Title
Assassin Fly (Diptera: Asilidae) Systematics and Predator Ecology

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Publication Date
2023

Assassin Fly (Diptera: Asilidae) Systematics
and Predator Ecology

By

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DOCTORAL DEGREE – DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Entomology and Nematology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

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Torsten Dikow

Committee in Charge

2023

Dedication

I dedicate my dissertation to all the teachers, mentors, and family members who pushed me to believe in myself to accomplish what sometimes seemed impossible.

George Alberts & Family

Sally & Tim Herbert

Cynthia Howe

Tracy Malloy

Sheila McCoy

Karl McKnight

⁂

Abstracts

Chapter 1

The Nearctic species of *Saropogon* Loew, 1847 north of Mexico are reviewed, with 19 species recognized and one described as new: *Saropogon pyrodes* **sp. nov.** from Arizona. This previously recognized new species has awaited description since its first collection in 1964. Only after a community scientist posted photographs taken in nature to an online database did its description become a priority. All species of *Saropogon* occurring in the Nearctic Region north of the Mexican border have been reexamined. Photographs and diagnoses of all species are provided with a distribution map of the included specimens studied. An updated key to the Nearctic species north of Mexico is provided. Finally, the need for a review of the diverse Mexican fauna is expressed.

Chapter 2

More than 3,400 Asilidae specimens with their associated prey have been specimen-level databased, by examining 15 natural history collections in the USA. The orders of arthropods preyed upon are, in order of representation, Hymenoptera, Diptera, Coleoptera, Orthoptera, Blattodea, Odonata, Araneae, Neuroptera, Thysanoptera, Siphonaptera, and Trichoptera. Asilidae genera with sufficient data to warrant special attention are: Asilinae (Efferia, Mallophora, Megaphorus, Proctacanthus, Promachus, and Triorla), Brachyrhopalinae (Ceraturus, Cyrtopogon, Heteropogon, Holopogon, and Nicocles), Dasypogoninae (Diogmites and Saropogon), Dioctriinae (Dioctria), Laphriinae (Atomosia and Laphria), Leptogastrinae (Leptogaster), Ommatiinae (Ommatius), Stenopogoninae (Callinicus, Microstylum, Ospriocerus, Scleropogon, and Stenopogon), Stichopogoninae (Stichopogon), and Trigonomiminae

(Holcocephala). Most Asilidae prefer a generalist or polyphagous diet consisting of only arthropod prey. However, several genera appear oligophagous – Ceraturgus on Coleoptera, Diogmites on Hymenoptera, Laphria on Lampyridae, Mallophora on Apidae, Megaphorus on Hymenoptera, Nicocles on Diptera, Ospriocerus on Meloidae, Promachus on Apidae, Saropogon on Hymenoptera, and Stichopogon on Diptera. This dataset also supports previous findings that female asilid predators outnumbered males in a 1.5 to 1 ratio.

Chapter 3

Assassin flies (Diptera: Asilidae) are a diverse family that plays an essential ecological role as top aerial and venomous predators. Little is known about the evolution of their predatory habits. This study provides a novel phylogenetic hypothesis of Asilidae along with prey preference and ancestral state reconstruction in a maximum likelihood framework. This study is based on 176 assassin fly species, 35 Asiloidea outgroup species, prey preference data accumulated from literature and museum collections, and approximately 7,913 bp of nuclear DNA from five genes (18S and 28S rDNA, AATS, CAD, and EF-1α protein-encoding DNA) and mitochondrial DNA from one gene (COI). Of the 12 asilid subfamilies included in the analysis the monophyly of six was supported. We used ancestral state reconstruction and stochastic character mapping to test whether a polyphagous arthropod predator is the ancestral state for Asilidae. Assassin flies are polyphagous arthropod predators, with specialized arthropod prey preferences evolving 20 independently across the Asilidae phylogeny.

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LIST OF SUPPLEMENTAL MATERIAL

A new species of *Saropogon* Loew, 1847 (Diptera, Asilidae) from Arizona, with a review of the Nearctic species north of Mexico

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ZooBank: http://zoobank.org/E6B79A47-F684-4AC1-ACA4-1E162DEDA5D3

Abstract

The Nearctic species of *Saropogon* Loew, 1847 north of Mexico are reviewed, with 19 species recognized and one described as new: *Saropogon pyrodes* **sp. nov.** from Arizona. This previously recognized new species has awaited description since its first collection in 1964. Only after a community scientist posted photographs taken in nature to an online database did its description become a priority. All species of *Saropogon* occurring in the Nearctic Region north of the Mexican border have been reexamined. Photographs and diagnoses of all species are provided with a distribution map of the included specimens studied. An updated key to the Nearctic species north of Mexico is provided. Finally, the need for a review of the diverse Mexican fauna is expressed.

Keywords

assassin flies, community science, identification key, Nearctic, robber flies, taxonomy

Introduction

New and undescribed species of insects are increasingly photographed and posted to online databases by the public (e.g., Mesaglio et al. 2021). Online images and identification databases are excellent resources through which community naturalists and scientists can interact with experts of their interest groups, sometimes resulting in the joint discovery of a new species (e.g., Winterton et al. 2012). Herein we describe a case where a known new species had been awaiting description in a personal collection for many years, but it was not until images were posted online that the naming of the species became a priority. This charismatic and 'fire-like' species of assassin fly (Diptera: Asilidae; Fig. 1.1) has inspired the reexamination of the Nearctic species of the globally diverse and taxonomically confounding genus, *Saropogon* Loew, 1847.

Figure 1.1. *Saropogon pyrodes* sp. nov. male in nature at ~ 0.7 km ENE of Amado in southern Arizona on Sep. 5, 2017, Photograph by Jeff Gruber.

Saropogon (Fig. 1.1; Fig. 1.6) includes at least 128 species and two subspecies (Sakhvon 2020). It is one of few Asilidae genera believed to occur in almost all zoogeographic regions (Londt 1997; Sakhvon 2020). It is, however, found mainly in temperate and tropical climates. In the Nearctic, *Saropogon* occurs primarily in the southwestern within the USA, in Texas, Arizona, New Mexico, and California, with some species scattered in the adjacent states. Some species occur as far north as Colorado and Nebraska and as far south as Nayarit, Mexico (Fig. 1.2). This manuscript focuses on the species found in Arizona but provides locality information of all specimens examined in the Supplemental material.

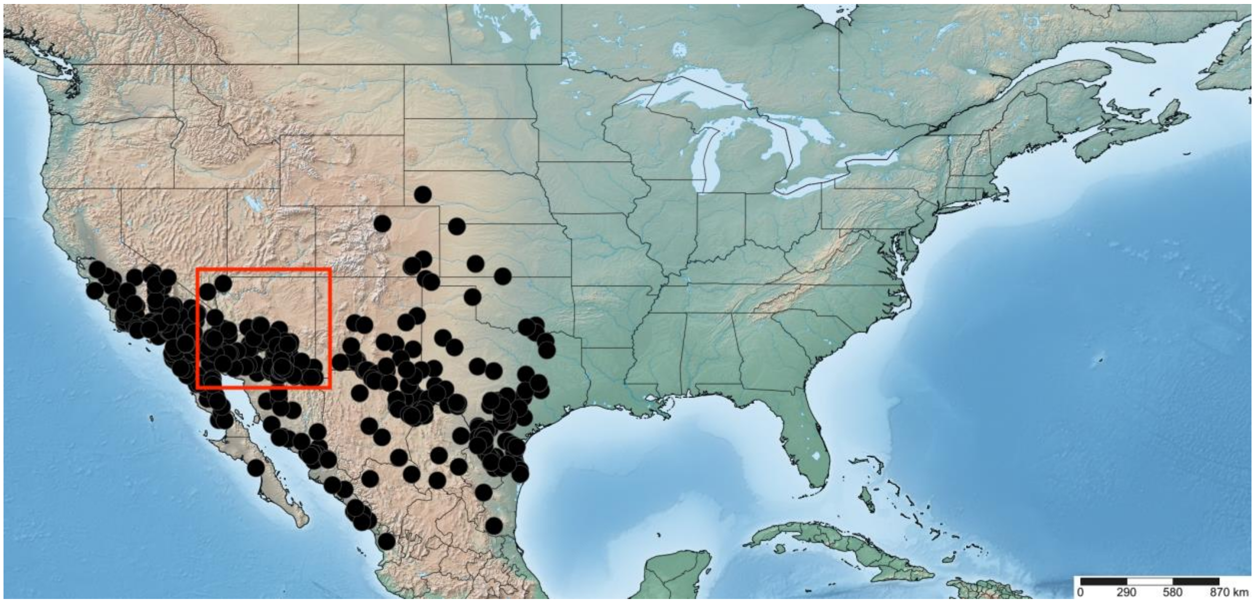

Figure 1.2. Distribution of Nearctic *Saropogon* (Diptera: Asilidae) examined. Red box indicates focused distribution for Fig. 1.10. Map created with SimpleMappr on 25 January 2022, and available at: https://www.simplemappr.net/map/17061

Wilcox (1966) most recently provided descriptions and an identification key to the then known Nearctic species. The status of several species has changed over the years, mainly due to the wide distribution and strong sexual dimorphism of many Nearctic species. We summarize the status history as follows:

Loew (1847) described *Saropogon* as a subgenus of *Dasypogon* (type species *Dasypogon luctuosus* Wiedemann, 1820).

Loew (1874) described the first Nearctic *Saropogon* species from Texas (*S. combustus* (male) and *S. adustus* (female)).

Osten-Sacken (1887) described *Saropogon senex* from Mexico (Sinaloa).

Coquillett (1902) described *Saropogon dispar* from Texas.

Johnson (1903) described *Saropogon abbreviates* and *S. bicolor* from Texas.

Coquillett (1904) described *Saropogon semiustus*, *S. luteus*, and *S. hyalinus* from California.

Back (1904) described *Saropogon albifrons* from Arizona and *S. rufus* from California.

Back (1909) synonymized *Saropogon albifrons* with *S. semiustus* (in part, see Wilcox 1966: 131), synonymized *S. adustus* with *S. combustus,* synonymized *S. rufus* with *S. luteus,* and described *S. coquillettii* from New Mexico. He also gave descriptions and a key to the known Nearctic species.

Curran (1930) described *Saropogon aridus* and *S. purus* from Arizona and published a key to the species.

Curran (1931) described *Saropogon birdi* from Oklahoma and provided a revised key to the species.

Bromley (1934) described *Saropogon fletcheri* and *S. pritchardi* from Texas and Oklahoma and gave a key to the Texas species.

Wilcox (1936) described the female of *Saropogon aridus*.

Bromley (1951) described *Saropogon laparoides* and *S. solus* from Texas.

Martin and Wilcox (1965) found that *Saropogon aridus* from Arizona was a synonym of *S. senex* described from Sinaloa, Mexico. Included *Saropogon hypomelas* (*Diogmites*) in their catalog.

Wilcox (1966) described *Saropogon bryanti* and *S. mohawki* from Arizona as well as *S. sculleni* and *S. nitidus* from Texas, noted of the synonymy of *S. albifrons* with *S. semiustus,* and discussed a personal communication with Bromley in 1936, who, after examining the type of *Diogmites hypomelas* decided that it belonged to *Saropogon* and Wilcox included the change in his identification key.

Fisher and Wilcox (1997; unpublished) proposed that *Saropogon sculleni* was a junior synonym of *S. laparoides.*

Current North American species:

Saropogon abbreviatus Johnson, 1903

Saropogon albifrons Back, 1904

Saropogon birdi Curran, 1931

Saropogon bryanti Wilcox, 1966

Saropogon combustus Loew, 1874

Saropogon coquillettii Back, 1909

Saropogon dispar Coquillett, 1902

Saropogon fletcheri Bromley, 1934

Saropogon hyalinus Coquillett, 1904

Saropogon hypomelas Loew, 1866

Saropogon laparoides Bromley, 1951

Saropogon luteus Coquillett, 1904

Saropogon mohawki Wilcox, 1966

Saropogon nitidus Wilcox, 1966

Saropogon pritchardi Bromley, 1934

Saropogon purus Curran, 1930

Saropogon pyrodes sp. nov.

