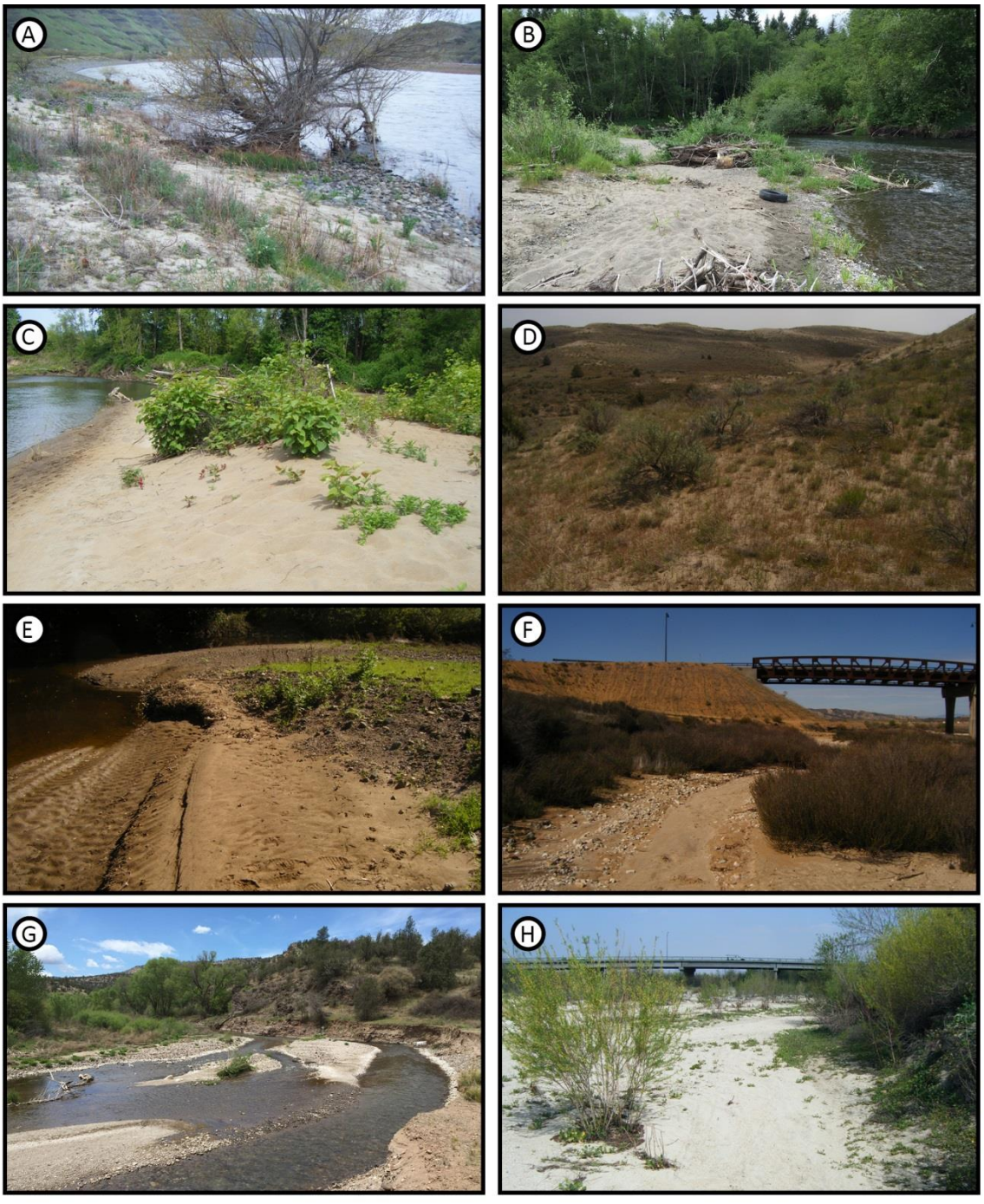

A
B
C
D
E
F
G
H

Fig. III.7. Habitats for inland sand-perching Lasiopogon species in this revision.
A) U.S.A.: Washington: Asotin Co., Snake River, sandy bank 4 mi S of Asotin jct Hwy 129, N 46.3037° W 117.0038°, 21.iv.2014 (L. ripicola)
B) U.S.A.: Washington: Thurston Co., Tumwater, Deschutes River @ Pioneer Park, N 46.9940° W 122.8881°, 15.v.2015 (L. puyallupi stat. nov.)
C) U.S.A.: Oregon: Linn Co., Crabtree Creek @ Hwy 226 bridge 8 mi N of Lebanon, N 44.6548° W 122.8519°, 19.v.2012 (L. willametti)
D) U.S.A.: Washington: Franklin Co., Juniper Dunes Wilderness, N entrance, 18 mi NE of Pasco, N 46.4249° W 118.8301°, 20.iv.2014 (L. albidus)
E) U.S.A.: California: Marin Co., San Antonio Creek, San Antonio Rd 4.5 mi S of Petaluma, N 38.1790° W 122.6283°, 15.iii.2014 (L. zonatus, L. esau sp. nov.)
F) U.S.A.: California: Riverside Co., Little San Gorgonio Creek @ Potrero blvd bridge, 2 mi NW of Beaumont, N 33.9411° W 117.0156°, 9.iii.2014 (L. wilcoxi sp. nov.)
G) U.S.A.: New Mexico: Grant Co., Gila River below Forks campsite, N 33.1842° W 108.2044°, 6.v.2015 (L. karli sp. nov.)
H) U.S.A.: California: Riverside Co., Santa Ana River at Mt. Rubidoux, N 33.9895° W 117.3928°, 4.iii.2013 (L. drabicolum)

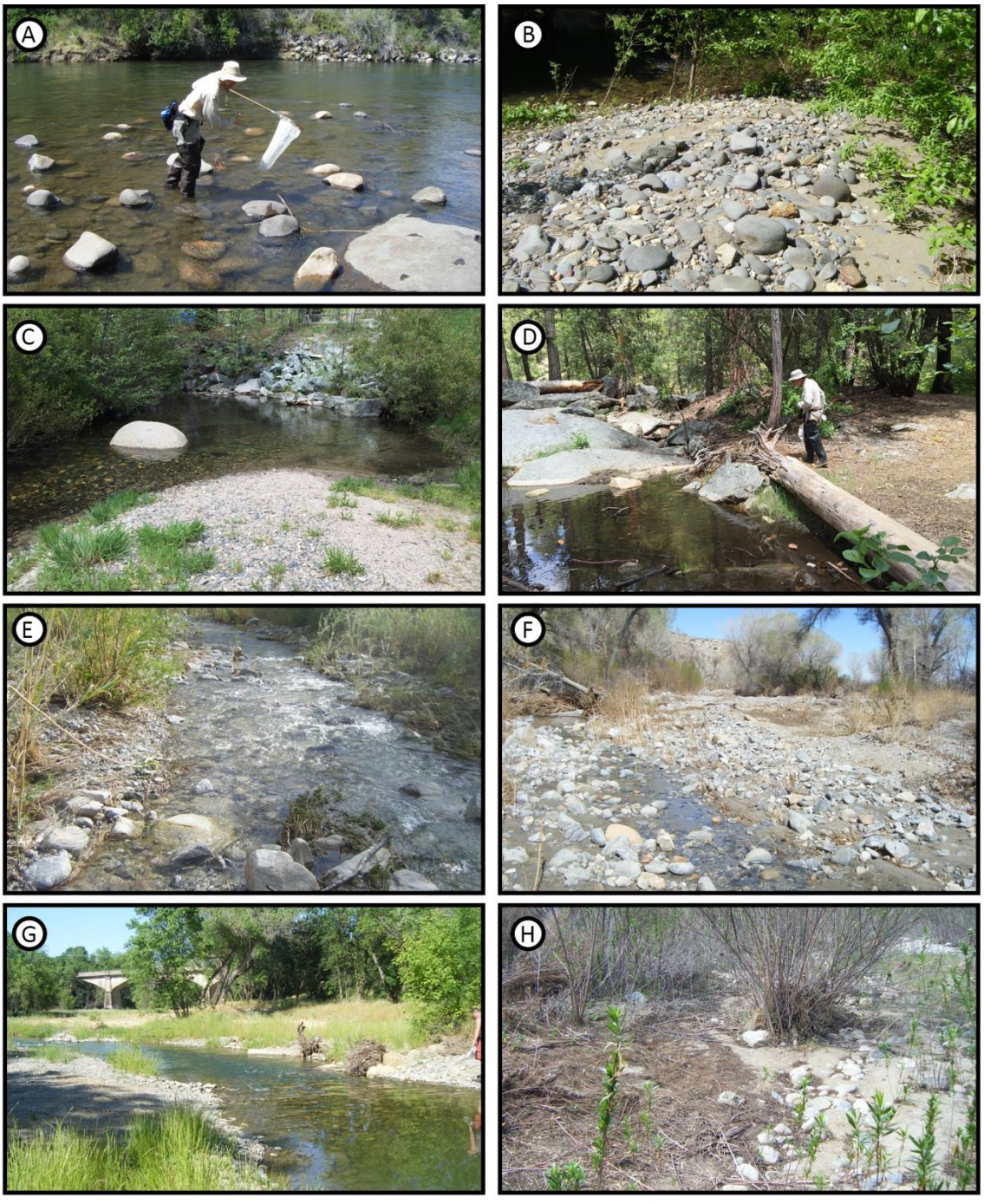

A
B
C
D
E
F
G
H

Fig. III.8. Habitats for inland rock-perching Lasiopogon species in this revision.
A) U.S.A.: Nevada: Washoe Co., Mogul, Truckee River @ Mayberry Crossing Park, N 39.5026° W 119.8974°, 13-14.v.2012 (L. sierra sp. nov.)
B) U.S.A.: California: Shasta Co., Little Cow Creek, Hwy 299 turnoff 4.2 km SW jct Oak Run Road, N 40.7392° W 122.0710°, 14.v.2012 (L. sierra sp. nov.)
C) U.S.A.: California: Mariposa Co., Summerdale campground, Big Creek, N 37.4895° W 119.6341°, 22.v.2016 (L. anaphlecter sp. nov.)
D) U.S.A.: California: Madera Co., Willow Creek, pools by Angle Falls parking lot, 1 mi N of Bass Lake, N 37.3352° W 119.5703°, 22.v.2016 (L. anaphlecter sp. nov.)
E) U.S.A.: California: Los Angeles Co., Big Tujunga River, 4 km NE of Sunland, N 34.2916° W 118.2878°, 7.iii.2014 (L. nelsoni sp. nov.)
F) U.S.A.: California: Los Angeles Co., Rock Creek Wash jct Valyermo Rd, 4 mi SE of Pearblossom, N 34.4637° W 117.8643°, 8.iii.2014 (L. nelsoni sp. nov.)
G) U.S.A.: California: Solano Co., Winters, Putah Creek @ jct Winters Rd and Putah Creek Rd, N 38.5201° W 121.9676°, 12.v.2012 (L. californicus)
H) U.S.A.: California: San Diego Co., San Luis Rey River, 5 km SE of Pauma Valley city, N 33.2605° W 116.9449°, 6.iii.2013 (L. gabrieli)

Table III.1. Taxonomy, collection data, genetic sampling, and voucher information for specimens used in the *Lasiopogon* species tree. If multiple voucher numbers are listed for a specimen, the first is for the DNA extract and the second is for the physical specimen.

Taxon	Locality	GenBank #				Specimen Voucher(s)
		AATS	COI	PEPCK	WG	
Lasiopogon actius Melander	USA: Oregon: Douglas Co., Ziolkouski Beach Park, 2 mi W of Winchester Bay, N 43.66264° W 124.2067°, 16.v.2012, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-331-2
Lasiopogon actius Melander	USA: Oregon: Lincoln Co., Newport, S side Yaquinna River mouth, dunes E of South Jetty Rd, N 44.61255° W 124.069057°, 17.v.2012, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-334-1
Lasiopogon actius Melander	Canada: Haida Gwaii: Graham Island, Tlell, upper beach, vii.2014, col. B. Wijdeven	-	x	x	x	(DNA extract completely consumed) RBCM ENT017-001081
Lasiopogon albidus Cole and Wilcox	USA: Washington: Franklin Co., Juniper Dunes Wilderness, N entrance, 18 mi NE of Pasco, N 46.42486° W 118.83005°, 20.iv.2014, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-576-3
Lasiopogon albidus Cole and Wilcox	USA: Oregon: Lake Co., dunes 2 mi N of Alkali Lake, N 43.02169° W 119.98963°, 30.iv.2014, col. T. McKnight	-	x	-	x	UMMZ-TAM-622-1
Lasiopogon ald-1	USA: California: Del Norte Co., Jedediah Smith Redwoods State Park, shore of Mill Creek, N 41.7870° W 124.089°, 11.vii.1989, col. E.M. Fisher	-	BOLD	-	-	RBCM ENT011-013309
Lasiopogon ald-1	USA: California: Del Norte Co., Jedediah Smith Redwoods State Park, shore of Mill Creek, N 41.7870° W 124.089°, 11.vii.1989, col. E.M. Fisher	-	BOLD	-	-	RBCM ENT011-013311
Lasiopogon ald-2	USA: Oregon: Hood River Co., E Fork Hood River at Sherwood campground, 6	x	x	x	x	UMMZ-TAM-472-1

	mi E of Mt. Hood peak, N 45.39434° W 121.56982°, 15.vi.2013, col. T. McKnight					
Lasiopogon ald-2	USA: Oregon: Hood River Co., E Fork Hood River at Sherwood campground, 6 mi E of Mt. Hood peak, N 45.39434° W 121.56982°, 15.vi.2013 , col. T. McKnight	x	x	-	x	UMMZ-TAM-472-2
Lasiopogon ald-2	USA: Washington: Yakima Co., American River, 9.5 mi SW jct Hwy 410 & Bumping River Rd, N 46.95361° W 121.29615°, 10.vii.2014, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-666-1
Lasiopogon aldrichii Melander	USA: Colorado: Summit Co., Vail Pass, conifer forest openings, N 39.5247° W 106.2217°, 22.vii.2015, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-821-1
Lasiopogon aldrichii Melander	USA: Wyoming: Albany Co., Medicine Bow Mtns, Hwy 130, Green Rock trailhead, meadow, stream, 5 mi NW of Centennial, N 41.34826° W 106.21773°, 23.vi.2016, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-896-1
Lasiopogon aldrichii Melander	USA: Colorado: Las Animas Co., below Cordova Pass, 17.vii.2012, col. W. Cranshaw, B. Kondratieff, D. Leatherman	x	x	x	x	UMMZ-TAM-CSU-4
Lasiopogon anaphlecter sp. nov.	USA: California: Tuolumne Co., Carlon day area, S Fk Tuolumne River banks, N 37.81243° W 119.85957°, 20.v.2016, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-859-1
Lasiopogon anaphlecter sp. nov.	USA: California: Tuolumne Co., Carlon day area, S Fk Tuolumne River banks, N 37.81243° W 119.85957°, 20.v.2016, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-859-2
Lasiopogon anaphlecter sp. nov.	USA: California: Mariposa Co., Summerdale campground, Big Creek, N 37.48948° W 119.63408°, 22.v.2016, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-871-1

Lasiopogon apache Cannings	USA: Utah: Garfield Co., Pine Creek at The Box Trailhead, E of Pine Cr. Rd., N 37°51'44" W 111°38'14", 1.v.2001, col. K.F. Kuehnl	-	x	x	x	UMMZ-TAM-BYU-1
Lasiopogon apache Cannings	USA: Utah: Garfield Co., Pine Creek at The Box Trailhead, E of Pine Cr. Rd., N 37°51'44" W 111°38'14", 1.v.2001, col. K.F. Kuehnl	-	x	x	x	UMMZ-TAM-BYU-2
Lasiopogon apache Cannings	USA: Arizona: Santa Cruz Co., Coronado Nat'l For., Medera Crk nr. Bog Sprgs. Capgrd., N 31°43'41" W 110°52'43", 16.vii.1995, col. S.D. Gaimari	-	x	-	x	UMMZ-TAM-INHS-17
Lasiopogon appalachensis Cannings	USA: Kentucky: Rockcastle Co., Rockcastle River at Fester Rd crossing, 6 mi SE of Mt. Vernon, N 37.30155° W 84.23158°, 13.v.2013, col. T. McKnight	-	x	x	x	UMMZ-TAM-405-1
Lasiopogon appalachensis Cannings	USA: Tennessee: Scott Co., Big South Fork Cumberland River, Hwy 297 at Leatherwood Crossing, 8 mi W of Oneida, N 36.47751° W 84.66856°, 14.v.2013, col. T. McKnight	-	x	-	-	UMMZ-TAM-409-1
Lasiopogon appalachensis Cannings	USA: Tennessee: Scott Co., Big South Fork Cumberland River, Hwy 297 at Leatherwood Crossing, 8 mi W of Oneida, N 36.47751° W 84.66856°, 14.v.2013, col. T. McKnight	x	x	-	x	UMMZ-TAM-409-3
Lasiopogon arenicola (Osten Sacken)	USA: California: San Mateo Co., Half Moon Bay State Beach, N 37.47997° W 122.45096°, 5.vi.2013, col. T. McKnight	-	x	-	-	UMMZ-TAM-431-1
Lasiopogon arenicola (Osten Sacken)	USA: California: San Mateo Co., Half Moon Bay State Beach, N 37.47997° W 122.45096°, 5.vi.2013, col. T. McKnight	-	x	-	x	UMMZ-TAM-431-2

Lasiopogon arenicola (Osten Sacken)	USA: California: San Mateo Co., Half Moon Bay State Beach, N 37.47997° W 122.45096°, 5.vi.2013, col. T. McKnight	-	x	x	x	UMMZ-TAM-431-3
Lasiopogon asilomar sp. nov.	USA: California: Monterey Co., Pacific Grove golf course, dunes in SW corner, N 36.63303° W 121.93624°, 11.v.2012, col. T. McKnight	-	x	-	x	UMMZ-TAM-314-2
Lasiopogon asilomar sp. nov.	USA: California: Monterey Co., Pacific Grove golf course, dunes in SW corner, N 36.63303° W 121.93624°, 11.v.2012, col. T. McKnight	-	x	-	x	UMMZ-TAM-314-4
Lasiopogon asilomar sp. nov.	USA: California: Monterey Co., Pacific Grove golf course, dunes in SW corner, N 36.63303° W 121.93624°, 11.v.2012, col. T. McKnight	-	x	x	x	UMMZ-TAM-314-6
Lasiopogon bitumineus sp. nov.	USA: California: San Luis Obispo Co., Oceano dunes at Pismo State beach, 1 km S of Oceano, *Ericameria* gully, N 35.08746° W 120.61552°, 12.iii.2014, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-546-2
Lasiopogon bitumineus sp. nov.	USA: California: San Luis Obispo Co., Oceano dunes at Pismo State beach, 1 km S of Oceano, *Ericameria* gully, N 35.08746° W 120.61552°, 12.iii.2014, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-546-3
Lasiopogon bitumineus sp. nov.	USA: California: San Luis Obispo Co., Montaña de Oro State Park, dunes at Sand Spit trailhead, upper (*Ericameria*), N 35.30111° W 120.87299°, 12.iii.2014, col. T. McKnight	-	x	-	x	UMMZ-TAM-547-1
Lasiopogon bivittatus Loew	USA: California: San Francisco Co., Fort Funston, dunes by Battery Davis, N 37.71862° W 122.50398°, 14.iii.2014,	-	x	-	-	UMMZ-TAM-556-1

	col. T. & K. McKnight					
Lasiopogon bivittatus Loew	USA: California: Marin Co., Point Reyes beach, streams S of N beach parking lot, N 38.07444° W 122.97589°, 14.iii.2014, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-557-2
Lasiopogon bivittatus Loew	USA: California: Marin Co., Point Reyes beach, streams S of N beach parking lot, N 38.07444° W 122.97589°, 14.iii.2014, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-557-3
Lasiopogon californicus Cole and Wilcox	USA: California: Solano Co., Winters, Putah Creek at jct Winters Rd and Putah Creek Rd, N 38.52012° W 121.96758°, 12.v.2012, col. T. McKnight, E.M. Fisher, M. Hauser	x	x	x	x	UMMZ-TAM-318-1
Lasiopogon californicus Cole and Wilcox	USA: California: Yolo Co., Putah Creek, Winters, N 38° 28' 53.05" W 122° 01' 38.27", 21.v.2016, col. C.E. Herbert	-	x	x	x	(DNA extract completely consumed) UMMZ-TAM-CEH-20160521-1
Lasiopogon californicus Cole and Wilcox	USA: California: Mendocino Co., Hendy Woods S.P., Navarro R., N 39° 04' 37" W 123° 28' 19", 12.vi.2009, E.M. & J. Fisher	-	x	x	x	UMMZ-TAM-RBCM-22 RBCM ENT017-001082
Lasiopogon californicus Cole and Wilcox	USA: California: Mendocino Co., Hendy Woods S.P., Navarro R., N 39° 04' 37" W 123° 28' 19", 12.vi.2009, E.M. & J. Fisher	x	x	-	x	UMMZ-TAM-RBCM-23 RBCM ENT017-001083
Lasiopogon can-1	CANADA: Alberta: Edmonton, McKinnon Ravine, 10.v.2010, col. John H. Acorn	x	x	x	x	(DNA extract completely consumed) RBCM ENT011-013321
Lasiopogon can-1	CANADA: Alberta: Edmonton, upstream of McKinnon Ravine, 16.vi.2009, col. John H. Acorn, Christianne McDonald	x	x	x	x	UMMZ-TAM-RBCM-15 RBCM ENT011-013322
Lasiopogon canningsi sp.	USA: California: Humbolt Co., Trinidad State Beach, Trinidad, N 41.05807° W	x	x	x	X	UMMZ-TAM-328-3

nov.	124.149325°, 15.v.2012, col. T. & K. McKnight					
Lasiopogon canningsi sp. nov.	USA: California: Humbolt Co., Trinidad State Beach, Trinidad, N 41.05807° W 124.149325°, 15.v.2012, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-328-5
Lasiopogon canningsi sp. nov.	USA: Oregon: Curry Co., Crissey Field SP, beach dunes, N 42.0022° W 124.2133°, 13.v.2015, col. T. McKnight	-	x	x	x	UMMZ-TAM-780-1
Lasiopogon canningsi sp. nov.	USA: California: Mendocino Co., MacKerricher State Park, N 39° 29' 25" W 123° 47' 39", 10.vi.2009, col. E.M. Fisher	X	x	x	x	UMMZ-TAM-RBCM-1 RBCM ENT017-001084
Lasiopogon canus Cole and Wilcox	CANADA: Yukon, Desadeash River dunes, N 60.66817° W 137.8001°, 26.vi.2008, col. L. Randall	X	x	x	x	UMMZ-TAM-RBCM-12 RBCM ENT011-013329
Lasiopogon canus Cole and Wilcox	CANADA: Yukon, Desadeash River dunes, N 60.66817° W 137.8001°, 26.vi.2008, col. L. Randall	X	x	x	x	UMMZ-TAM-RBCM-8 RBCM ENT011-013328
Lasiopogon chaetosus Cole and Wilcox	USA: Oregon: Lake Co., Abert Lake, N end, E Side Highway 395, N 42°44'21" W 120°06'46", 27.v.1995, col. R.A. Cannings, H. Nadel	-	BOLD	-	-	RBCM ENT998-005085
Lasiopogon chaetosus Cole and Wilcox	USA: Oregon: Lake Co., Alkali Lake, 2.5 km N on Hwy 395, N 42°59.5' W 119°59.6', 27.v.1995, col. R.A. Cannings, H. Nadel	-	x	-	-	UMMZ-TAM-RBCM-38 RBCM ENT998-005042
Lasiopogon chrysotus Cannings	USA: Tennessee: Scott Co., Big South Fork Cumberland River, Hwy 297 at Leatherwood Crossing, 8 mi W of Oneida, N 36.47751° W 84.66856°, 14.v.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-409-2
Lasiopogon cinctus	Belarus: Minsk: Molodechno dist., vic. Radoshkovichi town, sandy road in pine	x	x	x	x	UMMZ-TAM-BELA-1

(Fabricius)	forest, N 54° 12' 24.38'' E 27° 15' 8.13", 25.v.2014, col. V. Sakhvon					
Lasiopogon cinctus (Fabricius)	Sweden: SÖ: Nyköping Strandbadet Byggninge, path to beach near parking; N 58.7801° E 17.3917°; 30 May 2009; col. K.C. Holston	KY914514	KY914514	KY914497	KY914530	(DNA extract completely consumed) UMMZ-TAM-RBCM-17
Lasiopogon cinctus (Fabricius)	Sweden: SÖ: Nyköping Strandbadet Byggninge, path to beach near parking; N 58.7801° E 17.3917°; 30 May 2009; col. K.C. Holston	x	x	x	x	UMMZ-TAM-RBCM-7 RBCM ENT017-001085
Lasiopogon cinereus Cole	USA: Oregon: Deschutes Co., Sisters, Whychus Creek, N 44.29001° W 121.53302°, 13.vi.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-464-1
Lasiopogon cinereus Cole	USA: Washington: Yakima Co., Naches River 100 m W jct Tieton River, at Hwy 12 bridge, N 46.74597° W 120.78862°, 18.vi.2013, col. T. McKnight	-	x	x	x	UMMZ-TAM-479-1
Lasiopogon cinereus Cole	USA: California: Del Norte Co., Jedediah Smith Redwoods SP, Mill Creek at DRA grove, N 41.7867° W 124.0893°, 14.vii.2014, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-687-2
Lasiopogon coconino Cannings	USA: Arizona: Coconino Co., Oak Creek, 0.5 mi S of Cave Springs campground, N 34.9945° W 111.7376°, 3.v.2015, col. T. & K. McKnight	x	x	-	x	UMMZ-TAM-741-1
Lasiopogon coconino Cannings	USA: New Mexico: Grant Co., Black Canyon campground, sandbar above river, N 33.1853° W 108.0318°, 5.v.2015, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-750-1
Lasiopogon coconino Cannings	USA: Arizona: Yavapi Co., West Fork Oak Creek, Oak Creek Canyon, 3.vi.2003, col. B. Kondratieff, J. Schmidt	x	x	x	x	UMMZ-TAM-CSU-1
Lasiopogon currani Cole	USA: NY: St. Lawrence Co., Glen Meal State Park, clearing opposite N entrance,	-	x	x	x	UMMZ-TAM-59-1

and Wilcox	N 44.53135° W 75.01994°, 3-4.v.2010, col. T. McKnight					
Lasiopogon currani Cole and Wilcox	USA: NY: St. Lawrence Co., Glen Meal State Park, clearing opposite N entrance, N 44.53135° W 75.01994°, 3-4.v.2010, col. T. McKnight	-	x	x	x	UMMZ-TAM-59-2
Lasiopogon currani Cole and Wilcox	USA: NY: St. Lawrence Co., Glen Meal State Park, clearing opposite N entrance, N 44.53135° W 75.01994°, 3-4.v.2010, col. T. McKnight	x	x	x	x	UMMZ-TAM-59-4
Lasiopogon dimicki Cole and Wilcox	USA: Oregon: Lincoln Co., Newport, South Beach State Park trailhead, N 44.60146° W 124.06497°, 17.v.2012, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-333-1
Lasiopogon dimicki Cole and Wilcox	USA: Oregon: Lincoln Co., Newport, Agate Beach State Park dunes, N 44.65795° W 124.05732°, 21.vi.2013, col. T. McKnight	-	x	-	x	UMMZ-TAM-487-2
Lasiopogon dimicki Cole and Wilcox	USA: Oregon: Lincoln Co., Newport, Agate Beach State Park dunes, N 44.65795° W 124.05732°, 21.vi.2013, col. T. McKnight	-	x	x	x	UMMZ-TAM-487-3
Lasiopogon drabicolum Cole	USA: California: San Luis Obispo Co., San Simeon Creek, rapids above bridge ~4 mi E of San Simeon, N 35.60795° W 121.09053°, 10.v.2012, col. T. McKnight	-	x	-	x	(DNA extract completely consumed) UMMZ-TAM-312-9
Lasiopogon drabicolum Cole	USA: California: Riverside Co., Santa Ana River at Mt. Rubidoux, N 33.98948° W 117.39281°, 4.iii.2013, col. T. McKnight	-	x	x	x	UMMZ-TAM-391-1
Lasiopogon drabicolum Cole	USA: California: Riverside Co., Santa Ana River at Mt. Rubidoux, N 33.98948° W 117.39281°, 4.iii.2013, col. T. McKnight	-	x	x	x	UMMZ-TAM-391-2
Lasiopogon esau sp. nov.	USA: California: Marin Co., San Antonio Creek, San Antonio Rd 4.5 mi S of	-	x	x	x	UMMZ-TAM-562-4