Saropogon semiustus Coquillett, 1904

Saropogon senex Osten Sacken, 1887

Saropogon solus Bromley, 1951

Materials and methods

This study is based on examined specimens from the following institutions and online resources:

ASUHIC –The Hasbrouck Insect Collection, Arizona State University, Tempe, Arizona, U.S.A.

BMEC –The Bohart Museum of Entomology, University of California Davis, Davis, California U.S.A.

BugGuide – www.bugguide.net;

BYU – Brigham Young University, Provo, Utah, U.S.A.

CASENT – California Academy of Sciences Entomology Collection, San Francisco, California U.S.A.

Flickr – www.flickr.com

iNaturalist – www.inaturalist.org

LACM ENT – Natural History Museum of Los Angeles County Entomology Collection, Los Angeles, California, U. S. A.

MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

NHMUK – Natural History Museum, London, England, U.K.

NMSU – New Mexico State University Arthropod Collection, Las Cruces, New Mexico, U.S.A.

TAM – personal collection of Dr. Tristan McKnight, Tucson, Arizona U.S.A.

SEMC – Snow Entomological Museum Collection, The University of Kansas, Lawrence, Kansas, U.S.A.

TAMUIC – Texas A&M University Insect Collection, College Station, Texas, U.S.A.

UAIC – The University of Arizona Insect Collection, Tucson, Arizona, U.S.A.

UCR – University of California Riverside Entomology Research Museum, California, U.S.A.

USNM – Smithsonian National Museum of Natural History, Washington, D.C., U.S.A.

Repository abbreviations are from the 2022 GBIF Registry of Scientific Collections with some additions of preferred names from the collection's website, or personal communications.

Morphological terminology follows Dikow (2009a) and Cumming and Wood (2017). In the descriptions, abdominal tergites are abbreviated with '**T**,' and sternites are abbreviated with '**S**.' Prothoracic, mesothoracic, and metathoracic segments are abbreviated to 'pro,' 'mes,' and 'met,' respectively. Pubescence refers to the short, fine microtrichia densely covering certain body parts. Other generalized terms follow Nichols (1989).

Species descriptions are based on all specimens examined (Supplemental Material 1.1) and not exclusively on the holotype. A total of 1522 specimens of *Saropogon* was examined. The sole specimen of *S. birdi* Curran, 1931 was examined from photographs provided by the AMNH staff. The female wing of *Saropogon pyrodes* was not photographed because only two female specimens were available (the method used is destructive), and because there is no apparent sexual dimorphism present in this species.

Not all holotypes were examined in person. During the research portion of this manuscript, many collections were closed for visits and loans due to the Covid-19 pandemic and specimens were unavailable to the authors. All holotypes were at least examined through photographs. When available, links to all holotype photographs have been provided in the comments section for each species.

In all instances, specimens were dry-mounted on pins. Morphological features were examined using a Wild stereomicroscope. Wing length is measured from the tegula to the distal tip of the wing. The left wing was removed or, if previously broken, taken from the unit tray from a representative specimen from each species examined. After being photographed, the wing was then placed in a plastic pill capsule and pinned underneath the relevant specimen. Wing length is used in the species descriptions instead of body length because *Saropogon* abdomens are sometimes curved and difficult to measure. We have found more consistent measurements with wing lengths. The male terminalia were removed, placed in 10% potassium hydroxide (KOH) at 55 ^{o}C, neutralized in acetic acid (CH_3COOH) and rinsed in distilled water (H_2O). They were temporarily stored in 75 % ethanol (C_2H_5OH) for further examination and illustration, eventually sealed in polyethylene vials containing 100 % glycerin ($C_3H_8O_3$), and pinned underneath the corresponding specimen.

Most whole habitus photographs of pinned specimens and wings were taken at the BMEC by the first author, using a GIGAmacro Magnify^2 system, a Canon MP-E 65 mm macro-lens, Canon EOS Rebel T5i. The specimens were illuminated with a Macro Twin Lite MT-24EX through a simple paper light diffuser tube. The images were then processed through Lightroom and stacked using Zerene stacker. Finally, spot cleaning, color fixing, and inserting scale bars were done in Adobe Photoshop. At USNM, photographs appearing as Fig. 1.9A–G of the female and male terminalia were taken on a Zeiss SteREO Discovery V12 stereo microscope with a PlanApo S 1.0x lens at 40–95x magnification and an attached Olympus OM-D E-M1 MicroFourThirds digital camera. The dissected terminalia were placed in 75% ethanol in a glass dish and illuminated by a Schott VisiLED light source using mixed bright-field (dorsal), dark-field (lateral), and transillumination (ventral). The MicroFourThirds camera was tethered to a laptop computer and controlled by Olympus Capture software (version 2.2.1), and the vertical movement for obtaining photographs for later image stacking was done manually using the fine drive. Some whole habitus photographs of pinned specimens in the USNM were taken with a GIGAmacro Magnify^2 system, a Canon EOS D5 Mark IV full-frame DSLR, a Canon MP-E 65 mm F/2.8 macro-lens and illuminated by a Canon ring-lite flash. Individual RAW-format images taken at USNM were stacked using HeliconFocus Pro (version 7+) and exported in Adobe DNG-format.

SimpleMappr was used to generate the distribution maps of all specimens with defined localities (Shorthouse 2010). All localities and elevation not stated explicitly on the original label were estimated using Google Earth Pro version 7.3.4.8248 (Google Earth Pro 2021) and noted as estimates in Supplemental Material 1.1. Google Earth Pro uses digital elevation model (DEM) to calculate elevation.

Taxonomy

Saropogon Loew, 1847

Saropogon Loew, 1847: 439 (as subgenus of *Dasypogon*).

Type species: *Dasypogon luctuosus* Wiedemann, 1820; Coquillett (1910: 603); by designation.

= Sarapogon Williston, 1889: 74; incorrect spelling.

= *Araiopogon* Carrera, 1949: 122; junior synonym.

Type species: *Dasypogon gayi* Macquart, 1838: 37).

= *Lycomax* Hull, 1962: 278; as a subgenus of *Saropogon* Loew, 1847.

Type species: *Saropogon flavofacialis* Hull, 1956: 133.

= *Oberon* Carrera and Papavero, 1962: 57; junior synonym.

Type species: *Oberon velutinus* Carrera and Papavero, 1962: 58.

Subfamily: Dasypogoninae (Hull 1962; Papavero 1973; Lehr 1988; Artigas and Papavero 1988; Geller-Grimm 2004; Dikow 2009a; Cohen et al. 2021).

Tribe: Saropogonini (Hardy 1926; Martin and Papavero 1970; Dikow 2009a, 2018).

Diagnosis

Saropogon has a stout and often twisted spur at the antero-ventral apex of the fore tibiae (Fig. 1.3A), the same as related genera in the subfamily Dasypogoninae. It differs from other Nearctic taxa such as *Diogmites* Loew and *Blepharepium* Rondani by having cell m_3 open (Fig. 1.3B), and an antennal stylus composed of a single element with an apical seta-like element positioned apically in a cavity on the stylus (Fig. 1.3C). However, some *S. pritchardi* have cell m_3 almost closed, but never stalked. *Saropogon* differs from *Lestomyia* Williston by having a mystax confined to the oral margin (Fig. 1.3D) and its face is slightly concave (Fig. 1.3E) when viewed laterally. Some species of *Lestomyia* have a mystax confined to the oral margin, which can be distinguished from *Saropogon* by *having* strong anterior (presutural) dorsocentral bristles (absent in *Saropogon* (Wilcox 1966)). *Cophura* can be distinguished from *Saropogon* by its fore tibial spur on the postero-ventral surface being thin, and sigmoid rather than stout, hooked and on the antero-ventral surface (Dikow 2009a). *Cophura* also has a midtibia with a large, usually black, apical spine, which is absent in all *Saropogon* studied. Length 10–27 mm.

Figure 1.3. *Saropogon nitidus* Wilcox, 1966 illustrating distinguishing characters of the genus. **A** fore tibia with a distinct spur. **B** open m_3 cell on wing, **C** antennal style, **D** mystax of *S. nitidus* restricted to oral margin, and **E** face slightly concave. Scale bar 2 mm.

Sexual Dimorphism and wing variation in *Saropogon*

Back (1909) and Wilcox (1966) have called attention to many species of *Saropogon* that represent prime examples of sexual dimorphism. Species like *S. abbreviatus* (Fig. 1.4A, B), *S. combustus* (Fig. 1.4C, D), *S. purus* (Fig. 1.4E, F), and *S. senex* (Fig. 1.4G, H) have the male abdomen predominantly black, whereas the female abdomen is largely red. However, there can be color variation within these species. Curran (1931) reported a female *S. combustus* with a black abdomen. Leg color is also sexually dimorphic in most Nearctic *Saropogon,* with male legs tending to be black and female legs mainly reddish. Exceptions occur: the male of *Saropogon purus* has reddish hind femora and middle femora, and the female of *S. senex* has mainly black legs except for reddish hind femora. Setal patterns can also be dimorphic: males have long, erect, or semierect hairs on the mesonotum, abdomen, and legs in *Saropogon bryanti*, *S. combustus*, *S. coquillettii*, *S. dispar*, *S. laparoides*, and *S. mohawki*. In the females of these species, these hairs are short, appressed, and inconspicuous.

Wilcox (1966) emphasized that the wings of many species of *Saropogon* contain diagnostic features. Wings of *Saropogon abbreviatus* (Fig. 1.5A, B), *S. bryanti* (Fig. 1.5C, D), *S. combustus* (Fig. 1.5E, F), *S. dispar* (Fig. 1.5G, H), *S. hypomelas* (Fig. 1.5I, J), *S. luteus* (Fig. 1.5K, L), *S. purus* (Fig. 1.5M, N), and *S. senex* (Fig. 1.5O, P) are sexually dimorphic: they are brown in males, yellowish in females. Species with brown wings in both sexes are *Saropogon senex*, *S. abbreviatus*, *S. purus*, and *S. pritchardi*; *S. luteus* and *S. pyrodes* sp. nov., have yellowish wings in both sexes.