	Petaluma, N 38.17899° W 122.62826°, 15.iii.2014, col. T. & K. McKnight					
Lasiopogon esau sp. nov.	USA: California: Trinity Co., Hayfork, Hayfork Creek near Forest Ave, N 40.54509° W 123.16681°, 24.v.2016, col. T. & K. McKnight	-	-	-	x	UMMZ-TAM-879-2
Lasiopogon esau sp. nov.	USA: California: Humboldt Co., S Fork Eel River, Hwy 254 1.2km N of Miranda, sandbars at forest edge, N 40.248° W 123.824°, 10.v.1995, col. R.A. Cannings, H. Nadel	-	BOLD	-	-	RBCM ENT010-002770
Lasiopogon fumipennis Melander	USA: Oregon: Hood River Co., E Fork Hood River at Sherwood campground, 6 mi E of Mt. Hood peak, N 45.39434° W 121.56982°, 15.vi.2013, col. T. McKnight	KY906304	KY914521	KY914504	KY914536	UMMZ-TAM-472-3
Lasiopogon fumipennis Melander	USA: Washington: Yakima Co., Lodgepole campsite on American River, 18 mi E of Mt. Rainier peak, N 46.91474° W 121.38525°, 18.vi.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-480-1
Lasiopogon fumipennis Melander	USA: Washington: Clallam Co., stream at Switchback trailhead jct Hurricane Ridge Rd, 10 mi S of Port Angeles, N 47.9871° W 123.4613°, 13.vii.2014, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-682-2
Lasiopogon gabrieli Cole and Wilcox	USA: California: San Diego Co., Pala, San Luis Rey River wash jct Bompas Wash, N 33.36298° W 117.06455°, 6.iii.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-395-1
Lasiopogon gabrieli Cole and Wilcox	USA: California: San Diego Co., San Luis Rey River, 5 km SE of Pauma Valley city, N 33.26048° W 116.94488°, 6.iii.2013, col. T. McKnight	-	x	x	-	UMMZ-TAM-396-1
Lasiopogon	USA: California: Riverside Co., San	x	x	-	x	UMMZ-TAM-543-1

gabrieli Cole and Wilcox	Jacinto River, Hwy 74, 2 mi E of NF boundary, dry sagebrush slopes, N 33.72265° W 116.80581°, 10.iii.2014, col. T. McKnight					
Lasiopogon gabrieli Cole and Wilcox	USA: California: Riverside Co., San Jacinto River, Hwy 74, 2 mi E of NF boundary, cattails/sand in wash, N 33.72741° W 116.80946°, 10.iii.2014, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-544-2
Lasiopogon hinei Cole and Wilcox	MONGOLIA: Hovsgol Aimag: Renchinlhumbe Soum, Arsayn Gol, 16.2 km N of Renchinlhumbe town, N 51.25356° E 99.66687°, 2.vii.2006, col. C.R. Nelson, Selenge River Project	-	x	x	x	UMMZ-TAM-CRN-8478-1
Lasiopogon hinei Cole and Wilcox	MONGOLIA: Hovsgol Aimag: Renchinlhumbe Soum, Arsayn Gol, 16.2 km N of Renchinlhumbe town, N 51.25356° E 99.66687°, 2.vii.2006, col. C.R. Nelson, Selenge River Project	-	x	-	x	UMMZ-TAM-CRN-8478-2
Lasiopogon hinei Cole and Wilcox	CANADA: Alberta, Gull Lake summer village, 25.v.2009, col. J.H. Acorn	-	x	x	x	UMMZ-TAM-RBCM-24 RBCM ENT017-001086
Lasiopogon hinei Cole and Wilcox	CANADA: Alberta, Jackpine woods E of Redwater, 12.vi.2009, col. J.H. Acorn, J. Glasier, C. Lecourtoise	x	x	x	x	UMMZ-TAM-RBCM-5 (No morphological voucher for this specimen.)
Lasiopogon karli sp. nov.	USA: New Mexico: Catron Co., Taylor Creek, 0.5 mi SW of Wall Lake, N 33.35° W 108.0831°, 5.v.2015, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-748-1
Lasiopogon karli sp. nov.	USA: New Mexico: Grant Co., Gila River below Forks campsite, N 33.1842° W 108.2044°, 6.v.2015, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-753-1
Lasiopogon	USA: Colorado: Mineral Co., East Fork	x	x	x	x	UMMZ-TAM-CSU-3

lavignei Cannings	Rd, FR 667, N Tie Creek, 11.vi.1998, col. B. Kondratieff, D. Leatherman					
Lasiopogon leleji Cannings	SOUTH KOREA: Kangwon Prov., E. coast, Hamaeanbang Maengbang Beach, N 37°23.458' E 129°13.793', 17.v.2006, col. C.L. Young	-	x	x	x	UMMZ-TAM-BISH-3
Lasiopogon littoris Cole	USA: California: Santa Barbara Co., Rancho Guadalupe Dunes 1 mi S of parking lot, N 34.94991° W 120.65542°, 9.v.2012, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-309-5
Lasiopogon littoris Cole	USA: California: San Luis Obispo Co., Oso Flaco Lake Preserve, path through dunes, N 35.03187° W 120.62658°, 9.v.2012, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-310-5
Lasiopogon littoris Cole	USA: California: San Luis Obispo Co., Atascadero State Beach, dunes 1 km N of Morro Rock, N 35.37927° W 120.86261°, 9.v.2012, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-311-1
Lasiopogon marshalli Cannings	USA: Virginia: Giles Co., New River at Pembroke, N 37.31504° W 80.64922°, 23.v.2013, col. T. McKnight	-	x	-	-	UMMZ-TAM-429-1
Lasiopogon marshalli Cannings	USA: Virginia: Giles Co., New River at Pembroke, N 37.31504° W 80.64922°, 23.v.2013, col. T. McKnight	-	x	-	x	UMMZ-TAM-429-2
Lasiopogon montanus Schiner	ITALY: Val. D'Aosta Prov.: Alpi Pennine, 2250m, vic. Montseuc, 0.75 km S Cogne, N 45°36'01" E 7°21'45", 28.vi.2008, col. E.M. Fisher	x	x	x	x	UMMZ-TAM-RBCM-16 RBCM ENT017-001087
Lasiopogon monticola Melander	USA: Oregon: Deschutes Co., Three Creek Meadow, 13 mi S of Sisters, N 44.11505° W 121.62432°, 13.vi.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-466-1
Lasiopogon	USA: Oregon: Deschutes Co., Three	x	x	x	x	UMMZ-TAM-466-2

monticola Melander	Creek Meadow, 13 mi S of Sisters, N 44.11505° W 121.62432°, 13.vi.2013, col. T. McKnight					
Lasiopogon monticola Melander	USA: Washington: Yakima Co., Lodgepole campsite on American River, 18 mi E of Mt. Rainier peak, N 46.91474° W 121.38525°, 18.vi.2013, col. T. McKnight	-	x	x	x	UMMZ-TAM-480-3
Lasiopogon monticola Melander	USA: Wyoming: Lincoln Co., FOBU, Millet Spring, Primary, 1.vii.2005, col. S. Griswold	x	x	x	x	UMMZ-TAM-MNAZ-3 MNA DIP 5.1635
Lasiopogon nelsoni sp. nov.	USA: California: San Luis Obispo Co., San Simeon Creek, rapids above bridge ~4 mi E of San Simeon, N 35.60795° W 121.09053°, 10.v.2012, col. T. McKnight	x	x	x	x	UMMZ-TAM-312-1
Lasiopogon nelsoni sp. nov.	USA: California: Monterey Co., Andrew Molera State Park, path to campsites 0.5 mi W of parking lot, N 36.28741° W 121.84907°, 10.v.2012, col. T. McKnight	-	x	x	x	UMMZ-TAM-313-1
Lasiopogon nelsoni sp. nov.	USA: California: Los Angeles Co., Big Tujunga River, 4 km NE of Sunland, N 34.2916° W 118.2878°, 7.iii.2014, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-526-1
Lasiopogon nelsoni sp. nov.	USA: California: San Diego Co., Descanso, malaise in damp creek bed, 1280 m, N 32°50.1' W 116°37.4', 31.v-6.vi.2002, col. M.E. Irwin, F.D. Parker	-	x	-	-	UMMZ-TAM-INHS-19 (Other conspecifics from this collection event are INHS 798968.)
Lasiopogon odontotus sp. nov.	USA: California: El Dorado Co., Coloma, Little American River S Fork At Hwy 43 Bridge, N 38°48'25" W 120°54'10", 23.v.1993, col. R.A. Cannings, H. Nadel, E.M. Fisher	-	BOLD	-	-	RBCM ENT010-002810
Lasiopogon odontotus sp.	USA: California: El Dorado Co., Coloma, Little American River S Fork At Hwy 43	-	x	-	-	UMMZ-TAM-RBCM-51 RBCM ENT017-001088

nov.	Bridge, N 38°48'25" W 120°54'10", 23.v.1993, col. R.A. Cannings, H. Nadel, E.M. Fisher					
Lasiopogon oklahomensis Cole and Wilcox	USA: Arkansas: Izard Co., White River at Mt. Olive boat launch, N 35.99604° W 92.09174°, 15.v.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-411-1
Lasiopogon oklahomensis Cole and Wilcox	USA: Arkansas: Stone Co., N Sylamore Creek at Gunner Pool, 3 mi N of Fifty-Six, N 35.99602° W 92.21417°, 15.v.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-412-1
Lasiopogon opaculus Loew	USA: North Carolina: Henderson Co., Blantyre (Etowah), Little Willow Creek 1 km S of Pleasant Grove Rd, N 35.2932° W 82.5954°, 22.iv.2015, col. T. & K. McKnight	x	x	-	x	UMMZ-TAM-710a-1
Lasiopogon opaculus Loew	CANADA: Ontario: Lambton Co., Port Franks, Watson property near L-lake, malaise, 8.vi.1996, col. J. Skevington	-	BOLD	-	-	RBCM ENT010-002815
Lasiopogon pacificus Cole and Wilcox	USA: Oregon: Lane Co., Sutton Creek campground, forest trail to Alder dunes, 6 mi N of Florence, N 44.05552° W 124.10598°, 21.vi.2013, col. T. McKnight	KY906305	KY914522	KY914505	KY914537	UMMZ-TAM-488-1
Lasiopogon pacificus Cole and Wilcox	USA: Oregon: Lane Co., Sutton Creek campground, forest trail to Alder dunes, 6 mi N of Florence, N 44.05552° W 124.10598°, 21.vi.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-488-3
Lasiopogon polensis Lavigne	USA: Colorado: Boulder Co., aspen/pine meadow slope above tributary Lefthand Creek, 2 mi SSW of Ward, N 40.05355° W 105.52553°, 22.vi.2016, col. T. McKnight	x	x	x	x	(DNA extract completely consumed) UMMZ-TAM-892-1
Lasiopogon polensis	USA: Wyoming: Albany Co., Pole Mtn, Telephone Cyn, dry wash, N 41.26149°	x	x	x	-	UMMZ-TAM-893e-1

Lavigne	W 105.46016°, 23.vi.2016, col. T. & K. McKnight					
Lasiopogon polensis Lavigne	USA: Wyoming: Albany Co., Pole Mtn, Telephone Cyn, dry wash, N 41.26149° W 105.46016°, 23.vi.2016, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-893e-2
Lasiopogon prima Adisoemarto	CANADA: Alberta: Rocky Mountain House, bridge on Hwy #11 at N Saskatchewan River, sandy/mud/gravel bar in *Picea*/ *Populus* woods, N 52°24'43.9" W 114°57'13.4", 19.vi.2008, col. R.A. Cannings, J.H. Acorn	x	x	x	x	UMMZ-TAM-RBCM-10 RBCM ENT017-001089
Lasiopogon prima Adisoemarto	CANADA: Alberta: Rocky Mountain House, bridge on Hwy #11 at N Saskatchewan River, sandy/mud/gravel bar in *Picea*/ *Populus* woods, N 52°24'43.9" W 114°57'13.4", 19.vi.2008, col. R.A. Cannings, J.H. Acorn	x	x	x	x	UMMZ-TAM-RBCM-6 RBCM ENT017-001090
Lasiopogon puyallupi stat. nov.	USA: Oregon: Hood River Co., E Fork Hood River at Nottingham campground, 6 mi E of Mt. Hood peak, N 45.36815° W 121.57066°, 15.vi.2013, col. T. McKnight	-	x	-	x	UMMZ-TAM-474-1
Lasiopogon puyallupi stat. nov.	USA: Washington: Thurston Co., Tumwater, Deschutes River at Pioneer Park, N 46.994° W 122.8881°, 15.v.2015, col. T. McKnight	-	x	x	x	UMMZ-TAM-784-1
Lasiopogon puyallupi stat. nov.	USA: Washington: Mason Co., Fernwood, Skokomish River beach at Skokomish River Road mile 4, 10T 4844762E 5240515N NAD 83, 7.vi.2009, col. J. Miskelly	x	x	-	x	UMMZ-TAM-RBCM-4 (No morphological voucher for extracted specimen, but conspecifics from this collection event are RBCM ENT017-001091)
Lasiopogon quadrivittatus	USA: Utah: Wayne Co., Sand Creek crossing ~2 mi NW Torrey, Fishlake	x	x	x	x	UMMZ-TAM-308-7