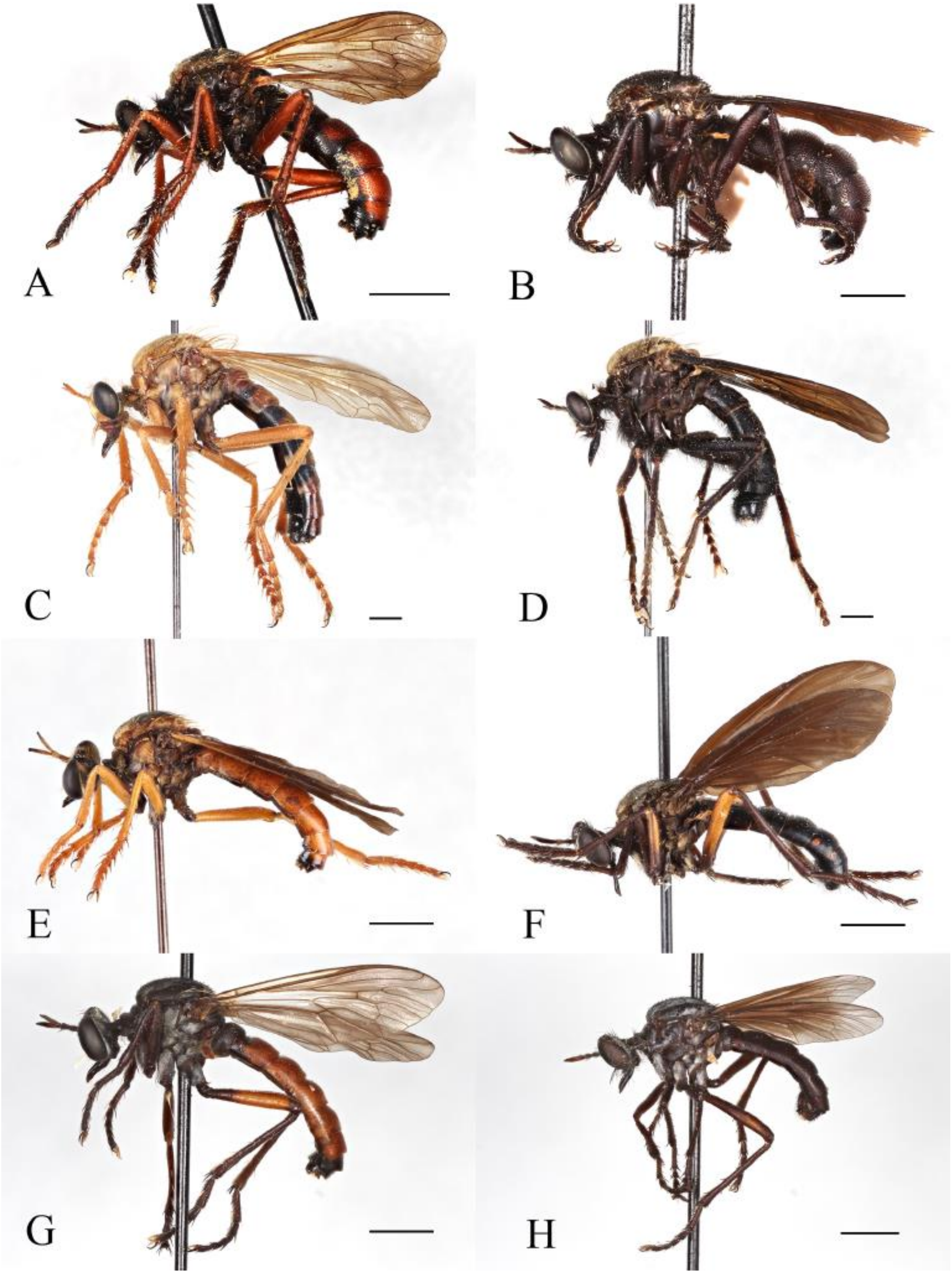

Figure 1. 4. Sexual color dimorphism **A** *Saropogon abbreviatus* female, **B** *S. abbreviatus* male, **C** *S. combustus* female, **D** *S. combustus* male, **E** *S. purus* female, **F** *S. purus* male, **G** *S. senex* female, and **H** *S. senex* male. Scale bars 2 mm.

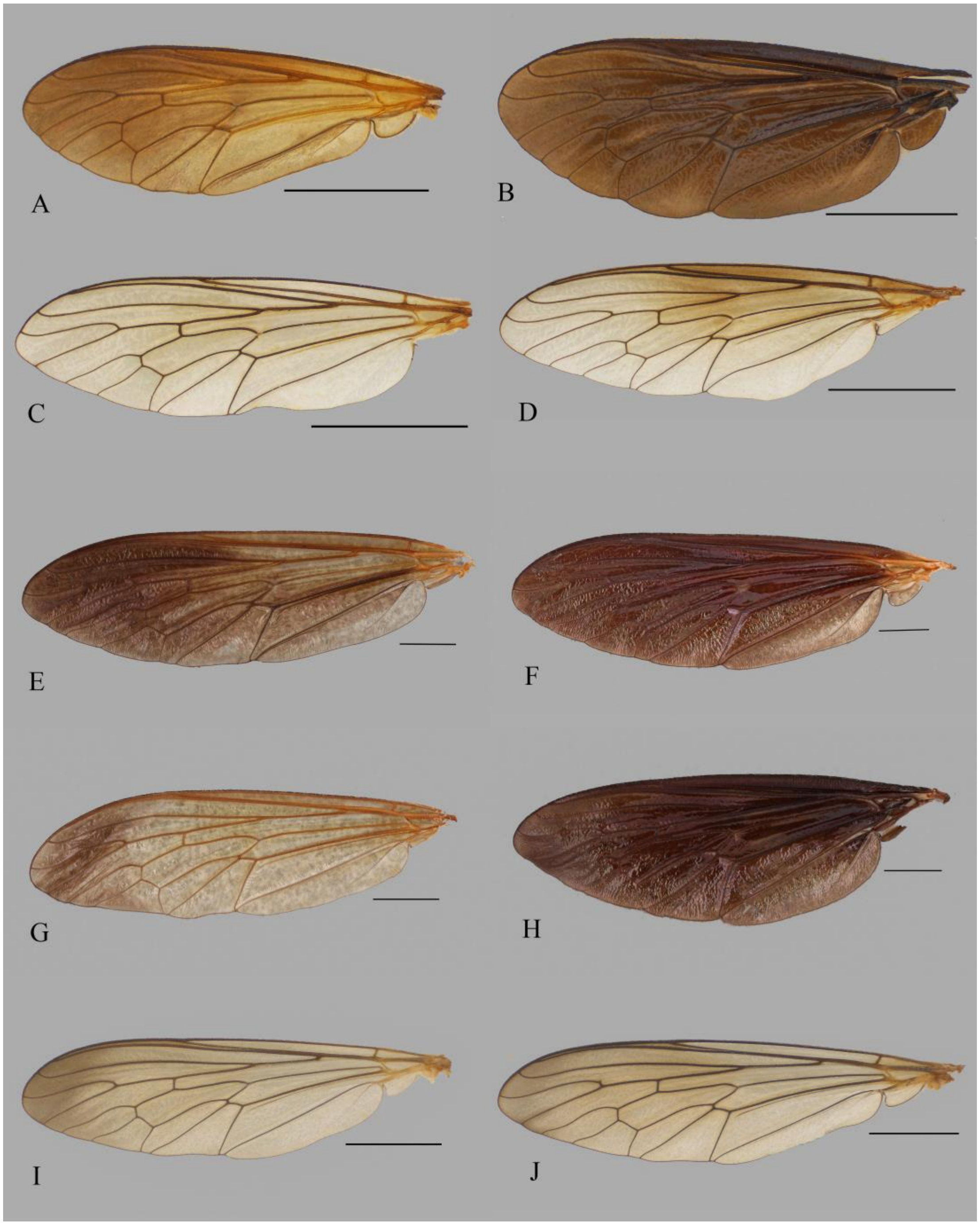

Figure 1.5. Representative *Saropogon* wings of **A** *S. abbreviatus* female, **B** *S. abbreviatus* male, **C** *S. bryanti* female, **D** *S. bryanti male,* **E** *S. combustus* female, **F** *S. combustus* male, **G** *S. dispar* female, **H** *S. dispar* male, **I** *S. hypomelas* female, and **J** *S. hypomelas* male, Scale bars 2 mm.

Biology

Dasypogoninae and *Saropogon* apparently tend to prefer Hymenoptera prey (Lavigne 2016, Pollock 2021; Table 1.1). *S. combustus* and *S. pritchardi* show a particular interest in the workers of *Pogonomyrmex* harvester ants (Pollock 2021). There is currently only one record of *Saropogon* as prey to another genus of Asilidae in North America. Bromley (1934a) recorded *Diogmites symmachus* Loew, 1872 feeding on *Saropogon dispar* in Texas.

Table 1.1. Adult *Saropogon* (Diptera: Asilidae) predation records in North America. Records gathered from Lavigne, 2016 online database (specimens were not examined personally); Arizona State University, Hasbrouck Insect Collection (ASUHIC); Bellamy, 2002; Brigham Young University, Provo, Utah (BYU); University of California, Davis, The Bohart Museum of Entomology (BMEC); Bromley, 1934; Hurd, 1952; Hurd and Linsley, 1975; New Mexico State University Arthropod collection (NMSU); Pollock 2021; Sweetman, 1958; Texas A&M University insect collection (TAMUIC); Thorp, 1973; University of Arizona Insect Collection (UAIC); University of California, Riverside, Entomology Research Collection (UCR), and the Smithsonian's National Museum of Natural History (USNM) pinned collection. Duplicate prey records for the same species are not included.

Predator	**Prey order**	**Prey family**	**Original source or collection**	**Country (state)**
S. abbreviatus	Hymenoptera	Apidae	BYU	USA (TX)
S. albifrons	Hymenoptera	Crabronidae	UCR	USA (CA)
S. bryanti	Hymenoptera	Apidae	USNM	USA (AZ)
S. bryanti	Hymenoptera	Vespidae	UAIC	USA (AZ)

S. bryanti	Hymenoptera	(?)	ASUHIC	USA (AZ)
S. bryanti	Hymenoptera	Apidae	Photograph – Jacob Smith	USA (AZ)
S. combustus	Coleoptera	Carabidae	Pollock, 2021	USA (NM)
S. combustus	Coleoptera	Chrysomelidae	Pollock, 2021	USA (NM)
S. combustus	Coleoptera	Tenebrionidae	Pollock, 2021	USA (NM)
S. combustus	Diptera	Asilidae	Pollock, 2021	USA (NM)
S. combustus	Diptera	Bombyliidae	Pollock, 2021	USA (NM)
S. combustus	Diptera	Culicidae	Pollock, 2021	USA (NM)
S. combustus	Hemiptera	Cicadidae	Pollock, 2021	USA (NM)
S. combustus	Hemiptera	Membracidae	Pollock, 2021	USA (NM)
S. combustus	Hemiptera	Rhopalidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Andrenidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Apidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Apoidea	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Braconidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Crabronidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Formicidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Formicidae	Pollock, 2021	USA (TX)
S. combustus	Hymenoptera	Halictidae	NMSU	USA (NM)
S. combustus	Hymenoptera	Ichneumonidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Mutillidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Pompilidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Sphecidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Thynnidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Tiphiidae	Pollock, 2021	USA (NM)
S. combustus	Hymenoptera	Vespidae	Pollock, 2021	USA (NM)
S. combustus	Araneae	(?)	Pollock, 2021	USA (NM)
S. coquillettii	Hymenoptera	Apidae	TAMUIC	USA (TX)
S. coquillettii	Hymenoptera	Apidae	Hurd and Linsley, 1975	USA (NM)
S. coquillettii	Hymenoptera	Megachilidae	Hurd and Linsley, 1975	USA (NM)

S. coquillettii	Hymenoptera	Vespidae	NMSU	USA (NM)
S. dispar	Coleoptera	Cerambycidae	USNM	USA (TX)
S. dispar	Coleoptera	Elateridae	Sweetman, 1958	USA (?)
S. dispar	Coleoptera	Scarabaeidae	Sweetman, 1958	USA (?)
S. dispar	Diptera	Bombyliidae	TAMUIC	USA (TX)
S. dispar	Diptera	Bombyliidae	Bromley, 1934	USA (TX)
S. dispar	Diptera	Calliphoridae	USNM	USA (TX)
S. dispar	Diptera	Muscidae	TAMUIC	USA (TX)
S. dispar	Diptera	Syrphidae	Bromley 1934	USA (TX)
S. dispar	Hemiptera	Coreidae	Bromley 1934	USA (TX)
S. dispar	Hymenoptera	Andrenidae	Bromley 1934	USA (TX)
S. dispar	Hymenoptera	Andrenidae	Linsley, 1960	USA (?)
S. dispar	Hymenoptera	Apidae	BYU and Bromley, 1934	USA (TX)
S. dispar	Hymenoptera	Apidae	BMEC and Thorp, 1973	USA (OK)
S. dispar	Hymenoptera	Apidae	USNM	USA (TX)
S. dispar	Hymenoptera	Crabronidae	BMEC	USA (OK)
S. dispar	Hymenoptera	Halictidae	Bromley, 1934	USA (TX)
S. dispar	Hymenoptera	Halictidae	Thorp, 1973	USA (OK)
S. dispar	Hymenoptera	Halictidae	Linsley, 1944	USA (?)
S. dispar	Hymenoptera	Pompilidae	Bromley, 1934	USA (TX)
S. dispar	Hymenoptera	Pompilidae	Hurd, 1952	USA (?)
S. dispar	Hymenoptera	Pompilidae	TAMUIC	USA (TX)
S. dispar	Hymenoptera	Scoliidae	Bromley, 1934	USA (TX)
S. dispar	Hymenoptera	Sphecidae	Bromley, 1934	USA (TX)
S. dispar	Hymenoptera	Sphecidae	BMEC and Thorp, 1973	USA (OK)
S. dispar	Hymenoptera	Vespidae	Bromley, 1934	USA (TX)
S. dispar	Hymenoptera	Vespidae	TAMUIC	(?)
S. dispar	Orthoptera	Acrididae	Bromley, 1934	USA (TX)
S. fletcheri	Coleoptera	Buprestidae	BYU	USA (TX)
S. fletcheri	Hymenoptera	Scoliidae	BYU	USA (TX)

S. fletcheri	Hymenoptera	Vespidae	BYU	USA (TX)
S. fletcheri	Hymenoptera	(?)	BYU	USA (TX)
S. hypomelas	Hymenoptera	Ichneumonidae	TAMUIC	USA (TX)
S. hypomelas	Hymenoptera	Vespidae	TAMUIC	USA (TX)
S. hypomelas	Hymenoptera	Vespidae	USNM	USA (TX)
S. mohawki	Coleoptera	Buprestidae	Bellamy, 2002	USA (CA)
S. mohawki	Coleoptera	Buprestidae	USNM	USA (CA)
S. mohawki	Hymenoptera	Halictidae	USNM	MEX (B.C.N.)
S. mohawki	Hymenoptera	(?)	ASUHIC	USA (AZ)
S. pritchardi	Coleoptera	Carabidae	Pollock, 2021	USA (NM)
S. pritchardi	Coleoptera	Tenebrionidae	Pollock, 2021	USA (NM)
S. pritchardi	Hymenoptera	Formicidae	Pollock, 2021	USA (NM)
S. pritchardi	Hymenoptera	Formicidae	Pollock, 2021	USA (TX)
S. purus	Diptera	(?)	ASUHIC	USA (AZ)
S. purus	Hymenoptera	(?)	ASUHIC	USA (AZ)
S. pyrodes	Hymenoptera	Apidae	Photograph – Jeff Gruber	USA (AZ)
S. senex	Coleoptera	Elateridae	USNM	MEX (Nay)
S. senex	Hymenoptera	Formicidae	USNM	MEX (Nay)

Saropogon females oviposit in soil with the aid of the acanthophorite spines (Fig. 1.9D) at the tip of their ovipositor. They use the spines to dig into the ground, to lay the eggs, and to sweep soil over the eggs after oviposition (Dennis and Lavigne 1975).

Key to species of North American *Saropogon,* modified from Wilcox (1966)

1	Apical scutellar macrosetae absent or short, shorter than ½ length of scutellum	**2**
-	Apical scutellar macrosetae present, as long or longer than length of scutellum	**4**
2	Apical scutellar macrosetae absent; both sexes with reddish abdomen; wing length 8 mm (USA: Texas; Mexico: Tamaulipas) Fig. 1.30	***S. solus* Bromley**
-	Apical scutellar macrosetae present; male abdomen black, female abdomen reddish	**3**
3	Discal scutellar setae developed as short macrosetae; anepisternum (except dorsally), katepisternum, proepimeron, and anepimeron non-pubescent with large, uniformly arranged circular depressions; male legs black, female legs red (USA: California, Texas; Mexico: Baja California, Tamaulipas) Fig. 1.7	***S. abbreviatus* Johnson**
-	Discal scutellar setae absent; anepisternum, katepisternum, proepimeron, and anepimeron with grayish pubescence, without uniformly arranged circular depressions; legs predominantly black, both sexes with metathoracic femora red (USA: Arizona; Mexico: Sinaloa, Sonora, Nayarit) Fig. 1.29	***S. senex* Osten Sacken**
4	Wings hyaline, without microtrichia or sparse microtrichia apically with no or slight color staining	**5**
-	Wings infuscate, males with brown or black wings, females lighter but with staining and/or microtrichia concentrated apically and around veins; generally larger flies (except *S. purus* and *S. luteus*)	**12**
5	Predominantly black abdomen; fore coxae with long, fine, white setae (USA: Texas) Fig. 1.17	***S. laparoides* Bromley**
	Predominantly reddish or yellowish abdomen; fore coxae with macrosetae or bare	**6**
6	Anepisternum and katepisternum with non-pubescent spot on the anterior half (e.g., Fig. 1.20B, F)	**7**
	Anepisternum and katepisternum pubescent throughout	**8**
7	Red non-pubescent spot on anepisternum and katepisternum; femora reddish; antennae dark red to yellow; wings with slight microtrichia apically (USA: Arizona) Figs 1.6, 1.23 – 1.27	***S. pyrodes* sp. nov.**
	Black non-pubescent spot on anepisternum and katepisternum; femora yellowish; antennae black to brown; wings entirely bare of microtrichia (USA: New Mexico, Texas; Mexico: Chihuahua, Coahuila) Fig. 1.20	***S. nitidus* Wilcox**
8	White macrosetae on scutum and scutellum; scutellum with gray pubescence.	**9**
	Yellowish macrosetae on scutum and scutellum; scutellum with gold pubescence	**10**

9	Face and anepisternum with light gold pubescence; male legs black with distally red femora, female with reddish legs; wings completely hyaline (USA: California, Arizona; Mexico) Fig. 1.28	***S. semiustus* Coquillett**
	Face and anepisternum with gray pubescence; both sexes with reddish legs; wings mostly hyaline but with slight brown tinge anteroproximally (USA: Arizona, California; Mexico: Baja California) Fig. 1.8	***S. albifrons* Back**
10	Wings mostly hyaline but always with slight microtrichia apically; male femora proximally black over half the length, females with entirely reddish legs (USA: Arizona, New Mexico, Texas; Mexico: Sonora) Fig. 1.12	***S. coquillettii* Back**
	Wings completely hyaline; both sexes with reddish legs, sometimes femora proximally darker but never more than half the length	**11**
11	Abdomen T4 and 5 anterolaterally black in both sexes; four apical scutellar macrosetae; male femora sometimes proximally black and reddish distally, female legs entirely reddish (USA: Arizona, California, Nevada, Utah; Mexico: Baja California, Sonora) Fig. 1.19	***S. mohawki* Wilcox**
	Abdomen yellow; two apical scutellar macrosetae; both sexes have entirely reddish legs (USA: New Mexico, Texas; Mexico: Chihuahua, Coahuila) Fig. 1.15	***S. hyalinus* Coquillett**
12	Small flies (body length < 15 mm; wing length < 11 mm)	**13**
	Large flies (body length > 15 mm; wing length > 11 mm)	**14**
13	Wings light orange stained especially around veins, microtrichia apically, thin (width < 1/3 of length); both sexes with thorax and abdomen orange (USA: California; Mexico: Baja California) Fig. 1.18	***S. luteus* Coquillett**
	Wings entirely dark brown from microtrichia and wide (width > 1/3 of length); male with black thorax and abdomen, female with dark brown thorax and orange abdomen (USA: Arizona; Mexico: Sinaloa, Sonora) Fig. 1.22	***S. purus* Curran**
14	Femora entirely red (e.g., Fig. 1.14B)	**15**
	Femora entirely black or at least with a dorsal black stripe (e.g., Fig. 1.9B, C)	**17**
15	T2–4 non-pubescent to sparse white pubescence on posterolateral margin, narrowly black on the anterior margins forming a thin band (USA: Texas) Fig. 1.14	***S. fletcheri* Bromley**
	T2–4 white pubescence on posterolateral margin, if black on the anterior margin, never forming a thin band	**16**
16	Wings entirely dark brown from microtrichia; antennae brown (USA: New Mexico, Oklahoma, Texas) Fig. 1.21	***S. pritchardi* Bromley**
	Wings light orange stained especially around veins, microtrichia apically; antennae orange (USA: Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas) Fig. 1.4, 1.11	***S. combustus* Loew - in part (females)**

17	Coxae and katatergite with black setae (USA: Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas) Figs 1.4, 1.11	***S. combustus*** **Loew - in part (males)**
	Coxae and katatergite with white or yellow setae	**18**
18	Abdomen predominantly black; T3 red is restricted to the posterior half if any	**19**
	Abdomen predominantly red; T3 black is restricted to the antero-lateral surface	**20**
19	Female with black basal segments of the palpi, segment 2 reddish; abdomen mostly black; two apical scutellar macrosetae (USA: Oklahoma) Fig. 1.9	***S. birdi*** **Curran – (females)**
	Female with orange basal segments of the palpi, male with black; female abdomen with some black; male abdomen mostly black; four apical scutellar macrosetae (USA: Oklahoma, Texas) Fig. 1.13	***S. dispar*** **Coquillett**
20	Male face and frons with white pubescence, female golden with ocellar tubercle and area around it white; male femur, sometimes tibia, black; female femur proximally black or with proximal black dorsal stripe, legs reddish; scutum with yellowish gray pubescence median stripe with brown pubescence without sub-lateral spots (USA: Arizona, New Mexico, Texas; Mexico: Coahuila, Nuevo Leon) Fig. 1.16	***S. hypomelas*** **(Loew)**
	Both sexes face and frons with golden pubescence; femur in both sexes reddish with black dorsal stripe; scutum yellowish with broad central stripe and elongated sub-lateral spots with gray pubescence (USA: Arizona, New Mexico, Texas; Mexico: Sonora) Fig. 1.10	***S. bryanti*** **Wilcox**

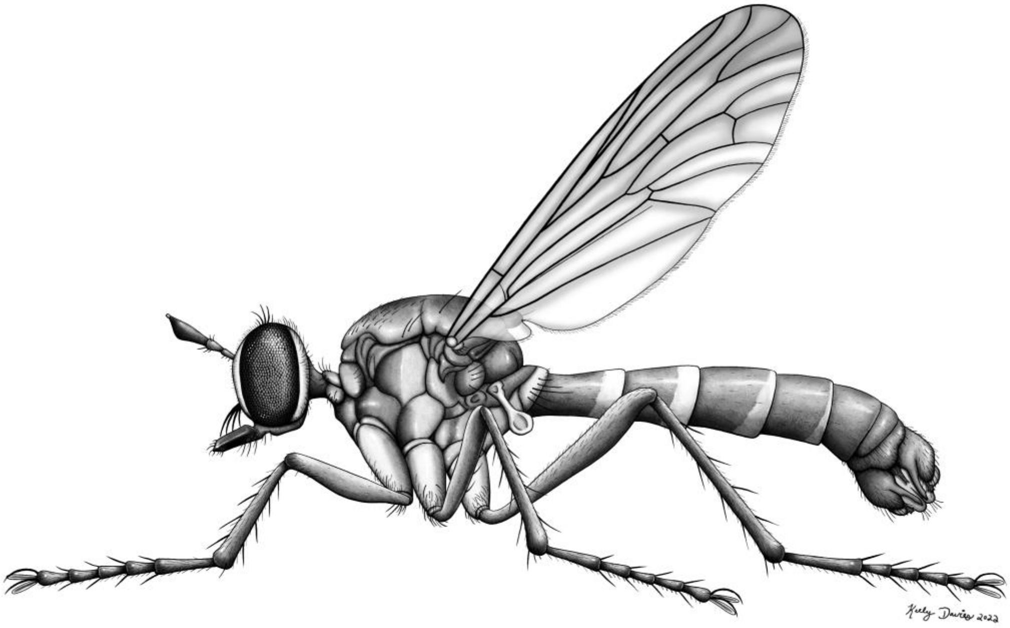

Figure 1.6. Habitus drawing of male *Saropogon pyrodes* sp. nov. by Keely Davies.

Saropogon abbreviatus **Johnson, 1903**

Figs 1.4A, B, 1.5A, B, 1.26, 1.7, 1.31

Saropogon abbreviatus Johnson, 1903: 113.

Saropogon bicolor Johnson, 1903: 113, junior synonym [homonym of *Saropogon bicolor* Jaennicke, 1867 (currently recognized as *Diogmites bicolor* Jaennicke, 1867)].

References. Back 1909: 345 (key and redescription); Curran 1930: 2 (key), 1931: 2 (key); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 128 (key); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. Has a rather short and stout abdomen with uniformly arranged circular depressions. The male is black with black or brown wings and the female is reddish with brown wings, darker apically. Body length 9–12 mm; wing length 7–9 mm. Flight time April – August.