Jones	National Forest, N 38.317975° W 111.441989°, 7 May 2012 col. T. McKnight					
Lasiopogon quadrivittatus Jones	USA: Utah: Wayne Co., Sand Creek crossing ~2 mi NW Torrey, Fishlake National Forest, N 38.317975° W 111.441989°, 7 May 2012, col. T. McKnight	x	x	x	x	UMMZ-TAM-308-9
Lasiopogon quadrivittatus Jones	CANADA: Alberta: Edmonton, river valley, on mud, 16.vi.2009, col. J.H. Acorn	x	x	-	x	UMMZ-TAM-RBCM-2 (No morphological voucher for this specimen, but it is from same collection event as RBCM ENT017-001093.)
Lasiopogon quadrivittatus Jones	CANADA: Alberta, Gull Lake summer village, 30-31.v.2009, col. J.H. Acorn	-	x	x	x	UMMZ-TAM-RBCM-26 RBCM ENT017-001092
Lasiopogon quadrivittatus Jones	CANADA: Alberta: Edmonton, river valley, on mud, 16.vi.2009, col. J.H. Acorn	x	x	x	x	UMMZ-TAM-RBCM-27 RBCM ENT017-001093
Lasiopogon ripicola Melander	USA: Idaho: Canyon Co., Boise River jct Hwy 95, 4 mi SE of Parma, N 43.74877° W 116.91538°, 18.iv.2014, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-568-2
Lasiopogon ripicola Melander	USA: Idaho: Boise Co., Horseshoe Bend, Payette River sandbank, N 43.90385° W 116.19717°, 18.iv.2014, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-569-3
Lasiopogon ripicola Melander	USA: Washington: Asotin Co., Snake River, sandy bank 1.6 mi S of Asotin jct hwy 129, N 46.33185° W 117.02672°, 21.iv.2014, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-582-1
Lasiopogon schizopygus Cannings	USA: Georgia: Rabun Co., North Fork Chattooga River jct Hwy 28, 2 mi SE of Pine Mountain, N 34.91898° W	-	x	-	-	UMMZ-TAM-425-1

(dark)	83.16927°, 22.v.2013, col. T. McKnight					
Lasiopogon schizopygus Cannings (dark)	USA: Georgia: Rabun Co., W Fork Chattooga River jct Overflow Creek Rd, 1 mi W of Pine Mountain, N 34.94913° W 83.20567°, 22.v.2013, col. T. McKnight	-	x	x	x	UMMZ-TAM-426-2
Lasiopogon schizopygus Cannings (dark)	USA: South Carolina: Oconee Co., Little River jct Burnt Tanyard Rd, 3.5 mi S of Salem (direct), boulder beach, N 34.8373° W 82.98148°, 21.iv.2015, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-705e-1
Lasiopogon schizopygus Cannings (pale)	USA: Mississippi: Winston Co., Tombigbee National Forest, Noxubee River jct Rd 971 between sites 13 & 14, N 33.24909° W 89.09376°, 18.v.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-416-1
Lasiopogon schizopygus Cannings (pale)	USA: Alabama: Autauga Co., Swift Creek jct Hwy 82, 13 mi NW of Prattville, N 32.56801° W 86.67611°, 19.v.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-419-1
Lasiopogon schizopygus Cannings (pale)	USA: Alabama: Conecuh Co., Sepulga River jct Hwy 31, 9 mi E of Evergreen, N 31.45393° W 86.78655°, 19.v.2013, col. T. McKnight	-	x	x	x	UMMZ-TAM-421-2
Lasiopogon schizopygus Cannings (pale)	USA: Georgia: Murray Co., Conasauga River jct Old GA Hwy 2, 5.5 mi E of Cisco, N 34.97456° W 84.64503°, 21.v.2013, col. T. McKnight	-	x	-	-	UMMZ-TAM-424-1
Lasiopogon septentrionalis Lehr	RUSSIA: Far East Magadanskaya Obl., Kolymskaya Rd. at Nerucha River, 14.vii.1993, col. R.A. Cannings	-	BOLD	-	-	UMMZ-TAM-ASRMA-326-10
Lasiopogon septentrionalis Lehr	FINLAND: Utsjoki, Karigasniemi, N 69.411° E 25.823°, 25.6.2013, col. Iiro Kakko	-	x	-	x	UMMZ-TAM-FINN-1 RBCM ENT017-001094
Lasiopogon	USA: South Carolina: Oconee Co., Little	X	x	x	x	UMMZ-TAM-705a-1

shermani Cole and Wilcox	River jct Burnt Tanyard Rd, 3.5 mi S of Salem (direct), forest stream litter, N 34.83704° W 82.97937°, 21.iv.2015, col. T. & K. McKnight					
Lasiopogon shermani Cole and Wilcox	USA: South Carolina: Oconee Co., Chattooga River jct Hwy 76 at SC/GA border, N 34.8141° W 83.3063°, 21.iv.2015, col. T. & K. McKnight	X	x	x	x	UMMZ-TAM-707-1
Lasiopogon sierra sp. nov.	USA: Nevada: Washoe Co., Mogul, Truckee River at Mayberry Crossing Park, N 39.50262° W 119.89737°, 13-14 May 2012, col. T. McKnight	x	x	x	x	UMMZ-TAM-322-3
Lasiopogon sierra sp. nov.	USA: California: Shasta Co., Little Cow Creek, Hwy 299 turnoff 4.2 km SW jct Oak Run Road, N 40.73917° W 122.071°, 14.v.2012, col. T. McKnight	-	x	x	x	UMMZ-TAM-325-2
Lasiopogon sierra sp. nov.	USA: California: El Dorado Co., South Fork American River, 2 mi W of Riverton, N 38.76734° W 120.48353°, 7.vi.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-437-1
Lasiopogon sierra sp. nov.	USA: California: Trinity Co., Douglas City campground, Trinity River, 7 mi S of Weaverville, N 40.64661° W 122.95591°, 24.v.2016, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-878-1
Lasiopogon slossonae Cole and Wilcox	USA: Ohio: Licking Co., Dry River, sandbars W of Lazy River at Granville cmpgd, 6.5 mi NW of Newark, N 40.12144° W 82.50038°, 22.v.2014, col. T. McKnight	x	x	x	x	UMMZ-TAM-638-1
Lasiopogon slossonae Cole and Wilcox	USA: New York: Essex Co., West Branch Ausable River at 118 River Rd, nr Lake Placid, N 44.265871° W 73.95898°, 2.vi.2014, col. K.B McKnight	KY906297	KY914513	KY914496	KY914529	UMMZ-TAM-KBM-2014-6-2-2
Lasiopogon	USA: Michigan: Washtenaw Co., Pickerel	KY906303	KY914520	KY914503	KY914535	UMMZ-TAM-404-1

terricola (Johnson)	Lake, sandy blowout in forest SW of lake, N 42.41199° W 83.98824°, 10.v.2013, col. T. McKnight					
Lasiopogon terricola (Johnson)	USA: Michigan: Washtenaw Co., Pickerel Lake, sandy blowout in forest SW of lake, N 42.41199° W 83.98824°, 10.v.2014, col. T. McKnight	x	x	-	x	UMMZ-TAM-630-1
Lasiopogon tes-1	USA: California: Siskiyou Co., Mt. Shasta, Bunny Flat above trailhead, N 41.35681° W 122.23244°, 22.vi.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-491-1
Lasiopogon tes-1	USA: California: Siskiyou Co., Mt. Shasta, Bunny Flat above trailhead, N 41.35681° W 122.23244°, 22.vi.2013, col. T. McKnight	-	x	x	x	UMMZ-TAM-491-2
Lasiopogon tes-1	USA: California: Siskiyou Co., Mt. Shasta, Bunny Flat above trailhead, N 41.35681° W 122.23244°, 22.vi.2013, col. T. McKnight	x	x	x	x	UMMZ-TAM-491-3
Lasiopogon tes-2	USA: California: Mono Co., White Mtns, Patriarch Grove, 11200', 27.vii.1995, col. A.S. & N. Menke	-	x	-	-	UMMZ-TAM-NMNH-1 USNMENT 01100402
Lasiopogon tes-3	USA: Oregon: Deschutes Co., Tumalo, juniper/sage forest above Deschutes River, outside Tumalo SP, N 44.13151° W 121.32943°, 29.iv.2014, col. T. McKnight	x	x	x	x	UMMZ-TAM-615-1
Lasiopogon tes-3	USA: Oregon: Deschutes Co., Tumalo, juniper/sage forest above Tumalo SP, N 44.12916° W 121.32768°, 30.iv.2014, col. T. McKnight	x	x	x	x	UMMZ-TAM-616-1
Lasiopogon tes-3	USA: Oregon: Deschutes Co., Tumalo, juniper/sage forest above Tumalo SP, N 44.12916° W 121.32768°, 30.iv.2014,	x	x	x	x	UMMZ-TAM-616-2

	col. T. McKnight					
Lasiopogon tes-4	USA: California: San Bernardino Co., San Bernardino Mtns, Van Deusen Canyon near Holcomb Valley, forest/meadow edge, N 34.2986° W 116.8907°, 30.iv.2015, col. T. McKnight	x	x	x	x	UMMZ-TAM-733-1
Lasiopogon tes-4	USA: California: San Bernardino Co., San Bernardino Mtns, Van Deusen Canyon near Holcomb Valley, forest/meadow edge, N 34.2986° W 116.8907°, 30.iv.2015, col. T. McKnight	x	x	x	x	UMMZ-TAM-733-2
Lasiopogon tes-5	USA: Arizona: Coconino Co., Hart Prairie, Snowbowl DMY, 2775 m, 4.vi.2003, col. E. North	-	x	-	x	UMMZ-TAM-MNAZ-1 MNA DIP 3.0854
Lasiopogon testaceus Cole and Wilcox	USA: California: Mariposa Co., Summerdale campground, Big Creek, N 37.48948° W 119.63408°, 22.v.2016, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-871-2
Lasiopogon testaceus Cole and Wilcox	USA: California: Mariposa Co., Summerdale campground, Big Creek, N 37.48948° W 119.63408°, 22.v.2016, col. T. & K. McKnight	x	x	x	-	UMMZ-TAM-871-3
Lasiopogon tetragrammus Loew	CANADA: Ontario: Lambton Co., Ipperwash, beach #4 trails by road, N 43.20887° W 81.98092°, 24.v.2014, col. T. McKnight	x	x	x	x	UMMZ-TAM-645-1
Lasiopogon tetragrammus Loew	USA: New York: Essex Co., West Branch Ausable River at 118 River Rd, nr Lake Placid, N 44.265871° W 73.95898°, 2.vi.2014, col. K.B McKnight	x	x	x	x	UMMZ-TAM-KBM-2014-6-2-1
Lasiopogon trivittatus Melander	CANADA: Alberta: Cardston, Belly River at Birdseye Ranch, 1330 m, 14.viii.2011, col. L.E. Stevens	-	x	-	-	UMMZ-TAM-MNAZ-2 MNA DIP 12.0452
Lasiopogon	CANADA: Alberta, Kananaskis, Evan-	x	x	-	-	UMMZ-TAM-RBCM-18

trivittatus Melander	Thomas Creek, ?.vii.2001, col. J. Zloty					RBCM ENT017-001095
Lasiopogon tumulicola sp. nov.	USA: Oregon: Lane Co., Beach W of Siltcoos Lake, N 43.88153° W 124.15313°, 17.v.2012, col. T. McKnight	-	x	x	x	UMMZ-TAM-332-2
Lasiopogon tumulicola sp. nov.	USA: Oregon: Lincoln Co., Gleneden Beach, NW tip of Salishan Spit, N 44.92008° W 124.026942°, 17.v.2012, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-335-4
Lasiopogon tumulicola sp. nov.	USA: Oregon: Tillamook Co., Pacific City, Bob Straub State Park, dunes W of parking lot, N 45.19247° W 123.968284°, 18.v.2012, col. T. & K. McKnight	x	x	x	x	UMMZ-TAM-336-4
Lasiopogon tumulicola sp. nov.	USA: Oregon: Lane Co., Sutton Creek campground, Sutton Creek near vista point, 6 mi N of Florence, N 44.06864° W 124.12355°, 21.vi.2013, col. T. McKnight	x	x	-	x	UMMZ-TAM-489-3
Lasiopogon unc-11	MONGOLIA: Hovsgol Aimag: Ulaan-Uul Soum, Beltes Gol, 22 km NW of Sumber, N 50.31066° E 99.32199°, 28.vi.2006, col. C.R. Nelson, Selenge River Project	-	x	x	x	UMMZ-TAM-CRN-8458-1
Lasiopogon unc-12	PORTUGAL: Algarve: Carrapateira, beach dunes, N 37.19287° W 8.90332°, 21.iii.2011, col. V. Jacinto	-	x	-	x	UMMZ-TAM-RBCM-33 RBCM ENT017-001096
Lasiopogon wilcoxi sp. nov.	USA: California: Riverside Co., Noble Creek at Bogart Co Park, 5 mi N of Beaumont, N 33.99735° W 116.95277°, 10.iii.2014, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-540-1
Lasiopogon wilcoxi sp. nov.	USA: California: Riverside Co., Noble Creek at Bogart Co Park, 5 mi N of Beaumont, N 33.99735° W 116.95277°, 10.iii.2014, col. T. & K. McKnight	-	x	-	x	UMMZ-TAM-540-2
Lasiopogon	USA: California: Riverside Co., Noble	-	x	-	x	UMMZ-TAM-540-3

wilcoxi sp. nov.	Creek at Bogart Co Park, 5 mi N of Beaumont, N 33.99735° W 116.95277°, 10.iii.2014, col. T. & K. McKnight					
Lasiopogon willametti Cole and Wilcox	USA: Oregon: Marion Co., Willamette River, sandbars at Willamette Mission State Park, 4 mi W of Waconda, N 45.08213° W 123.06181°, 18.v.2012, col. T. & K. McKnight	KY906299	KY914515	KY914498	KY914531	UMMZ-TAM-338-8
Lasiopogon willametti Cole and Wilcox	USA: Oregon: Linn Co., Crabtree Creek at Hwy 226 bridge 8 mi N of Lebanon, N 44.65479° W 122.85185°, 19.v.2012, col. T. McKnight	x	x	x	x	UMMZ-TAM-339-1
Lasiopogon willametti Cole and Wilcox	USA: Oregon: Benton Co., Willamette River, NE corner of Kiger Island, 3 mi SE Corvallis, N 44.52681° W 123.23809°, 19.v.2012, col. T. & K. McKnight	-	x	x	x	UMMZ-TAM-341-2
Lasiopogon willametti Cole and Wilcox	USA: California: Del Norte Co., Jedediah Smith Redwoods SP, Howland Hill Rd nr Cedar Creek bridge, N 41.7893° W 124.0779°, 13.v.2015, col. T. McKnight	-	x	x	x	UMMZ-TAM-777-1
Lasiopogon woodorum Cannings	USA: Ohio: Hocking Co., Clear Creek, W of jct Hwy 33, 1 mi NW of Rockbridge, N 39.59615° W 82.55077°, 22.v.2014, col. T. McKnight	x	x	x	x	UMMZ-TAM-640-2
Lasiopogon yukonensis Cole and Wilcox	CANADA: Yukon: Carmacks, 24 km N, 670m, N 62.3514° W 136.4140°, 6.vi.2011, col. S. Cannings	-	x	-	x	UMMZ-TAM-RBCM-34 RBCM ENT017-001097
Lasiopogon yukonensis Cole and Wilcox	CANADA: Yukon: Yukon Crossing, 4.7 km E on Klondike Highway, hilltop sweep, N 62.3514° W 136.414°, 6.vi.2011, col. S.G. Cannings	x	x	x	x	UMMZ-TAM-RBCM-50 RBCM ENT015-007078
Lasiopogon zonatus Cole	USA: California: Marin Co., San Antonio Creek, San Antonio Rd 4.5 mi S of	-	x	x	x	UMMZ-TAM-562-3