Most similar to *S. senex* and *S. purus*. Differs from *S. purus* because *S. abbreviatus* has short apical scutellar macrosetae, whereas the apical scutellar macrosetae of *S. purus* are longer than the length of the scutellum. Differs from *S. senex* because *S. abbreviatus* has short discal scutellar macrosetae, and *S. senex* has none.

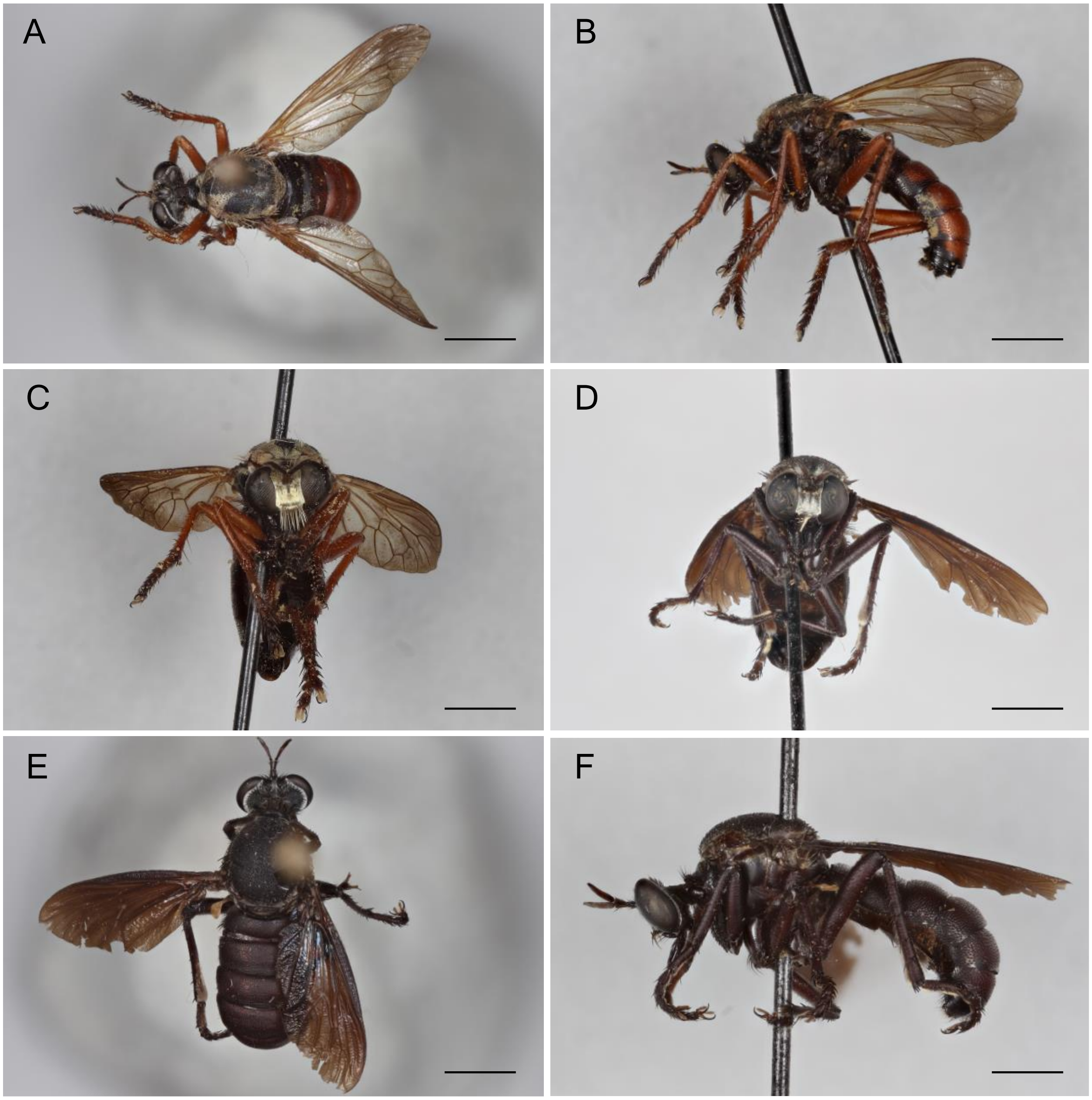

Figure 1.7. *Saropogon abbreviatus* Johnson, 1903 Female (USNMENT01830071): **A** dorsal view, **B** lateral view, **C** anterior view; Male (USNMENT01830070): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Distribution. USA: California, Texas; Mexico: Baja California, Tamaulipas

Type material examined. UNITED STATES OF AMERICA • 1 ♂, holotype; Texas; MCZ; Type 7582.

Other material examined. Supplemental material 1.1.

Comments. The holotypes of *Saropogon abbreviatus* and *S. bicolor* (jr. syn.) are currently in the Museum of Comparative Zoology at Harvard University. The collection provides photos of the types on their website MCZBase: https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:7582 and https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:32756.

Saropogon albifrons Back, 1904

Figs 1.8, 1.26, 1.32

Saropogon albifrons Back, 1904: 29.

Saropogon semiustus Coquillett, 1904: 186, junior synonym. In part.

References. Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 130 (key and redescription); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. Legs reddish orange in both sexes; face, scutum, and anepisternum entirely with white pubescence with white macrosetae; antennae yellowish; ~ 30 macrosetae forming mystax; wings hyaline with a slightly darker tinge proximally; veins brownish at the base of the wing, darker apically; T2–5 postero-laterally with white pubescence in both sexes; scutellum with only two marginal bristles. Body length 9–14 mm; wing length 7–9 mm. Flight time April – June.

Easily confused with *Saropogon semiustus*, especially females; white face pubescence is the best distinguishing character in *S. albifrons*.

Distribution. USA: Arizona, California; Mexico: Baja California

Type material examined. UNITED STATES OF AMERICA • 1 ♀, lectotype; Arizona, Mohave County, Bill Williams Fork; August; F. H. Snow; SEMC; SEMC1603972 • 1 ♀, paralectotype; same collection information as lectotype; SEMC; SEMC1603973.

Arizona material examined. UNITED STATES OF AMERICA • 6 ♀; La Paz County, Parker, Osborn Well Road, 1.6 km E. of Route 95, white sand dunes; 34°07' N, 114°15' W; 150 m; 02 May 2008; T. Dikow, E. Fisher; USNM; USNMENT00870564, USNMENT00870565, USNMENT00870566, USNMENT00870567, USNMENT00870568, USNMENT00870569 • 1 ?; Maricopa County, Bush Highway; 33°32' N, 111°35' W; 415 m; 09 May 1968; R. N. Foster; ASUHIC; ASUHIC0139490 • 1 ♀; Maricopa County, Gila Bend; 32°56'N, 112°43'W; 224 m; F. H. Parker; USNM; USNMENT0119937 • 3♂, 1♀; Maricopa County; Gila River, 10 km S. Arlington; 33°13'N, 112°45'W; 200 m; 03 June 2010; F. D. Parker, M. E. Irwin; UAIC • 1 ♀; Maricopa County; Queen Creek; 33°15'N, 111°38'17"W; 425 m; 06 June 1964; G. D. Butler Jr.; UAIC • 1 ?; Yuma County; 8 mi. SE of Parker; 34°01' N, 114°01' W; 176 m; 07 May 1966; S. A. Gorodenski, J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139489 • 1 ?; Yuma County, Mohawk Pass; 32°43’ N, 113°44’ W; 24 April, 1966; J. H. Davidson, J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139488.

Other material examined. Supplemental material 1.1.

Comments. *Saropogon albifrons* was not mentioned by Curran (1930, 1931), most likely because the species was not included in the Back (1909) identification key. [The authors are unsure as to why it was not included.] The co-types (syntypes) referenced in Back 1904 were deposited one in the Massachusetts Agricultural College collection and one at the University of Kansas collection (SEMC); however, both can be currently found at SEMC. The authors have designated the specimen in better condition to be the lectotype and the other the paralectotype. Information about them can be found here: https://biodiversity.ku.edu/node/1095/.

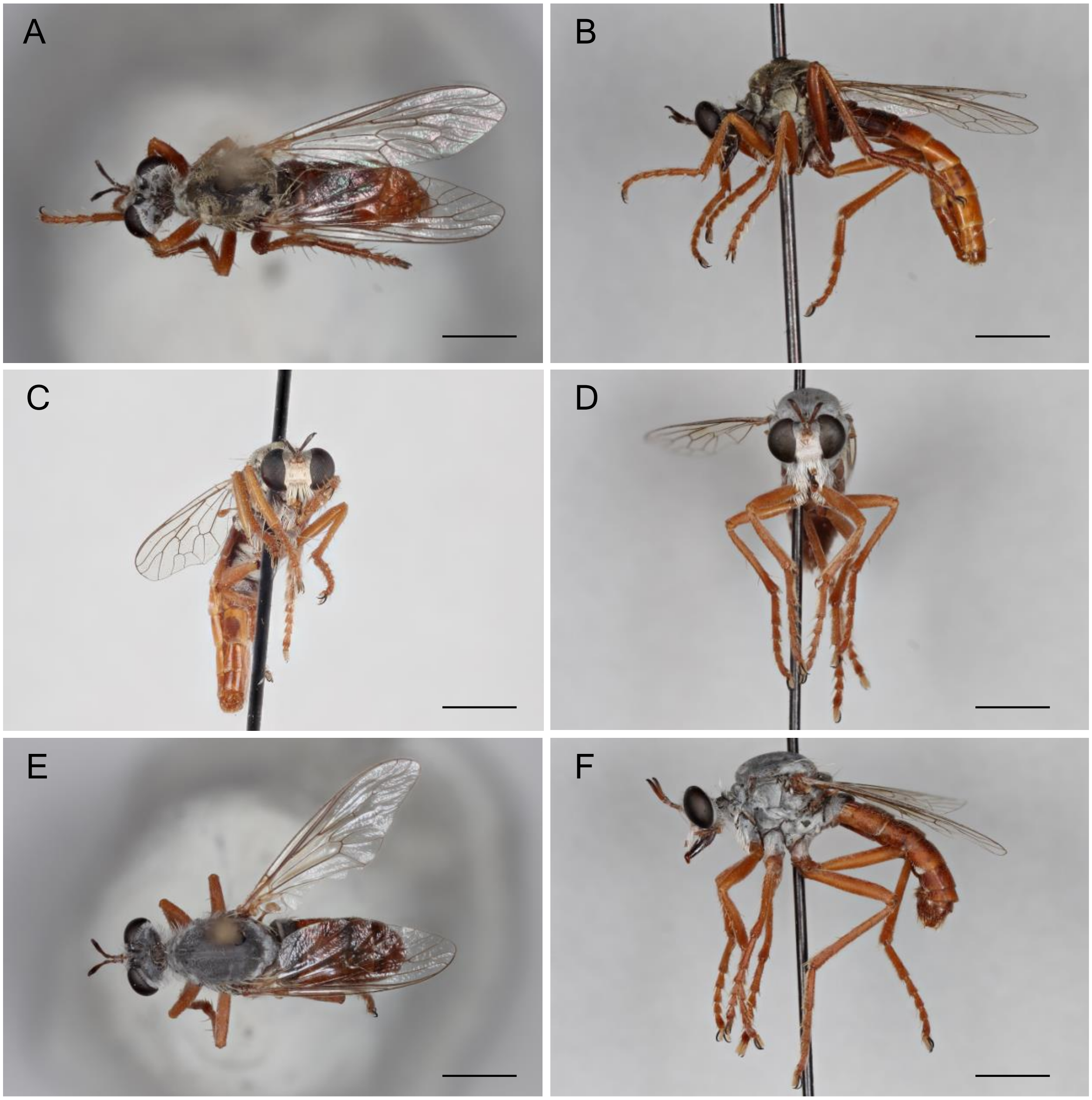

Figure 1.8. *Saropogon albifrons* Back, 1904 Female (USNMENT01819164): **A** dorsal view, **B** lateral view, **C** anterior view; Male (USNMENT01830072): **D** anterior view, **E** dorsal view, and **F** lateral view. Scale bars 2 mm.