and Wilcox	Petaluma, N 38.17899° W 122.62826°, 15.iii.2014, col. T. & K. McKnight					
Lasiopogon zonatus Cole and Wilcox	USA: Oregon: Baker Co., Burnt River 2 mi N of Huntington, N 44.36724° W 117.28899°, 1.v.2014, col. T. McKnight	x	x	x	x	UMMZ-TAM-623-1
Lasiopogon zonatus Cole and Wilcox	USA: California: San Benito Co., San Benito River, pantrap, N 36°22.72' W 120°54.12', 1.vi.1998, col. F.D. Parker	x	x	-	x	UMMZ-TAM-LACM-3 LACM ENT 334094
Lasiopogon zonatus Cole and Wilcox	USA: California: San Benito Co., San Benito River, pantrap, N 36°22.72' W 120°54.12', 1.vi.1998, col. F.D. Parker	-	x	x	x	UMMZ-TAM-LACM-4 LACM ENT 334093
Stackelbergini a cerberus McKnight	USA: Nevada: Clark Co., Wheeler wash, 6 mi NE of Pahrump, N 36.24678° W 115.89428°, 5.x.2013, col. T. McKnight	KY906307	KY914524	KY914507	KY914539	UMMZ-TAM-509-1
Stackelbergini a cerberus McKnight	USA: Nevada: Nye Co., Rock Valley wash jct Hwy 95, 5 mi E of Amargosa Valley city, N of highway, N 36.63359° W 116.31018°, 6.x.2013, col. T. McKnight	KY906308	KY914525	KY914508	KY914540	UMMZ-TAM-512-1
Stichopogon argenteus (Say)	USA: Michigan: Leelanau Co., Sleeping Bear dunes, W of D.H. Day grp campground, N 44.89486° W 86.04721°, 17.viii.2013, col. T. McKnight	KY906306	KY914523	KY914506	KY914538	UMMZ-TAM-502-1
Stichopogon trifasciatus (Say)	USA: Michigan: Mason Co., Ludington State Park, dunes S of Skyline dune, N 44.03177° W 86.49656°, 15.vi.2012, col. T. McKnight	KY906302	KY914518	KY914501	KY914533	UMMZ-TAM-366-2

CHAPTER IV

Ecological specialization in predatory *Lasiopogon* robber flies (Diptera: Asilidae) and its role in facilitating diversification and species coexistence

Introduction

Biologists have long sought to understand why some taxonomic groups are more diverse than others. Specialization in structured environments facilitates diversification by connecting processes of adaptation and drift at molecular and ecological scales with the patterns of diversity seen over evolutionary time (Bell 2008). Many of the best examples of adaptive radiation—Darwin's finches, Caribbean *Anolis*, Rift Lake cichlids—come from isolated systems such as islands, lakes, or mountaintops, likely because this provides a straightforward mechanism for structuring the environmental matrix so increased costs to dispersal will reduce recombination between developing varieties. Thus, the interaction between dispersal and niche breadth lies at the heart of diversification (Bell 2008), however, applying principles observed from contained islands to more complex continental systems can be problematic.

Specialization is also critical for understanding how taxa overcome limiting similarity to coexist in communities. The competition-niche similarity hypothesis (MacArthur & Levins 1967) anchors the common assumption that ecologically similar species should compete more intensely for resources than less similar taxa, and therefore should be less likely to coexist unless they are filtered by preexisting trait differences into different niches (e.g. ecological sorting, Ackerly 2003) or evolve divergent traits via character displacement upon secondary contact (Schluter 2000). By opening a window into a clade's evolutionary past, phylogeneies provide a crucial tool for recognizing these specialization processes, which has led to the burgeoning field of phylogenetic community ecology (Violle et al. 2011). However, it can remain difficult to disentangle the confounding effects of competitive exclusion, environmental filtering, and dispersal limitations (Pigot and Tobias 2013), and traits in the same species can evolve along

multiple pathways, leaving a variety of evolutionary history signatures (Germain et al. 2016, Kooyers et al. 2017).

Ecological specialization by robber flies (Diptera: Asilidae) provides a valuable new system for evaluating relationships between niche breadth, diversification, and coexistence. Robber flies, also known as assassin flies, are a fantastically diverse radiation of insectivorous predators widespread in terrestrial habitats across the globe (Dikow 2009a). As flying insects but not long-distance disperers, asilids represent an ideal compromise of site fidelity and dispersal, where adaptation to local environments can plausibly happen while still maintaining some gene flow between populations, and where the regional species pool can readily recolonize sites after local extinction (Levine and Rees 2002). Most asilid species are considered to be generalist ambush predators, and many taxa typically coexist in a given region with distinct ecological preferences suggesting that resource partitioning facilitated by ecological specialization, filtering, and character displacement may have directed diversification (Londt 1994, Shelly 1985, Haupt 2002). Asilids are known to be cannibalistic and are frequently seen chasing away nearby conspecifics or congeners, which suggests that competition is an active force in the community. While we do not know how asilids recognize each other, as visually-orienting predators they probably depend on body or setal color differences to some degree.

Diversity patterns in the robber fly subfamily Stichopogoninae suggest repeated episodes of fine-scale ecological specialization and character displacement (Lehr 1984). *Lasiopogon* is one of the largest genera in this clade, with over 60 species spread across North America, and is well represented by thousands of specimens in museum collections across the continent. These flies are fairly small-sized predators in open, sandy environments, with many species living in a given geographic region but differing in key aspects of microhabitat use, such as habitat type (dune, riverside, meadow), perch position (e.g., on open sand, on boulders, on fallen logs), or phenology (different seasonal emergence windows).

For this study, I examined disparity in four ecologically relevant traits (habitat, perch, phenology, and mystax color) among regionally coexisting *Lasiopogon* species in the light of their phylogenetic history to address whether ecological specialization can explain patterns of species coexistence. Character displacement and ecological filtering are two primary explanations for coexistence of *Lasiopogon* species. For species assembling from the same regional pool, these processes are expected to show different patterns of trait evolution between

sympatric and allopatric species (Kooyers et al. 2017). Because ecological filtering is the result of preexisting trait differences manifesting themselves once species are in geographic contact, trait divergence patterns should be similar in both sympatric and allopatric species, however, as divergent character displacement is the result of coevolution following secondary contact, trait divergences should be greater between sympatric species than in allopatric species. These patterns can be complicated if selection has followed different processes in different geographic regions, for different traits, or in different taxa (Kooyers et al. 2017). Finally, I examined whether climatic niches are constrained by tradeoffs at the continental scale in this system.

Materials and Methods

Molecular phylogeny

Details for estimation of the molecular phylogeny are covered in Chapter 2. In brief, a species tree was estimated with the STARBEAST UCLN template in BEAST 2.4.3 (Bouckaert et al., 2014, Drummond et al. 2006), which uses a Bayesian framework to simultaneously estimate tree topology and branch lengths from individual sequence data. Four loci were sequenced and partitioned independently during phylogenetic analysis: one mitochondrial (COI) and three nuclear protein coding genes (PEPCK, AATS, wingless); each species was represented by 1-4 specimens.

To ensure adequate ecological sampling, the species tree was pruned for this study to include only North American species known from at least three distinct collection localities; this left 59 species, which amounts to 87% of the known Nearctic diversity. New species that are still formally undescribed at this time are included using placeholder names following Cannings (2002) to better capture the true diversity of each clade.

Relative rates of trait evolution for different species were compared by calculating phylogenetic relatedness and diversification rates from the species tree. Patristic phylogenetic distances between species pairs were calculated in R using the fastHeight function of the phytools package (Revell 2012). Diversification rates for tips of the tree were estimated using the DR statistic (Jetz et al. 2012) implemented in R.

Niche characterization

Ecological information for North American *Lasiopogon* species was estimated from museum specimen localities and personal observations over five years of fieldwork (Table IV.2). My database of localities includes most collection localities currently known for these species, and was assembled from 4789 specimens personally inspected (for a list of institutions granting access to their collections, see Chapter 2) and 489 reports where identifications were deemed credible and uniquely identifiable, including published systematic literature (Cannings 2002, Adisoemarto 1967, James 1941, Cole and Wilcox 1938), online reports associated with verifiable photographs and detailed location information (Beaton 2016, BugGuide 2016, Ratnasingham and Hebert 2013), or correspondence with colleagues. After duplicates (e.g., individuals of the same species at the same locality on the same day) were removed, this left 1186 unique collecting events (Fig. IV.1). Specimens collected from the same site but on different days were included for phenology estimation, but excluded from geography-based analysis. Most museum labels did not come with latitude and longitude, so sites were georeferenced based on data from labels, notes by the original collectors, or my personal field experience to select an area of suitable habitat at or reasonably near the stated locality. For example, a species known to inhabit beach dunes would not have coordinates estimated at a city's post office or centroid but rather at that city's beach access, river species would be at a city's river access, species without established preferences would have sites estimated at generically and universally plausible *Lasiopogon* habitat. This was done to help provide the most realistic model of species occurences for downstream data use or for future workers seeking to locate new specimens, and does not impact environment estimates at the scale available for ecological niche modeling.

Species distributions and range sizes were calculated from these localities using minimum bounding geometry tools in ArcGIS 10.4. Species pairs with geographically overlapping distributions had the amount of overlap calculated individually for each member (e.g., the percent of species A's range that is overlapped by species B is distinct from the percent of species B's range that is overlapped by species A). Both overlap directions were included separately because interactions between species can be asymmetrical—i.e., competition can affect one species in a pair more than it does the other (Kooyers et al. 2017); this would be expected particularly between broadly distributed taxa and local endemics. As overlaps were calculated from imprecise bounding polygons and frequently included inconsequential slivers of

adjacent taxa, this provided a natural experiment to compare broadly codistributed (i.e., geographically sympatric) taxa with effectively allopatric species from the same regional pool (which frequently includes recently diverged allospecies). The cutoff for treating species pairs as geographically sympatric was conservatively set at overlap > 30% (Pigot and Tobias 2013).

Habitat and perching behaviors were compiled from specimen records and field notes, and trait disparities were scaled from 0 (no difference) to 1 (no overlap). Perches were characterized as primarily bare sand, primarily elevated features (e.g., rocks, logs, vegetation), or intermediate/both; mystax color was scored as white, black, or mixed. Perch and mystax differences were calculated in three classes (no difference, partial overlap, no overlap). Habitats were characterized as dune, river, meadow, or any combination of those three, and species differences were summarized as a binary function (at least one shared habitat vs no shared habitats).

Adult phenology was calculated by converting specimen records into the ordinal date (e.g., Jan 1^{st} = 1, Jan 2^{nd} = 2; specimens with missing date information were excluded) and then taking the 5–95 percentile interval for each taxon. Phenological disparity was calculated for each species pair as 1 minus the percent of species A's emergence window overlapping with species B. As with species ranges, phenological overlaps were calculated individually for each member of the species pair. Species phenology windows appeared to be correlated with elevation, so to check whether there was individual variation for species at a given site, I tested trait divergence for the three species (*L. asilomar, L. bitumineus, L. littoris*) that are apparently endemic to the isolated Oceano beach dune system in San Luis Obispo, California, U.S.A.

Climate information was extracted for each locality from the WorldClim 1 km^2 grids of temperature, precipitation, and bioclimatic variables (Hijmans et al. 2005). Mean annual temperature and mean annual precipitation (bio 1 and 12 respectively) were selected to ease interpretability in summarizing the fundamental climate parameter space; a PCA of all 19 variables showed these two as orthogonal to each other and primary (or essentially primary among other highly correlated variables) contributers to the principle components that explain the most variance (68%). The coefficient of variation (SD/mean) was calculated for each species' temperature and precipitation to get an approximation of climatic spread and then multiplied together to serve as an overall proxy for climatic niche breadth.

Correlations between traits and phylogenetic or geographic difference were tested using Spearman's rank test or ANOVA in R. Phylogenetic signal was tested using Pagel's λ and Blomberg's K.

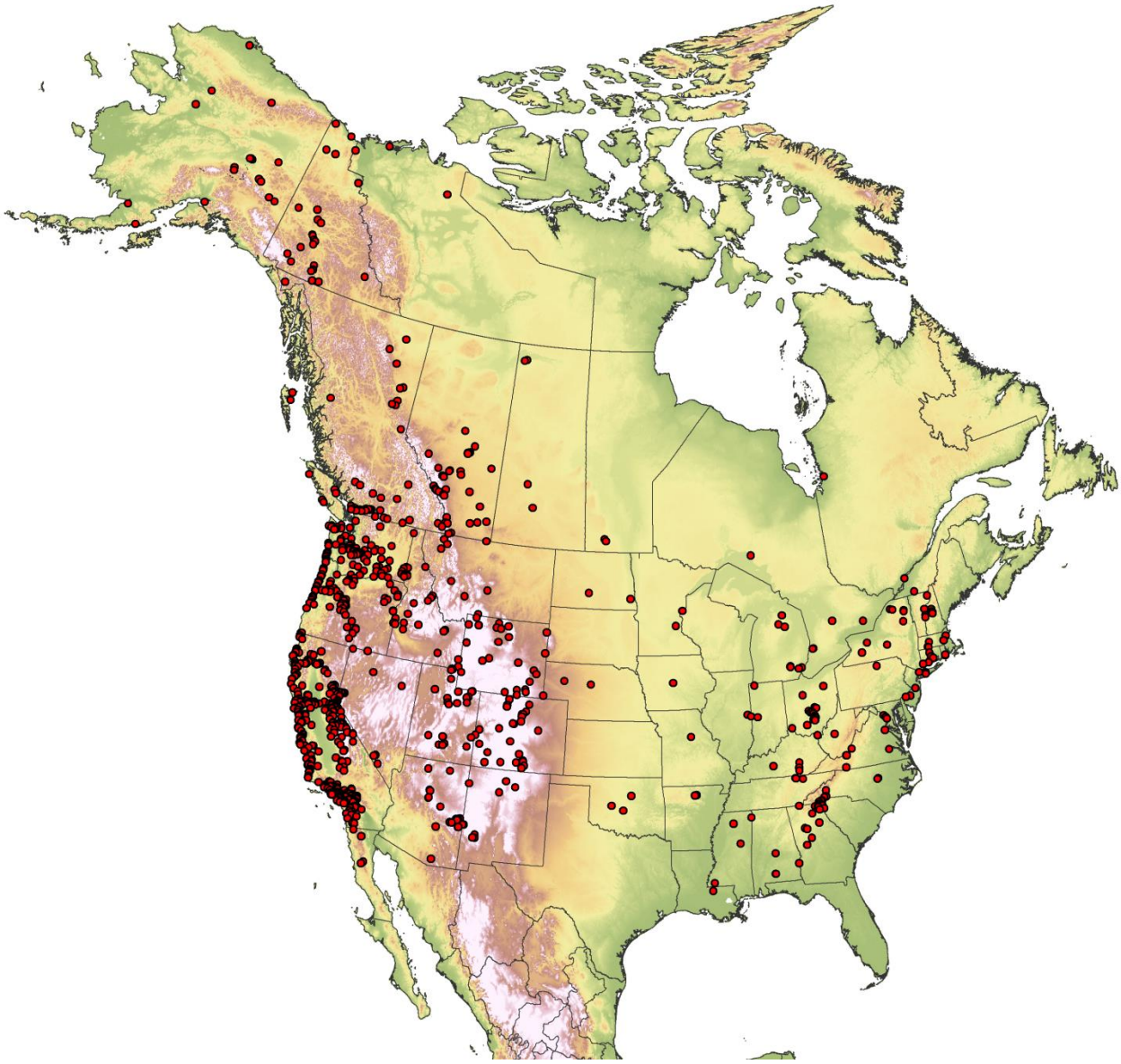


Fig. IV.1. Specimen localities for Nearctic Lasiopogon included in the ecological analysis.

Results

The three taxa endemic to the Oceano dune system have significantly different phenological windows (Fig. IV.2, $p<0.0001$, randomization F-test); perch and habitat are identical (as expected), while mystax color partially reinforces the phenological trait disparity (*L. bitumineus* is black, *L. littoris* and *L. asilomar* are white).

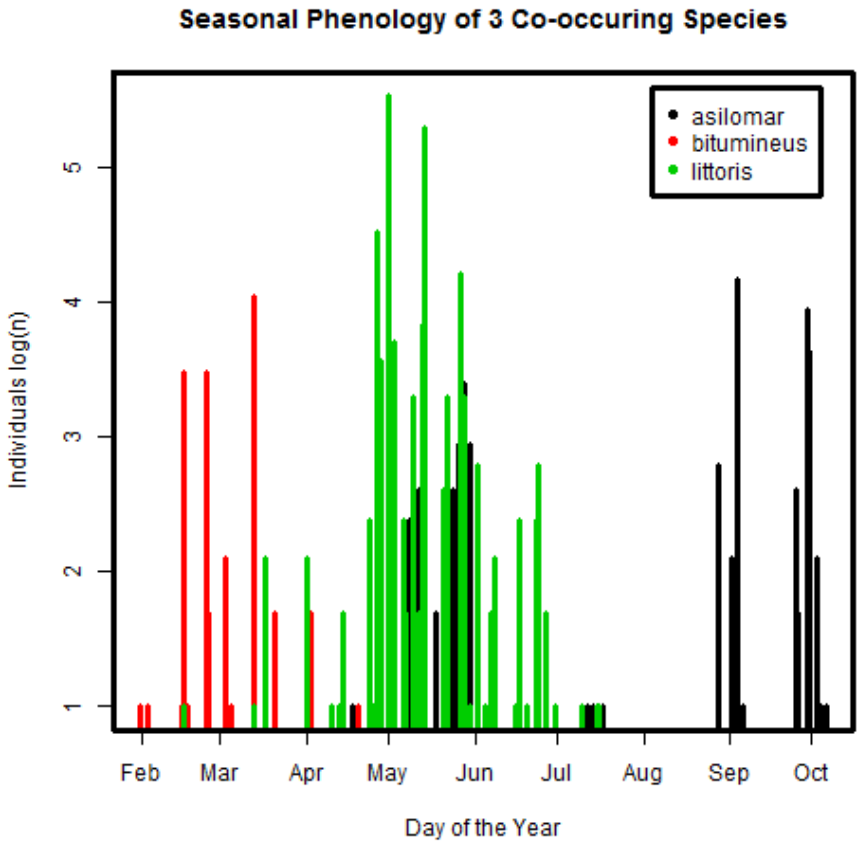


Fig. IV.2. Seasonal abundance (log transformed) for the three species (*L. asilomar, L. bitumineus, L. littoris*) codistributed at the Oceano dune system in San Luis Obispo, California.

The total number of species pairs with partial or complete geographic overlap was 378; 157 pairs (42%) were considered sympatric (i.e., geographic overlap >30%). There was no association between phylogenetic distance and the degree of geographic sympatry. The clades stemming from the basal split of the tree (the *bivittatus* + *opaculus* section (clade A) vs the *fumipennis* + *testaceus* + *aldrichii* + *canus* + *terricola* groups (clade B)) appeared to show fundamentally distinct patterns of trait disparity vs phylogenetic signal, and since these likely represent independent and replicate radiations across the continent, species pairs were split into separate pools for each clade for further testing. Clade A had 188 species pairs, of which 75 (40%) were sympatric; clade B had 36 species pairs, of which 14 (39%) were sympatric.

In general, species pairs from clade A show ecological disparity (phenology, perch, habitat, but not color) correlating with phylogenetic distance, but not with the degree of geographic overlap; whereas in clade B, ecological disparity (phenology and perch) is inversely correlated with the degree of geographic overlap and not with phylogenetic distance (except for

color). Allopatric species pairs showed weaker correlations, and usually with lower significance levels, but variables show the same basic trend (Table IV.1). For clade A, phenology and perch showed strong patterns of trait divergence

Table IV.1. Spearman's r correlations between phylogenetic distance and niche component disparity, or the degree of geographic sympatry and niche component disparity, for sympatric and allopatric species pairs of *Lasiopogon* clade A and clade B. ** = p < 0.05, * = p < 0.1.

		Clade A: sympatric	Clade A: allopatric	Clade B: sympatric	Clade B: allopatric
Phylogeny	Phenology	0.39**	0.21*	-0.13	-0.01
	Perch	0.20*	0.06	-0.05	0.33
	Habitat	0.44**	0.25**	0.04	-0.09
	Color	-0.04	-0.14	0.86**	0.48**
Geographic Sympatry	Phenology	0.01	-0.14	-0.52*	-0.36*
	Perch	-0.05	-0.03	-0.49*	0.23
	Habitat	-0.04	0.02	-0.45	0.02
	Color	-0.08	0.07	0.24	0.41*

Bioclimatic variables failed to provide much discriminatory power for coexisting *Lasiopogon* species and instead were mostly correlated with regional geographic factors. Larger ranges had broader bioclimatic niches ($r^2 = 0.44$, p= 9.7e-9), but specializations in one axis (e.g., variability in tempterature or precipitation) did not force tradeoffs in other variables (the coefficient of variation for temperature and precipitation were positively correlated, $r^2 = 0.18$, p = 0.0007). Despite spanning nearly 30° of latitude, there was no significant latitudinal gradient in temperature or precipitation variability, especially after excluding the four outlier species found north of the Arctic Circle. Niche breadth was weakly inversely correlated with diversification rate of phylogenetic tips, but this was not significant after correcting for shared phylogenetic history.

Discussion

When ecological interactions in the genus were analyzed as a whole, trait disparity patterns were muddled and insignificant; however, closer examination showed that this was because diversification in the two main subclades has apparently been influenced by different ecological processes. Analyzing the two clades separately showed that in one group (clade A) shifts in seasonal phenology and perch habit were correlated with phylogenetic distance significantly stronger among sympatric species pairs than allopatric species, as expected under a paradigm of divergent character displacement, likely from competition. Habitat shifts were strongly correlated with phylogenetic distance in both sympatric and allopatric species pairs,

which supports a model of ecological filtering instead. In the other group (clade B), shifts in color were significantly correlated with phylogenetic distance for both sympatric and allopatric species pairs, but phenology, habitat, and perch showed no significant trends.

The three species from the isolated Oceano dune system show that phenology windows can be significantly different between taxa even if their geographic and environmental distributions are identical. Thus, even though phenology generally tracks the spring green-up, there is some latitude for ecological character displacement to reduce competition within a community. The partial phenological overlap between *L. littoris* and *L. asilomar* was reinforced by similar mystax color instead of the expected trait shift, but differences in body size and geographic range size (*L. asilomar* flies are much bigger and have a geographic distribution 10x as large as the other two) can probably explain this coexistence. Furthermore, the presence of *L. asilomar* at these dunes is corroborated by only a few (8) museum specimens from the extreme southerly reach of this species' range and may thus represent ephemeral dispersal events; I have never personally observed it there myself in four trips to this region.

The phenological, habitat, and perch variables measured in this study are stabilizing differences, which promote coexistence by causing negative frequency dependence in interacting species (Germain et al. 2016). Species that have evolved in sympatry are expected to accumulate stabilizing differences faster than allopatric species, which should be evolutionarily naïve to each other (Germain et al. 2016). This pattern is moderately supported by the species pairs in clade A, but surprisingly contradicted by the pattern in clade B. This is perhaps a result of the different phylogenetic structure of the two groups: clade A is filled with recently split tips and is more diverse overall, whereas nodes in clade B are typically older and have fewer descendants. Clade A may thus represent a hotbed of evolution where taxa are actively involved in biotic interactions, while species in clade B may have already sorted into more "safe" niches.

While sympatric species pairs do show stronger correlations than taxa in allopatry, it is surprising that there isn't a more prominent difference (Germain et al. 2016) for some traits. This may be due to the fine scale of habitat structuring in invertebrate communities reducing the relevance of such coarse geography. As shown in classic examples of ecological speciation, fidelity to host plants or other microhabitats may effectively isolate species from each other even if they are close to each other and broadly codistributed (Rice 1987, Stireman et al. 2005, Mallet

et al. 2009), meaning species pools exist in a finely scaled mosaic of allopatry instead of true sympatry.

Lasiopogon is at heart a cool temperate or boreal group—the genus has the most northernly ranging robber flies (*L. canus*, *L. prima*, and *L. hinei* can be found at 68–70° N near the shores of the Arctic Ocean) while many species in the south are only found in high montane or subalpine environments, or are only active in the earliest phases of spring when the climate is still comparably harsh. Environmental filtering likely plays its main role via habitat selection and phenological emergence windows, and is not directly influenced by bioclimatic variables.

These results highlight the importance of finding the appropriate taxonomic, geographic, and ecological scales for analyses of community-level diversification processes. While it is common to apply models universally and to bin data for straightforward statistical strength, it is can be unreasonable to expect the complex biogeography, vagaries of historical contingency, and intricate developmental machinery that influence traits in a broadly distributed group to listen to a single drummer. Researchers should consider whether their system may require the use of mixed models or partitioning informed from deep knowledge of a group. Furthermore, the direction of trait evolution (from ecological filtering to different modes of character displacement) can vary within a single species due to an unrelated selection gradient, suggesting that different populations can find alternative but equivalent evolutionary solutions to a common competitive pressure (Kooyers et al. 2017). This may be driving some of the observed dissimilar trait divergence patterns in subclades of *Lasiopogon*.

Table IV.2. Summary of ecological traits for *Lasiopogon* species included in analysis (N is number of independent localities): perch, habitat (d= dune, r= river, m= mountain), mystax color, phenology window (5-95% confidence interval of ordinal dates), species distribution area, annual temperature mean and standard deviation, annual precipitation mean and standard deviation, climate variability (temp variance * ppt variance), species diversification rate (estimated from tip of phylogeny).

Species	**N**	**Perch**	**Habitat**	**Mystax color**	**Phenology interval 5-95%**	**Area (km^2)**	**Temperature mean, SD (°C)**	**Precipitation mean, SD (mm)**	**Climate variability**	**Diversification rate**
L. actius	33	sand	d	white	135-217	123000	10.1, 0.8	2041, 205	0.000295	183.1
L. albidus	8	sand	d	white	110-121	47700	10.4, 1.8	225, 25	0.000679	20.8
L. ald-1	3	rock/log	r	black	141-192	93	11.7, 0.6	1849, 396	0.000441	44.5
L. ald-2	7	rock/log	rm	black	170-200	17600	5.8, 2.4	1445, 631	0.00381	32.6
L. aldrichii	35	rock/log	rm	black	170-225	776000	2.6, 2.5	561, 114	0.001853	60.4
L. anaphlecter	10	both	r	black	130-179	2250	11.1, 1.7	1027, 135	0.000803	53.7
L. apache	8	both	rm	black	121-197	62200	8.4, 3.6	529, 159	0.00385	18.4
L. appalachensis	7	both	r	black	131-144	9670	12.6, 0.3	1284, 89	8.43E-05	31.9
L. arenicola	5	sand	d	white	77-163	576	13.5, 0.7	570, 108	0.000454	91.0
L. asilomar	13	sand	d	white	122-272	6020	13.7, 0.5	468, 109	0.000389	63.9
L. bitumineus	10	sand	d	black	45-92	680	13.8, 0.2	381, 27	0.000053	26.0
L. bivittatus	22	both	d	black	73-130	5920	13.2, 0.5	718, 185	0.000413	20.6
L. californicus	24	rock/log	r	black	101-168	40100	14.3, 1.3	667, 404	0.002632	53.7
L. can-1	11	sand	r	black	147-186	113000	2.5, 0.5	494, 88	0.00033	22.9
L. canningsi	15	sand	d	black	121-171	3570	11.4, 0.2	1337, 304	0.000165	35.8
L. canus	25	both	rm	black	153-212	1570000	-4.8, 3.6	299, 86	0.003843	23.6
L. chaetosus	15	sand	d	mixed/both	112-172	336000	9.0, 2.1	246, 60	0.001811	18.4
L. cinereus	80	rock/log	r	black	164-241	2320000	6.7, 3.3	857, 608	0.008338	15.2
L. coconino	11	both	r	black	125-183	25700	10.5, 2.8	506, 53	0.001041	27.3
L. currani	24	rock/log	rm	black	122-166	623000	8.6, 2.2	1124, 281	0.001922	21.9
L. dimicki	5	sand	d	black	123-157	11	10.6, 0.2	2000, 169	7.29E-05	56.1
L. drabicolum	20	sand	r	mixed/both	48-125	78600	16.1, 2.6	430, 162	0.003364	50.4
L. esau	24	both	r	mixed/both	93-145	24800	13.2, 1.6	1023, 340	0.001836	143.9