Saropogon birdi Curran, 1931

Figs 1.9, 1.26, 1.31

Saropogon birdi Curran, 1931: 2.

References. Curran 1931: 2 (key and original description); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 129 (key to females); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. Antennae mostly reddish except the style; base of palpi are black; femora black dorsally; coxal macrosetae yellowish; wings amber-colored with a tinge of brown apically; two apical scutellar macrosetae; abdomen mostly black. Body length 27 mm; wing length 15–21 mm. Flight time June.

Commonly confused with *S. pritchardi* but *S. birdi* has black on the femora dorsum. Distinguished from *S. dispar* by having two apical scutellar macrosetae, and black basal segments of the palpi. *S. dispar* has four apical scutellar macrosetae and the female has orange basal segments of the palpi.

Distribution. USA: Oklahoma

Type material examined. UNITED STATES OF AMERICA • 1 ♀, holotype; Oklahoma, Johnson County; 34°17’N, 96°37’W; 241 m; 20 June 1929; R. D. Bird; AMNH.

Comments. We were only able to examine the holotype from images sent from the American Museum of Natural History where it is housed. We have been unable to find any other specimens of this species to examine.

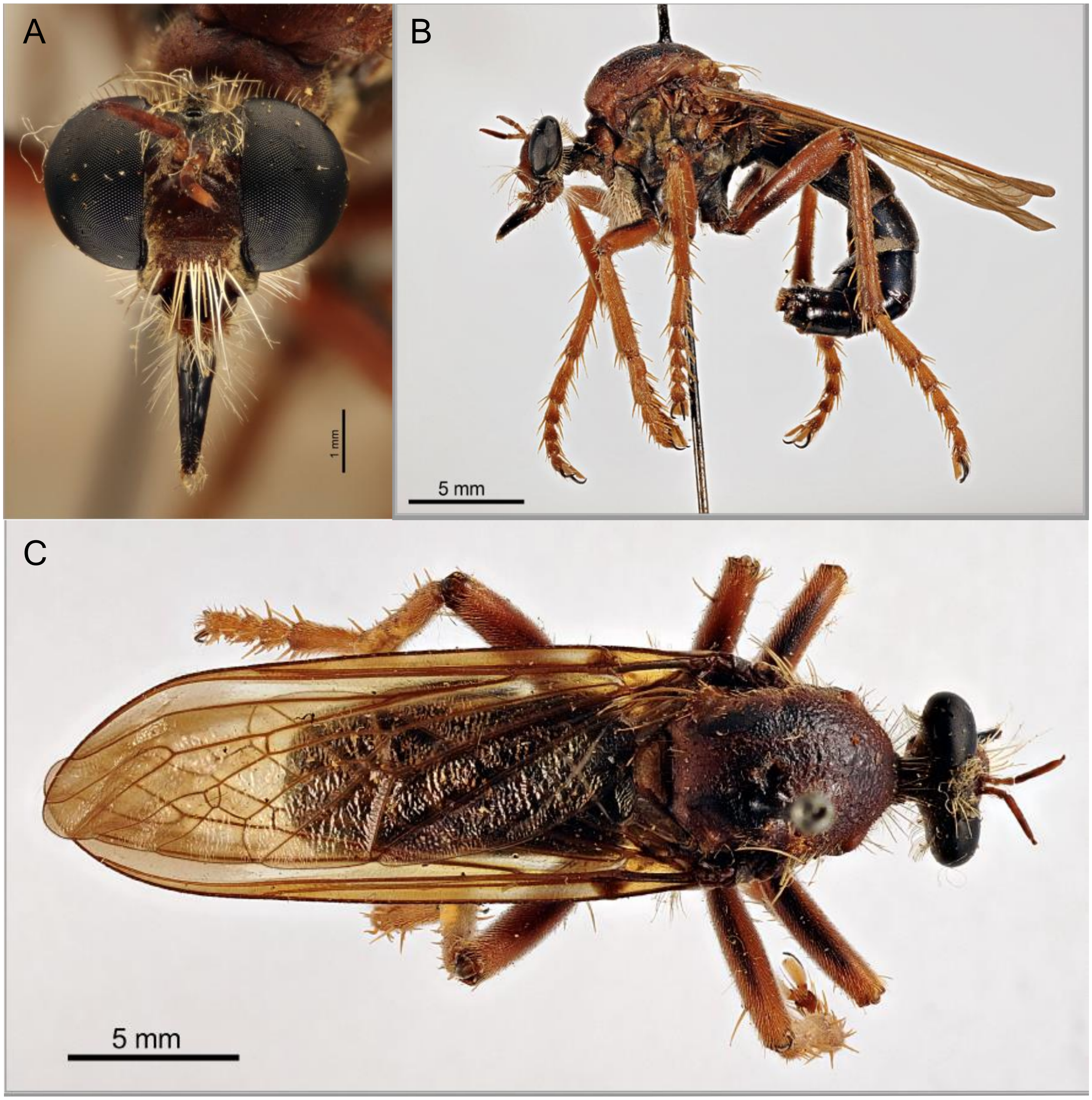

Figure 1.9. *Saropogon birdi* Curran, 1931 Female holotype **A** anterior view, **B** lateral view, **C** dorsal view. Photograph provided by American Museum of Natural History.

Saropogon bryanti Wilcox, 1966

Figs 1.5C, D, 1.10, 1.26, 1.33

Saropogon bryanti Wilcox, 1966: 132.

References. Wilcox 1966: 132 (key and original description); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. Femur in both sexes reddish with black dorsal stripe; male and female face and frons with golden pubescence; scutum yellowish with the broad central stripe and elongated sub-lateral spots with gray pubescence. Male wing covered in microtrichia, female wing with microtrichia especially around veins Body length 16–19 mm; wing length 16–18 mm. Flight time June – August.

Distinguishable from *Saropogon hypomelas* by the face and frons being with golden pubescence and the extent of the black on the femora.

Distribution. USA: Arizona, New Mexico, Texas; Mexico: Sonora

Type material examined. UNITED STATES OF AMERICA • 1 ♂, holotype; Arizona, Pima County, Baboquivari Canyon W. side Baboquivari Mts; 31°47’ N, 111°37’ W; 1124 m; 25 – 27 July 1952; H. B. Leech, J. W. Green; CASENT; Type no. 9278. • 1 ♀, allotype; same data as for holotype; CASENT; CASENT8427216 • 1 ♀, paratype; Arizona, Pima County, 8 mi. N. Tucson; 32°19’ N, 110°58’ W; 756 m; 11 June 1964; J. M. Davidson; USNM; USNMENT01830074.

Arizona material examined. UNITED STATES OF AMERICA • 1 ♂; Cochise County, 7 mi. N. Mescal; 32°04’N, 110°26’W; 1097 m; 24 July 1966; F. G. Werner family; UAIC • 1 ♂; Cochise County, Portal; 31°54’ N, 109°8’ W; 1433 m; 02 June 1964; J. M. Davidson; USNM; USNMENT01830117 • 1 ♀; Cochise County, San Pedro River, 2 mi. E. Benson; 31°57’N, 110°16’W; 1073 m; 30 June 1963; J. C. Bequaert, P. H. Johnson; UAIC • 1 ?; Maricopa County, 3.2 mi. SE. of St. Johns, E. of Sierra Estrellas; 33°17’ N, 112°10’ W; 320 m; 07 July 1973; M. Kolner, J. Alcock; ASUHIC; ASUHIC139498, ASUHIC139499, ASUHIC139400, ASUHIC139401, ASUHIC139402, ASUHIC139403 • 33 ?; same collection data as for preceding; 10 July 1973; O. Francke, M. Kolner; ASUHIC; ASUHIC139404, ASUHIC139405, ASUHIC139406, ASUHIC139407, ASUHIC139408, ASUHIC139409, ASUHIC139410, ASUHIC139411, ASUHIC139412, ASUHIC139413, ASUHIC139414, ASUHIC139415, ASUHIC139416, ASUHIC139417, ASUHIC139418, ASUHIC139419, ASUHIC139420, ASUHIC139421, ASUHIC139422, ASUHIC139423, ASUHIC139424, ASUHIC139425, ASUHIC139426, ASUHIC139427, ASUHIC139428, ASUHIC139429, ASUHIC139430, ASUHIC139431, ASUHIC139432, ASUHIC139433, ASUHIC139434, ASUHIC139435, ASUHIC139436 •1 ♀; Maricopa County, 6 mi. N. of Scottsdale; 33°32’N, 111°55’W; 397 m; 07 September 1969; S. McCleve; UAIC • 3 ?; same collection data as for preceding; 22 July 1973; M. Kolner; ASUHIC; ASUHIC139437, ASUHIC139438, ASUHIC139439 • 2 ♂, 2 ♀; Maricopa County, 3.2 mi. SE. St. Johns, E. of Sierra Estrellas; 33°16’ N, 112°13’ W; 320 m; 10 July 1973; O. Francke, M. Kolner; CASENT; CASENT8427206, CASENT8427213, CASENT8427214, CASENT8427215 • 1 ?; Maricopa County, Granite Reef Dam; 33°30’ N, 111°41’ W; 401 m; 29 August 1964; J. M. Davidson; USNM; USNMENT01830106 • 1 ♂; Maricopa County; Sierra Mts.; 33°34’ N, 111°42’ W; 914 – 1219 m; 19 August 1924; A. A. Nichol; USNM; USNMENT01199077 • 2 ♂; Pima County, 4mi. E. Sahuarita; 31°57’N, 110°53’W; 861 m; 10 July, 1968; F. Werner, J. Burger, J. LaFage; UAIC • 1♀; Pima County 4 mi. SE. Sahuarita; 31°54’N, 110°54’W; 882 m; 17 July 1968; F. Werner, M. Noller; UAIC • 1 ♂; Pima County, 12 mi. N. Sasabe; 31°40’ N, 111°58’ W; 1134 m; 27 July 1973; E. M. Fisher; USNM; USNMENT01830118 • 1 ♀; Pima County, Santa Rita Experimenal Range Reserve; 31°49’N, 110°51’W; 1130 m; 21 July 1970; UAIC • 1 ♂; Pima County; 18 mi. W. Robles Jct.; 32°4’ N, 111°37’ W; 861 m; 30 August 1970; P. H. Sullivan; USNM; USNMENT01830108 • 2 ♂, 1 ♀; Pima County, 12 mi. n. Sasabe; 31°39’ N, 111°32’ W; 1122 m; 27 July 1973; E. M. Fisher; USNM; USNMENT01830105, USMENT01830073; CASENT; CASENT8427411 • 1 ?; Pima County, Madera Canyon; 31°44’ N, 110°53’ W; 1354 m; 23 July 1966; J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139493 • 1 ♂; Pima County, Range Res. 7 mi. N. Sahuarite; 32°05’N, 110°58’W; 785 m; 19 July 1979; F. Werner, Olson, Nygard; UAIC • 1 ♂, 1 ♀; Pima County, Saguaro National Monument Cast.; 32°17’N, 111°09’W; 829 m; 23 July 1978; B. lipa; UAIC • 1 ♂, 1 ♀; Pima County, Santa Catalina Mountains; 32°26’ N, 110°47’ W; 2776 m; 13 August 1940; E. C. Van Dyke; CASENT; CASENT8427209, CASENT8427210 • 1 ?; Pima County; Santa Rita Range Reserve; 31°43’ N, 110°52’ W; 1797 m; 15 July 1970; M. Cazier, J. Bigelow, L. Welch; ASUHIC; ASUHIC0139494 • 1 ?; same collection data as for preceding; M. Kolner, S. Szerlip; ASUHIC; ASUCIC0139495 • 2 ♂, 3 ♀; same collection data as for preceding; 31°49’N, 110°51’W; 1130 m; 06 July 1979; F. Werner, Olson, Nygard; UAIC; • 1 ♂;

Pima County, Tucson; 32°13’ N, 110°58’ W; 724 m; 14 July 1947; USNM; USNMENT01199052 • 1 ♀; same collection data as for preceding; 18 July 1962; Wargo; UAIC • 1 ?; Pinal County, 12 mi. N. of Redington; 32°36’ N, 110°29’W; 950 m; 20 July 1966; J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139492 • 1 ♂; Pinal County, Apache Junction; 33°25’N, 111°34’W; 512 m; 30 July 1929; UAIC • 5 ♂, 2 ♀; Santa Cruz County, Santa Rita Mtns., Madera Canyon; 31°47’ N, 110°55’ W; 1049 m; 14 – 22 July 1971; D. G. Marqua, P. Sullivan; USNM; USNMENT0183007, USNMENT01830110, USNMENT01830111, USNMENT01830112, USNMENT01830113, USNMENT01830114, USNMENT01830115 • 1 ♂; same collection data as for preceding; 1503 m; 01 August 1960; S. L. Wood, J. B. Karren, H. Shurtleff; BYU; BYUC215968 • 3 ♂, 5 ♀; same collection data as for preceding; 12 July 1973; D. G. Marqua; CASENT; CASENT8427208; USNM; USNMENT01830116, USNMENT01830121, USNMENT01830122, USNMENT01830123, USNMENT01830124, USNMENT01830125, USNMENT01830126 • 1 ♀; Yavapai County, Congress; 34°9’ N, 112°51’ W; 931 m; 20 July 1930; T. F. Winburn, R. H. Painter; CASENT; CASENT8427207.