L. fumipennis	49	rock/log	rm	black	125-212	470000	5.6, 2.8	1518, 743	0.004933	15.5
L. gabrieli	31	both	r	black	41-89	20900	17.3, 1.4	343, 79	0.001136	26.0
L. hinei	15	both	rmd	black	147-212	1960000	-2.7, 4.3	411, 175	0.006723	8.6
L. lavignei	3	both	r	black	161-162	137	4.0, 1.1	449, 91	0.000828	65.9
L. littoris	15	sand	d	white	116-172	817	13.9, 0.3	391, 57	0.000145	15.4
L. marshalli	4	both	r	black	147-150	1400	11.4, 0.4	987, 96	0.000149	45.1
L. monticola	41	rock/log	m	black	149-226	935000	4.0, 2.7	1185, 842	0.007015	12.3
L. nelsoni	43	rock/log	r	black	77-165	47800	15.6, 1.9	445, 137	0.00202	37.2
L. odontotus	15	both	r	black	92-152	30400	13.6, 3.9	550, 181	0.004443	31.8
L. oklahomensis	6	both	r	white	100-135	24100	15.1, 0.6	961, 170	0.000359	47.9
L. opaculus	21	both	r	black	105-169	1140000	12.0, 2.8	1169, 305	0.002597	39.2
L. pacificus	16	sand	d	black	127-186	57500	9.9, 0.9	1835, 471	0.000852	60.4
L. polensis	11	rock/log	rm	black	140-193	91600	4.6, 3.4	462, 104	0.002722	21.9
L. prima	21	sand	rd	white	149-220	2080000	-2.6, 4.4	472, 268	0.00928	9.9
L. puyallupi	43	both	rd	black	110-204	117000	9.4, 1.0	1766, 803	0.001635	183.1
L. quadrivittatus	33	both	rmd	white	124-180	1940000	6.7, 2.9	334, 95	0.002918	35.3
L. ripicola	26	both	r	mixed/both	107-143	122000	10.7, 1.5	370, 133	0.001961	30.9
L. schizopygus	19	both	r	black	85-143	283000	15.3, 2.0	1445, 210	0.001004	45.1
L. shermani	7	both	rm	black	97-136	8000	14.6, 0.8	1509, 196	0.000348	22.7
L. sierra	26	rock/log	r	black	125-181	58600	10.2, 3.2	750, 349	0.005325	143.9
L. slossonae	25	both	r	black	119-182	391000	8.3, 3.1	1025, 65	0.000702	39.2
L. terricola	32	sand	rd	white	126-168	1830000	8.7, 3.0	909, 244	0.002853	9.9
L. tes-1	16	rock/log	rm	black	131-182	94900	8.3, 3.0	819, 282	0.003733	48.4
L. tes-2	10	both	m	black	156-209	1220	1.7, 2.0	531, 131	0.001789	37.3
L. tes-3	9	rock/log	m	black	134-155	1760	7.1, 0.7	534, 446	0.0022	48.4
L. tes-4	4	rock/log	m	black	123-150	121	8.2, 0.6	653, 29	9.64E-05	37.3
L. tes-5	3	rock/log	m	white	157-173	74	4.7, 0.3	606, 55	0.000095	17.4
L. testaceus	21	both	rm	black	144-213	82100	6.1, 2.8	909, 275	0.003067	34.9
L. tetragrammus	12	both	rd	mixed/both	142-190	767000	5.1, 3.0	896, 154	0.001848	65.9
L. trivittatus	22	rock/log	r	white	171-224	376000	2.2, 1.6	514, 123	0.001352	8.0

L. tumulicola	22	both	d	black	127-184	23300	10.3, 0.6	2102, 266	0.000249	35.8
L. wilcoxi	28	sand	r	black	61-151	21800	15.3, 1.9	496, 119	0.001594	35.3
L. willametti	16	sand	r	black	98-151	144000	10.9, 0.8	1091, 400	0.001078	98.2
L. woodorum	10	rock/log	r	black	119-161	85700	10.9, 1.0	992, 53	0.000195	47.9
L. yukonensis	10	sand	rd	black	158-182	12300	-2.8, 1.3	276, 11	0.000193	23.6
L. zonatus	48	sand	r	black	80-179	545000	13.7, 3.6	543, 316	0.007267	35.3

CHAPTER V
Conclusions and Future Directions

Despite being a group once characterized as belonging to "the problem children of the Asilidae" (Oldenberg 1924, translated in Cannings 2002), the genus *Lasiopogon* is an interesting and informative study system that illustrates the complexity of coexistence when species can diversify along multiple ecological axes. Reconciling patterns in such "messy" species radiations of non-model organisms across continental regions requires detailed data and a nuanced perspective of what is relevant for the focal taxa. This dissertation is the first to study robber fly ecology and evolutionary biology at the species level with molecular data, and hopefully will help bridge the usual divide between taxonomic and ecological schools of expertise.

This research shows the continuing value of detailed traditional taxonomic work, describing many species new to science and a newly recorded genus (*Stackelberginia*) for the relatively well-studied North American fauna. Cannings (2002) originally estimated the *bivittatus* group as having 13 named and 3 undescribed species, but after this work our current understanding is 25 species: 12 previously described, 1 elevated from subspecies (*L. puyallupi*), and 12 newly described. Two species are added to the *opaculus* section—one moved from the *bivittatus* group (*L. martinensis*), the other newly described (*L. karli*).

Genitalia dissections remain a valuable tool for identifying and classifying robber fly species, and will likely remain important for the foreseeable future, as many taxa are only known from old specimens with insufficient DNA quality for genetic analysis using current methods. As genitalia-based species groups were generally supported by the molecular phylogeny, it may be possible to graft species without DNA into the tree by using geometric morphometrics on genitalia shape. Identifications of lone female specimens can remain challenging, as female genitalia morphology was not investigated as fully as with males. Future work to describe the dissected spermathecae, ovipositor, and other traits should shed light on this problem. The recently discovered phenomenon of wing interference patterns (WIPs, Shevtsova et al. 2011) are another promising trait to investigate for taxonomic resolution and identification—my cursory

examination of *Lasiopogon* wings in a handful of species showed a promising balance of variation and stability in species and species groups.

The molecular phylogenies presented here corroborate some previous phylogenetic hypotheses for this group of flies, but update, add to, and sometimes contradict other preceeding work. *Lasiopogon* is confirmed as a basal member of the subfamily Stichopogoninae, and the overlooked genus *Stackelberginia* is placed as sister to *Lasiopogon* with relic species left in the deep deserts of Central Asia and the North American Great Basin. Species groups of *Lasiopogon* are largely unchanged from Cannings (2002) being well supported in the molecular tree, but the backbone of the tree is realigned to make the *bivittatus* and *opaculus* groups sister to the *fumipennis*, *testaceus*, *aldrichii*, *canus*, *terricola*, *cinctus*, and *montanus* groups. This topological shift was strongly supported by all four loci sampled in this analysis, and follows an intuitive clustering of morphological syndromes. Many other nodes remain poorly supported, some at fine scales and others deep in the tree, but this is expected given the diversity of the genus and the possible resolution from only sequencing four loci. Further work with more extensive genomic sampling will be needed to confidently tease apart the convoluted gene histories and species relationships for these taxa. Approximate Bayesian computation (ABC) could lend a useful framework for testing hypotheses with spatially explicit models of genetic differentiation at fine scales for taxa with complex geographic or ecological histories, such as in mountain sky islands or ephemeral beach habitats (Knowles and Massatti 2017, Papadopoulou and Knowles 2015).

Ecological coexistence of *Lasiopogon* species remains a complicated subject. Divergence in specific ecological traits (e.g., perch, habitat, phenology) are not straightforward explanatory variables for all coexistence and diversification in *Lasiopogon*, but are still relevant when used with caution. As different phylogenetic groups show diverse patterns of trait evolution, and traits variously show the signatures of character displacement or ecological filtering, it would be reasonable to use a mixed model to test patterns of community assembly. With the data examined here, the clade formed by the *bivittatus* and *opaculus* groups shows significantly stronger correlations between phylogenetic distance and trait displacement in phenology and perch in sympatric species pairs than allopatric species, suggesting that character displacement has played a role in shaping their evolution, while habitat differences were significantly correlated with phylogenetic distance in both sympatric and allopatric species, indicative of the signature for environmental filtering. Mystax color (presumably a species recognition tool) was

not a significant factor for this subclade, but in the other half of the phylogeny (the *fumipennis*, *testaceus*, *aldrichii*, *canus*, and *terricola* groups) phylogenetic distance was only correlated with color disparity and not with the other ecological variables. The degree of sympatry (geographic overlap) was not strongly correlated with trait differences, perhaps because asilid habitat preferences fracture the landscape into a much finer-scale mosaic. To better understand these patterns of trait divergence and coexistence we will need more observations of detailed and quantifiable species behavior in natural settings, especially around coexisting taxa, and to examine trait differences within individual species across more constrained selection gradients.

Five years of "chasing spring" to time my collecting expeditions for the weeks when adult flies are present has taught me that seasonal phenology is an important element of *Lasiopogon* niche specialization. Some phenological mismatch among codistributed species is undoubtedly attributable to altiduinal differences in the spring green-up, but there still remain individual differences. For example, the three species (*L. asilomar, L. bitumineus,* and *L. littoris*) recorded from the Oceano dune complex of central California have significantly segregated emergence seasons. In the *bivittatus* and *opaculus* groups, phenology mismatch was strongly correlated with phylogenetic distance but not with the degree of sympatry; this pattern was reversed for taxa in the other half of the phylogeny. Future studies may benefit from investigating the potential competitive influence of *Stichopogon,* a closely related and broadly distributed genus with similarly high species diversity and functionally equivalent foraging behavior. In the truncated growing seasons of the far north, *Lasiopogon* species can be the only asilids present, but in the south a given locality may have *Lasiopogon* emerging in the spring and *Stichopogon* in the summer. *Lasiopogon* phenology records may also be useful for conservation work, as the highly specific emergence periods compiled from specimen collected over the last century could illustrate year-to-year climatic variation and serve as a benchmark for measuring the extent of future climate change. This illustrates a frequently overlooked value of museum collections and the importance of digitizing and databasing specimen label information.

The research in this dissertation focused on a limited suite of traits thought to influence species coexistence and community stability, which provided some explanatory power, but several associations remain unexplained or uncompelling. Future work would benefit from studying other traits thought to be associated with fitness and resource use, such as body size, foraging rate and chase-away behavior, eyesight, venom efficacy, prey specificity, and resistance

to dessication. Other morphological traits not covered in this work, such as hairiness and ovipositor morphology, especially hypogynial valve shape, are thought to be directly linked to substrate adaptation and would likely improve resolution of environmentally adaptive ecotypes. Traits thought to be used by the flies themselves in species recognition (such as WIPs, tergite tomentum patterns, and setae color) should be investigated for evidence of biotic interactions—for example, the population and community structure of polymorphic traits potentially used in recognition (such as the variably black, white, or mixed-color mystaces in some species, e.g., *L. drabicolum*, *L. esau*, *L. ripicola*, and *L. chaetosus*) could be useful for testing hypotheses of competition-mediated trait evolution. Of course, the long period of virtually unknown larval behavior could also be an important factor explaining species coexistence, and future research should be directed at describing basic larval ecology including prey selection, feeding rate, cues for development, substrate choice, and environmental tolerances.

Intra-guild predation could also play an important role in structuring and mediating species interactions, as coexistence of competing species can arise solely if intraspecific competition is greater than interspecific competition (Barabás et al. 2016). Robber flies are documented cannibals, and as generalist predators they are likely competing for prey. Studying direct and indirect effects of robber flies on each other with help future analyses find the pulse of niche codiversification.

This litany of future directions has been provided to illustrate some of the many germane opportunities for intradisciplinary or institutional collaboration, training of future scientists, and deeper investigation of fundamental principles in ecology and evolutionary biology that are available with robber flies. As illustrated in this dissertation, the ubiquity and staggering diversity of insect clades like robber flies does make the story of asilid evolution more convoluted than the traditional lineup of textbook cases, but this difficulty is also part of their reward: they offer an accessible example of evolutionary radiation across the complex continental landscape.

BIBLIOGRAPHY

Ackerly, D.D. (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, 164, S165–S184. http://dx.doi.org/10.1086/368401

Adisoemarto, S. (1967) The Asilidae (Diptera) of Alberta. *Quaestiones Entomologicae*, 3, 3–90.

Adisoemarto, S. & Wood, D.M. (1975) The Nearctic species of *Dioctria* and six related genera (Diptera, Asilidae). *Quaestiones Entomologicae*, 11, 505–576.

Alexander, C.P. (1969) Baron Osten Sacken and his influence on American Dipterology. *Annual Review of Entomology*, 14, 1–19.

Back, E.A. (1909) The Robber-flies of America north of Mexico belonging to the subfamilies Leptogastrinae and Dasypogoninae. *Transactions of the American Entomological Society*, 35, 137–400.

Barabás, G., Michalska-Smith, M.J., and Allesina, S. (2016) The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities. *The American Naturalist*, 188, E1–E12. http://dx.doi.org/10.1086/686901

Beaton, G. (2016) Giff Beaton's robber flies (Asilidae) of Georgia and the southeast <http://www.giffbeaton.com/stichopogoninae.htm>. [Accessed May 2016]

Bell, G. (2008) *Selection: the mechanism of evolution. 2nd Ed*. Oxford University Press, Oxford. 553 pp.

Brown, R.W. (1956) *Composition of Scientific Words. Revised Edition.* Smithsonian Institution Press, Washington, D.C., 882 pp.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M.A., Rambaut, A. & Drummond, A.J. (2014) BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, 10 (4), e1003537. http://dx.doi.org/10.1371/journal.pcbi.1003537

BugGuide 2016. < http://bugguide.net/node/view/51556>. [Accessed May 2016]

Bybee, S.M., Taylor, S.D., Nelson, C.R. & Whiting, M.F. (2004) A phylogeny of robber flies (Diptera: Asilidae) at the subfamilial level: molecular evidence. *Molecular Phylogenetics and Evolution*, 30, 789–797.