Other material examined. Supplemental material 1.1.

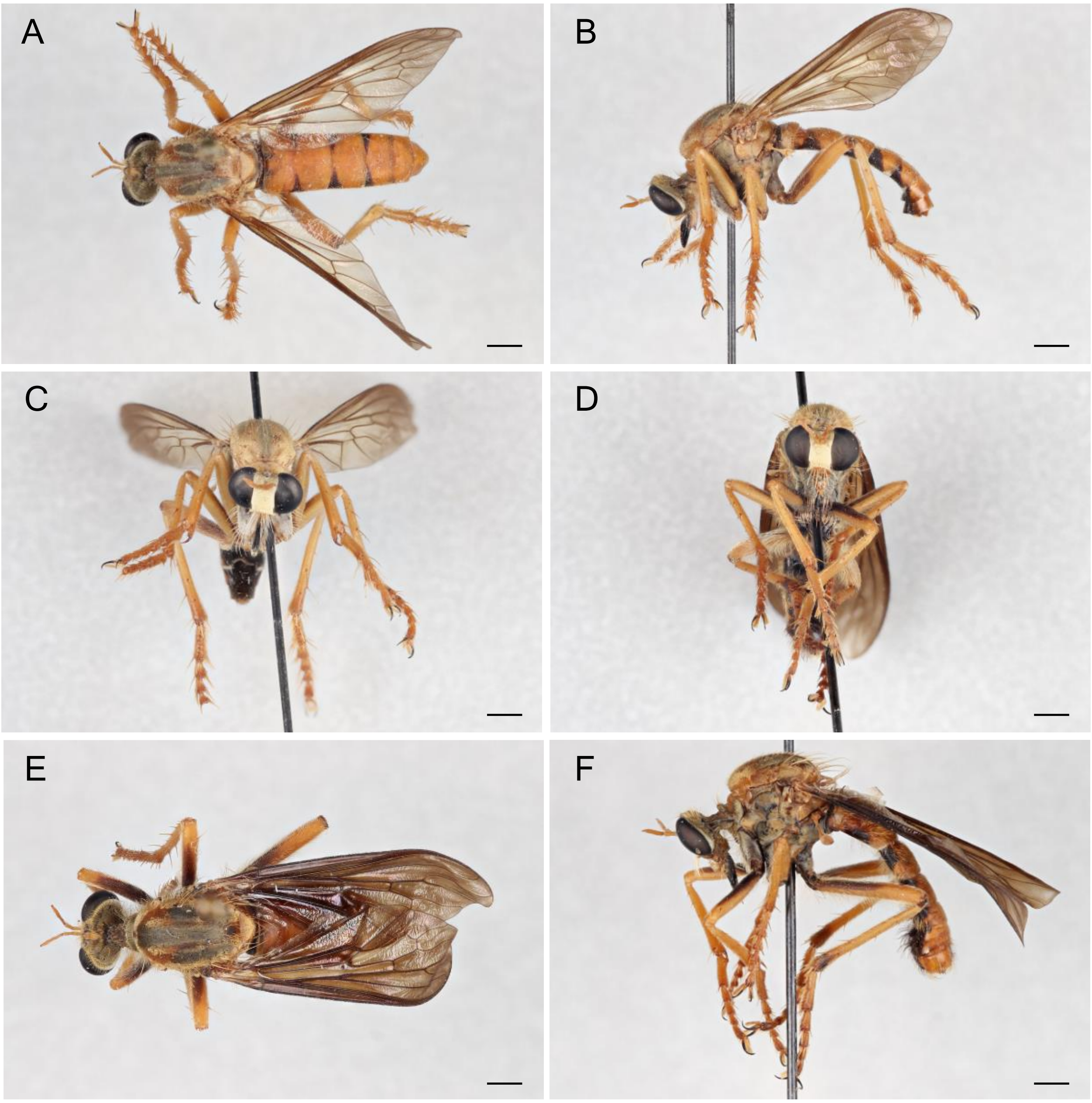

Figure 1.10. *Saropogon bryanti* Wilcox, 1966 Female (USNMENT01830074): **A** dorsal view, **B** lateral view, **C** anterior view; Male (USNMENT01830073): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Comments. One specimen we examined was from Iowa (CASENT8427218, Supplemental material 1.1), though the species seems to be identified correctly, this is still an unusual occurrence and may be a mistake, so it is not included in the known distribution for this species. Photographs of the *Saropogon bryanti* holotype can be found at: https://monarch.calacademy.org/taxa/index.php?tid=679454

Saropogon combustus Loew, 1874

Figs 4C–D, 5E–F, 1.11, 1.26, 1.34

Saropogon combustus Loew, 1874: 373.

Saropogon adustus Loew, 1874: 375, junior synonym.

References. Osten-Sacken 1874:185 (catalog); Back 1909: 347 (key and redescription); Curran 1930: 2 (key), 1931: 2 (key and notes); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 129 (key); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. This species is sexually dimorphic: males mostly black, wings brown, four scutellar bristles; females reddish, wings yellowish, anterior corners of T2–5 black. Body length 13–19 mm; wing length 14–17 mm. Flight time May – October.

The male is easily distinguished from *S. fletcheri* and *S. pritchardi* because it is significantly darker and more robust than the other males. The female is a bit more challenging but can be separated from *S. fletcheri* because it does not have the black anterior bands on its abdomen. The female *S. pritchardi* also has significantly darker wings than *S. combustus* which is light brown and darker apically.

Distribution. USA: Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas

SimpleMappr: https://www.simplemappr.net/map/16981

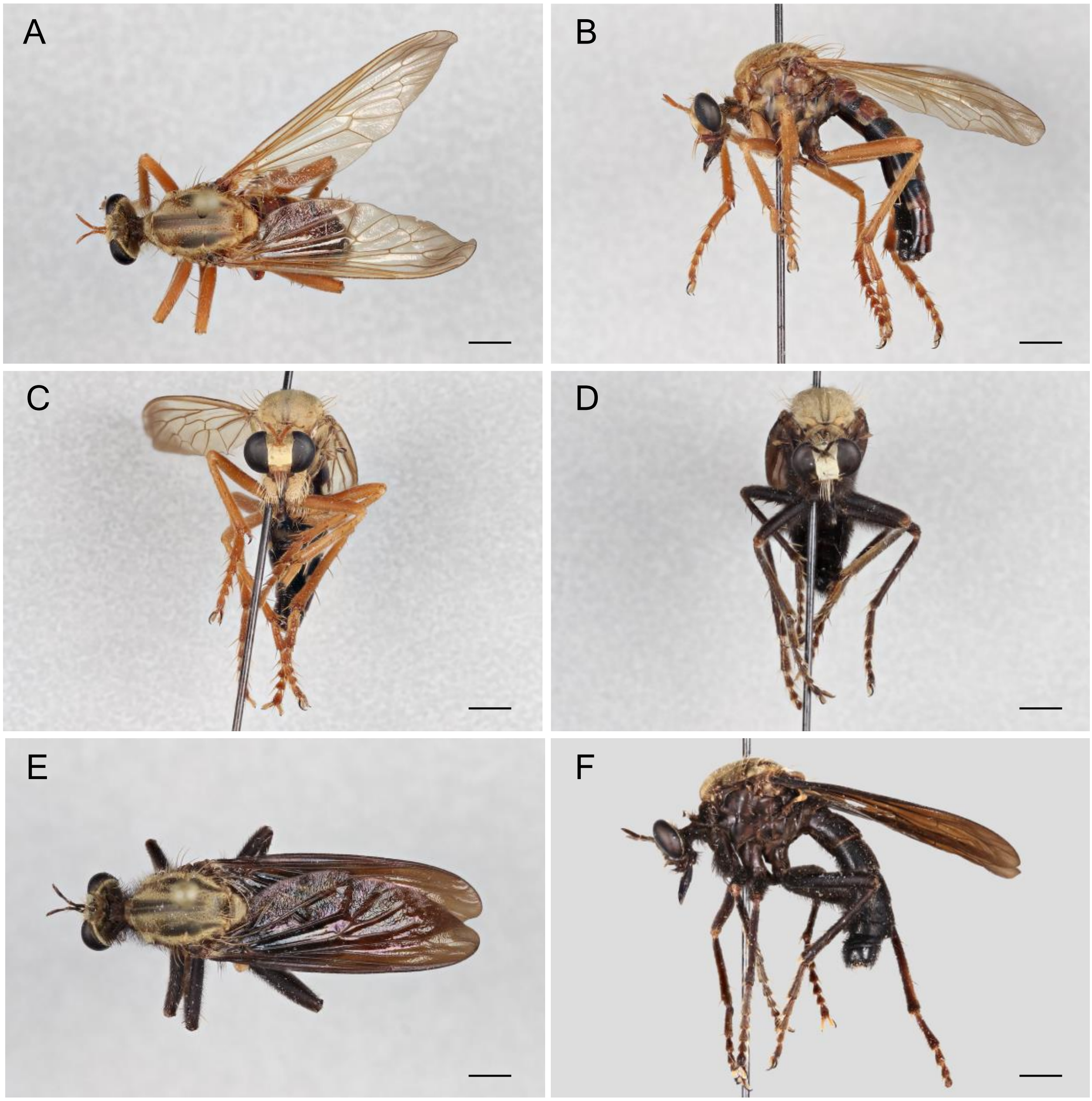

Figure 1.11. *Saropogon combustus* Loew, 1874 Female (USNMENT01819131): **A** dorsal view, **B** lateral view, **C** anterior view; Male (USNMENT01819138): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Type material examined. UNITED STATES OF AMERICA • 1 ♂, holotype; Loew; photographed pinned specimen; MCZ; Type 12819 • 1 ♀; Loew; MCZ; Type 12818.

Other material examined. Supplemental material 1.1.

Comments. The holotypes of both *Saropogon combustus* and *S. adustus* (junior synonym) are in the Museum of Comparative Zoology at Harvard University. The collection provides photos of the types on their website MCZBase: https://mczbase.mcz.harvard.edu/MediaSearch.cfm?action=search&media_id=99135,99136,99137,99138,99139 and https://mczbase.mcz.harvard.edu/MediaSearch.cfm?action=search&media_id=99130,99131,99132,99133,99134

Saropogon coquillettii Back, 1909

Figs 1.12, 1.26, 1.32

Saropogon coquillettii Back, 1909: 348.

Saropogon coquilletti auctt: common misspelling.

References. Back 1909: 348 (original description and key); Curran 1930: 2 (key), 1931: 2 (key); Martin and Wilcox 1965: 383 (catalog); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. *Saropogon coquillettii* is similar to *S. semiustus, S. hyalinus,* and *S. luteus,* but can be separated from them because it has four scutellar bristles instead of two. It has nearly hyaline wings with only a tinge of color apically and is more slender than *Saropogon combustus* and *S. dispar*. Body and wing length 14–16 mm. Flight time May – October.