Cannings, R.A. (1996) Taxonomy and distribution of *Lasiopogon montanus* Schiner and *L. bellardii* Jaennicke (Diptera: Asilidae), two common robber flies from the mountains of Western and Central Europe. *Entomologica Scandinavica*, 27, 347–59.

Cannings, R.A. (2002) *The Systematics of* Lasiopogon *(Diptera: Asilidae).* Royal British Columbia Museum, Victoria, 354 pp.

Cobb, N., Gruber, E., Heske, E., Flecker, E., Lightfoot, D., Masters, A., McClintock, N., Price, J., Seibert, T. & Smith, M. (1981) *An ecological study of the Alvord Basin dunes, southeastern Oregon.* Final Technical Report for National Science Foundation Grant No. SP-7905328. Oregon State University, Corvallis, 142 pp.

Cole, F.R. (1916) New species of Asilidae from southern California. *Psyche*, 23, 63–69.

Cole, F.R. (1924) Notes on the dipterous family Asilidae, with descriptions of new species. *Pan-Pacific Entomologist*, 1, 7–13.

Cole, F.R. & Lovett, A.L. (1921) An annotated list of the diptera (flies) of Oregon. *Proceedings of the California Academy of Sciences, Series 4*, 11, 197–344.

Cole, F.R. & Wilcox, J. (1938) The genera *Lasiopogon* Loew and *Alexiopogon* Curran in North America (Diptera-Asilidae). *Entomologica Americana*, 43, 1–91.

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, 9 (8), 772. http://dx.doi.org/10.1038/nmeth.2109

Diamond, J.M. (1975) Assembly of species communities. In: Cody, M.L. & Diamond, J.M. (Eds.), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge.

Dikow, R.B., Frandsen, P.B., Turcatel, M. & Dikow, T. (2017) Genomic and transcriptomic resources for assassin flies including the complete genome sequence of *Proctacanthus coquilletti* (Insecta: Diptera: Asilidae) and 16 representative transcriptomes. *PeerJ*, 5:e2951. http://dx.doi.org/10.7717/peerj.2951

Dikow, T. (2009a) Phylogeny of Asilidae inferred from morphological characters of imagines (Insecta: Diptera: Brachycera: Asiloidea). *Bulletin of the American Museum of Natural History*, 319, 1–174. http://dx.doi.org/10.1206/603.1

Dikow, T. (2009b) A phylogenetic hypothesis for Asilidae based on a total evidence analysis of morphological and DNA sequence data (Insecta: Diptera: Brachycera: Asiloidea). *Organisms Diversity & Evolution,* 9, 165–188. http://dx.doi.org/10.1016/j.ode.2009.02.004

Dikow, T. & Grimaldi, D.A. (2014) Robber flies in Cretaceous ambers (Insecta: Diptera: Asilidae). *American Museum Novitates*, 3799, 1–19. http://dx.doi.org/10.1206/3799.1

Drummond, A.J. & Suchard, M.A. (2010) Bayesian random local clocks, or one rate to rule them all. *BMC Biology,* 8, 114. http://dx.doi.org/10.1186/1741-7007-8-114

Evenhuis, N.L. (2016) The insect and spider collections of the world website. Available from: http://hbs.bishopmuseum.org/codens/ (accessed 30 March 2016)

Fisher, E.M. (1986) A reclassification of the robber fly tribe Andrenosomini, with a revision of the genus *Dasyllis* Loew (Diptera: Asilidae). Ph.D. dissertation, University of California Riverside, Riverside, CA.

Folmer, I., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.

Geller-Grimm, F. (2013) Asilidae homepage catalog of species. Available from: http://www.geller-grimm.de/asilidae.htm/ (accessed 1 July 2013).

Germain, R.M., Weir, J.T. & Gilbert, B. (2016) Species coexistence: macroevolutionary relationships and the contingency of historical interactions. *Proceedings of the Royal Society B,* 283, 20160047.

Guindon, S. & Gascuel, O. (2003) A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. *Systematic Biology*, 52, 696–704. http://dx.doi.org/10.1080/10635150390235520

Hardy, D.E. (1961) The Bibionidae of California. *Bulletin of the California Insect Survey*, 6 (2), 179–196.

Haupt, J. (2002) Choice of perching sites by East Asian robber flies (Diptera: Asilidae). *European Journal of Entomology,* 99, 35–42.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25, 1965–1978.

Huckett, H.C. (1975) The Muscidae of California exclusive of subfamilies Muscinae and Stomoxyinae. *Bulletin of the California Insect Survey*, l8, l–148.

James, M.T. (1941) The robber flies of Colorado (Diptera: Asilidae). *Journal of the Kansas Entomological Society*, 14, 27–53.

Karl, E. (1959) Vergleichend-morphologische Untersuchungen der männlichen Kopulationsorgane bei Asiliden (Diptera). *Beiträge Entomologie*, 9, 619–680. [in German]

Knowles, L.L. (2009) Species tree estimation: methods of phylogenetic analysis when there is incongruence across genes. *Systematic Biology*, 58, 463–467.

Knowles L.L. & Massatti R. (2016) Distributional shifts - not geographic isolation - as a probable driver of montane species divergence. *Ecography*, online in advance of print. http://dx.doi.org/10.1111/ecog.02893

Kooyers, N.J., James, B. and Blackman, B.K. (2017) Competition drives trait evolution and character displacement between *Mimulus* species along an environmental gradient. *Evolution*, 71, 1205–1221. http://dx.doi.org/10.1111/evo.13200

Lehr, P.A. (1964) [New genera and new species of the robber-flies (Diptera, Asilidae) in the fauna of the USSR]. *Entomologicheskoe Obozrenie*, 18 (4), 914–934. [in Russian]

Lehr, P.A. (1980) [Eurybiotic mode of life as the initial stage of evolution of a taxon, by the example of robber flies (Diptera, Asilidae)]. *In:* [Parallelism and Regularity in the Evolution of Insects] Far East Division of the Academy of Sciences of the USSR, Vladivostok, pp. 4–69. [in Russian]

Lehr, P.A. (1984) [Assassin flies of the tribe Stichopogonini (Diptera, Asilidae) of the fauna of the USSR. 2]. *Zoologicheskiy Zhurnal*, 63 (6), 859–864. [in Russian]

Lehr, P.A. (1988) Family Asilidae. *In:* Soós, Á. & Papp, L. (Eds.), *Catalogue of Palearctic Diptera, 5, Athericidae-Asilidae.* Akadémiai Kiadó, Budapest, pp. 197–326.

Levine, J.M. and Rees, M. (2002) Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *The American Naturalist*, 160, 452–467.

Loew, H. (1866) Diptera Americae septentrionalis indigena. *Berliner Entomologische Zeitschrift*, 10, 1–54.

Londt, J.G.H. (1994) Afrotropical Asilidae (Diptera) 26. Ethological observations, and a possible ecological classification based on habitats. *Annals of the Natal Museum*, 35, 97–122.

Mallet, J., Meyer, A., Nosil, P., & Feder, J.L. (2009) Space, sympatry, and speciation. *Journal of Evolutionary Biology* 22: 2332–2341.

MacArthur, R.H. & Levins, R. (1967) The limiting similarity, convergence and divergence of coexisting species. *American Naturalist*, 101, 377–385.

Maddison, W.P. & Maddison, D.R. (2016) Mesquite: a modular system for evolutionary analysis, version 3.02. Available from: http://mesquiteproject.org (accessed on 24 Mar 2015)

Matsuda, T., Morishita, M., Hinomoto, N. & Gotoh, T. (2014) Phylogenetic Analysis of the Spider Mite Sub-Family Tetranychinae (Acari: Tetranychidae) Based on the Mitochondrial COI Gene and the 18S and the 5′ End of the 28S rRNA Genes Indicates That Several Genera Are Polyphyletic. *PLoS One* 2014; 9(10): e108672. http://dx.doi.org/10.1371/journal.pone.0108672

McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Coordinators), (1981) *Manual of Nearctic Diptera. Vol. 1*. Agriculture Canada, Hull, 674 pp.

McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Coordinators), (1987) *Manual of Nearctic Diptera. Vol. 2*. Agriculture Canada, Hull, 1332 pp.

McKnight, T.A. & Cannings, R.A. (2017) *Stackelberginia cerberus* sp. n. (Diptera: Asilidae): morphological description, phylogenetic placement and first Nearctic records of the genus. *Zootaxa*, [in review]

Melander, A.L. (1923) The genus *Lasiopogon* (Diptera, Asilidae). *Psyche*, 30, 130–45.

Merritt, R.W., Cummins, K.W. & Berg, M.B. (Eds.) (2008) *An introduction to the aquatic insects of North America*. 4th Ed. Kendall Hunt, Dubuque, 1158 pp.

Metz, C.W. & Nonidez, J.F. (1924) The behavior of the nucleus and chromosomes during spermatogenesis in the robber fly *Lasiopogon bivittatus*. *Biological Bulletin*, 46, 153–62.

Nelson, C.R. (1987) Robber flies of Utah (Diptera: Asilidae). *Great Basin Naturalist*, 47, 38–90.

Oldenberg, L. (1924) Zur Kenntnis der Asiliden-Gattung *Lasiopogon* (Diptera). *Deutsche Entomologische Zeitschrift*, 5, 441–448. [in German]

O'Hara, J.E. (1982) Classification, phylogeny and zoogeography of the North American species of *Siphona* Meigen (Diptera: Tachinidae). *Quaestiones Entomologicae*, 18, 261–380.

Osten Sacken, C.R. (1877) Western Diptera: descriptions of new genera and species of Diptera from the region west of the Mississippi, and especially from California. *Bulletin of the U.S. Geological and Geographical Survey of the Territories*, 3 (2), 189–354.

Papadopoulou, A. & Knowles, L.L. (2015) Species-specific responses to island connectivity cycles: refined models for testing phylogeographic concordance across a Mediterranean Pleistocene Aggregate Island Complex. *Molecular Ecology*, 24, 4252–4268.

Pigot, A.L. & Tobias, J.A. (2013) Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters*, 16, 330–338.

Pybus, O.G. & Harvey, P.H. (2000) Testing macro-evolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society B*, 267, 2267–2272.

de Queiroz, K. (1998) The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. *In:* Howard, D.J. & Berlocher, S.H. (Eds.), *Endless Forms: Species and speciation*. Oxford University Press, Oxford, pp. 57–75.

Rambaut, A. (2012) Figtree v1.4. Available from: http://tree.bio.ed.ac.uk/software/figtree/ (accessed 8 June 2014)

Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) Tracer v1.6. Available from: http://beast.bio.ed.ac.uk/Tracer (accessed 9 June 2014)

Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes*, 7, 355–364. doi:10.1111/j.1471-8286.2006.01678.x

Revell, L.J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223. doi:10.1111/j.2041-210X.2011.00169.x

Rice, W.R. (1987) Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. *Evolutionary Ecology*, 1, 301–314. doi:10.1007/BF02071555

Schluter, D. (2000) Ecological character displacement in adaptive radiation. *The American Naturalist*, 156, S4–S16. http:dx.doi.org/10.1086/303412

Shelly, T.E. (1985) Ecological comparisons of robber fly species (Diptera: Asilidae) coexisting in a neotropical forest. *Oecologia*, 67, 57–70.

Shevtsova, E., Hansson, C., Janzen, D.H. & Kjaerandsen, J. (2011) Stable structural color patterns displayed on transparent insect wings. *Proceedings of the National Academy of Sciences of the USA*, 108, 668–673. doi: 10.1073/pnas.1017393108

Stevens, L.E. & Scarbrough, A.G. (2015) Additions to the robber fly fauna of southern Nevada, USA (Diptera: Asilidae). *Journal of the Arizona-Nevada Academy of Science*, 46 (2), 42–49. http://dx.doi.org/10.2181/036.046.0204

Stireman III, J.O., Nason, J.D. & Heard, S.B. (2005) Host-associated genetic differentiation in phytophagous insects: general phenomenon or isolated exceptions? Evidence from a goldenrod-insect community. *Evolution*, 59, 2573–2587.

Sukumaran, J. & Knowles, L.L. (2017) Multispecies coalescent delimits structure, not species. *Proceedings of the National Academy of Sciences of the United States of America*, 114 (7), 1607–1612. http://dx.doi.org/10.1073/pnas.1607921114

Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729. http://dx.doi.org/10.1093/molbev/mst197

Theodor, O. (1976) *On the Structure of the Spermathecae and Aedeagus in the Asilidae and their Importance in the Systematics of the Family*. Jerusalem: Israel Academy of Sciences and Humanities.

Violle, C., Nemergut, D.R., Pu, Z. & Jiang L. (2011) Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*, 14, 782–787.

Weinberg, M. (1978) Contribution to the knowledge of the morphology and biology of the species *Lasiopogon montanus* Schin. (Diptera, Asilidae) from the southern Carpathian mountains. *Traveaux du Museum d'Historie Naturelle "Grigore Antipa"*, 19, 293–296.

Wilcox, J. (1961) The genus *Hodophylax* James (Diptera: Asilidae). *Bulletin of the Brooklyn Entomological Society*, 61, 112–116. http://www.biodiversitylibrary.org/part/177278

Wilcox, J. (1965) New *Cophura*, with revised keys to the groups and to the Nearctic species (Diptera: Asilidae). *Annals of the Entomological Society of America*, 58 (6), 805–816. http://dx.doi.org/10.1093/aesa/58.6.805

Wilcox, J. (1966) *Efferia* Coquillett in America north of Mexico (Diptera: Asilidae). *Proceedings of the California Academy of Sciences*, 34 (2), 85–234. http://www.biodiversitylibrary.org/part/53305

Wild, A.L. & Maddison, D.R. (2008) Evaluating nuclear protein-coding genes for phylogenetic utility in beetles. *Molecular Phylogenetics and Evolution*, 48, 877–891. http://dx.doi.org/10.1016/j.ympev.2008.05.023

Winterton, S.L. (2004) Are hind coxal knobs a synapomorphy for therevids?: An unusual new species of *Anabarhynchus* Macquart from Australia (Diptera: Therevidae: Therevinae). *Zootaxa*, 413, 1–8. http://dx.doi.org/10.11646/zootaxa.413.1.1

Wood, G.C. (1981) Family Asilidae. *In:* McAlpine, J.R., Peterson, B.V., Shell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Eds.), *Manual of Nearctic Diptera. Vol. 1*. Agriculture Canada: Hull, pp. 549–573.