Distribution. USA: Arizona, New Mexico, Texas; Mexico: Sonora
SimpleMappr: https://www.simplemappr.net/map/16982

Type material examined. UNITED STATES OF AMERICA • 1♂, holotype; New Mexico, Doña Ana County, Las Cruces; 32°28'N, 106°52'W; 1247 m; Aug 1923; Townsend; USNM; USNMENT01199124 • 1♂, 1♀, topotype; same locality data as holotype; 28 Jul; Townsend; USNM; USNMENT01199038, USNMENT01199017.

Arizona material examined. UNITED STATES OF AMERICA • 2♂, 4♀; Comal County, Cañon Lake; 33°32' N, 111°27' W; 631 m; 02 September 1935; F. H. Parker; USNM; USNMENT01199096, USNMENT01199088, USNMENT01199036, USNMENT01199092, USNMENT01199119, USNMENT01199045 • 1♀; Gila County, Globe; 32°22' N, 110°51' W; 1237 m; August; D. K. Duncan; USNM; USNMENT01518366 • 1♀; same collection data as for proceeding; 24 August 1957; F. H. Parker; UAIC • 2♂, 1♀, 1?; Gila County, San Carlos Lake; 33°11' N, 110°28' W; 749 m; August; D. K. Duncan; CASENT; CASENT8427290, CASENT8427291; USNM; USNMENT01199029, USNMENT01199043 • 1♂; Maricopa County, Higley; 33°18' N, 111°42' W; 398 m; 24 July 1917; E. G. Holt; USNM; USNMENT01819460 • 1♂; Maricopa County, Phoenix; 33°26' N, 112°04' W; 334 m; 01 August 1960; R. E. Rice; USNM; USNMENT01830392 • 1♀; Pima County, 30 mi. SE Ajo; 32°07' N, 112°26' W; 612 m; 30 July 1966; R. L. Brumley; BME; BMEP0280586 • 10♂; Pima

County, Picacho Pass; 32°39’ N, 111°23’ W; 555 m; 13 September 1954; J. C. Hall; BME; BMEP0280451, BMEP0280590, BMEP0280593, BMEP0280599, BMEP0280616, BMEP0280594, BMEP0280619, BMEP0280534, BMEP0280533, BMEP0280618 • 1♂, 2♀, 1?; Pinal County, 15 mi. S. of Florence; 32°50’ N, 111°21’ W; 631 m; 20 August 1949; F. H. Parker; USNM; USNMENT01199016, USNMENT01199056, USNMENT01199073 • 1♀; Pinal County; 32°48’ N, 111°17’ W; 619 m; 18 August 1940; E. R. Leach; CASENT; CASENT8427292 • 3♀; Pinal County, Mt. Superstition near Higley; 33°28’ N, 111°11’ W; 1424 m; 24 July 1917; E. G. Holt; USNM; USNMENT01819540, USNMENT01819520, USNMENT01819530.

Other material examined. Supplemental material 1.1.

Comments. This species is often misspelled (e.g., Curran 1930, 1931) as *Saropogon coquilletti*, but the original description states *S. coquillettii*. Photographs of the holotype can be viewed at: http://n2t.net/ark:/65665/326f621b6-964b-4453-8fb5-715b5480ab6f

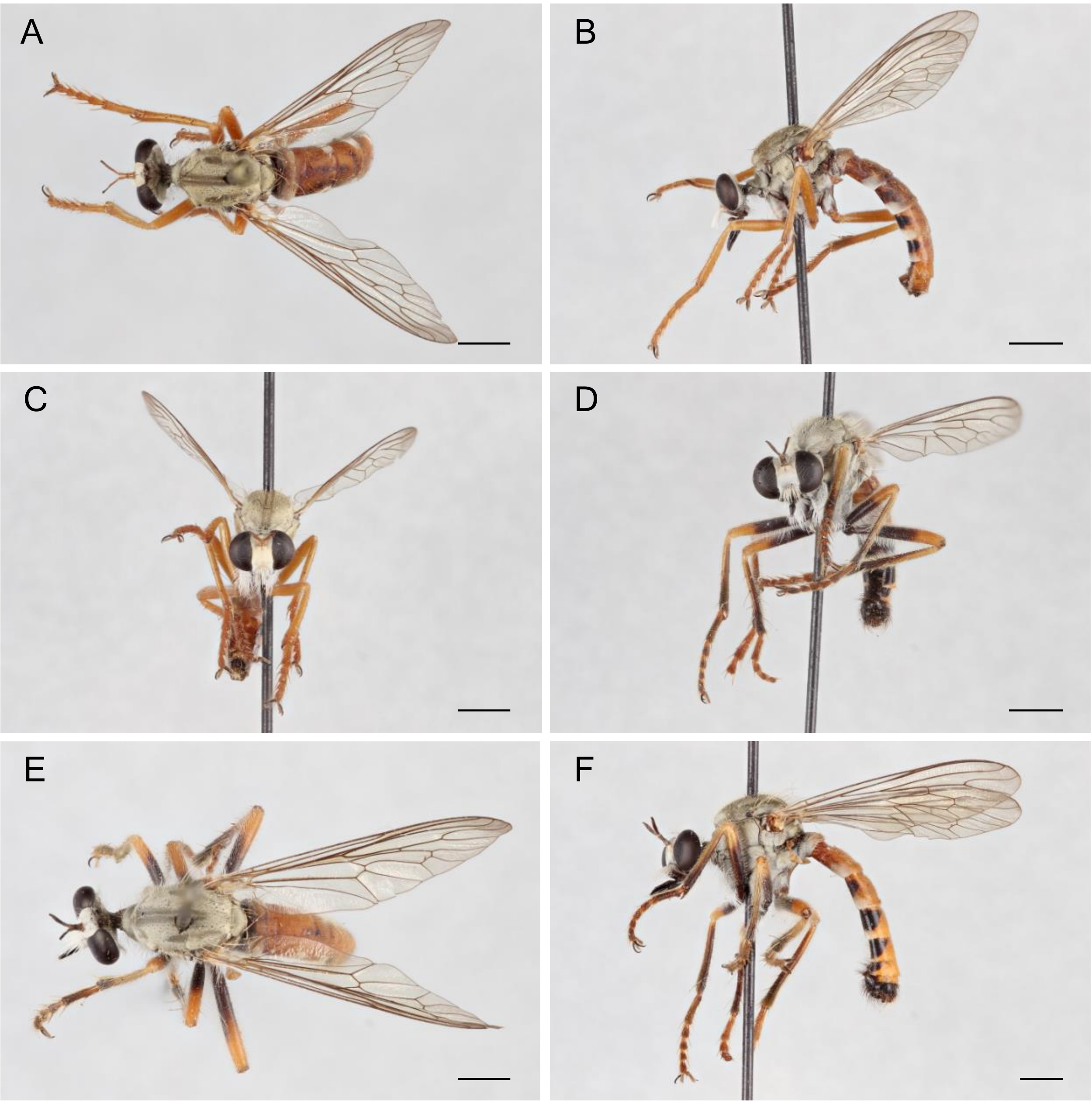

Figure 1.12. *Saropogon coquillettii* Back 1909 Female (USNMENT01830076): **A** dorsal view, **B** lateral view, **C** anterior view; Male (USNMENT01830075): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Saropogon dispar Coquillett, 1902

Figs 1.5G, H, 1.13, 1.32

Saropogon dispar Coquillett, 1902: 139.

References. Back 1909: 349 (key and redescription); Curran 1930: 2 (key), 1931: 2 (key and notes); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 129 (key); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. This species is sexually dimorphic: males with brown wings, black mesonotum and legs, brownish tibiae and tarsi; females with yellowish wings, brown mesonotum, reddish legs, distally blackish prothoracic and mesothoracic femora. Body length 20–23 mm; wing length 18–21 mm. Flight time May – August.

Saropogon dispar may be confused with *S. hypomelas* or *S. bryanti* but it is a significantly darker species than either.

Distribution. USA: Oklahoma, Texas

SimpleMappr: https://www.simplemappr.net/map/16983

Type material examined. UNITED STATES OF AMERICA • 1♂, holotype; Texas, DeWitt County, Cuero; 29°05’N, 97°17’W; 57 m; 06 Jun.; USNM; USNMENT01199066

Other material examined. Supplemental material 1.1.

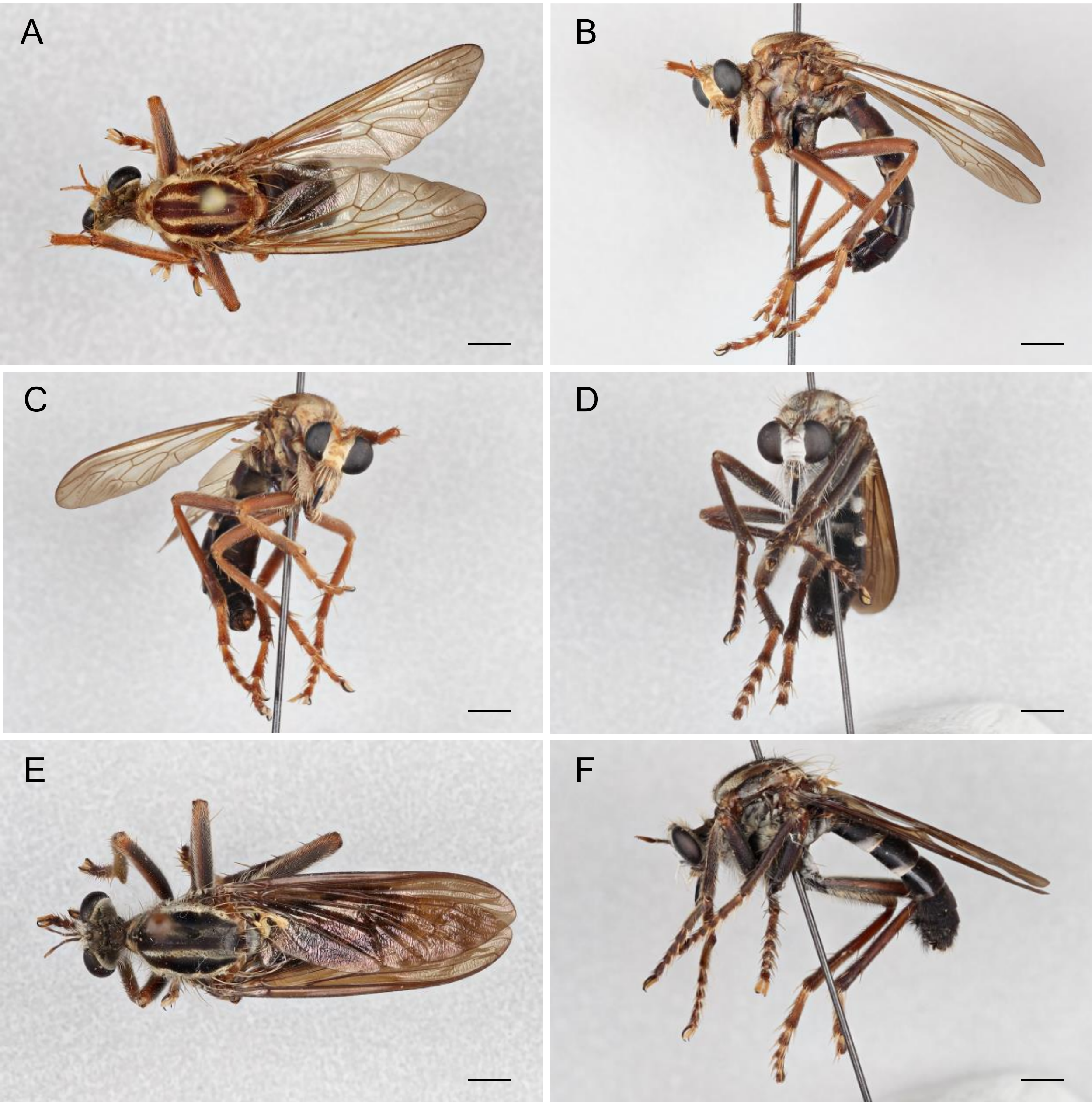

Figure 13. *Saropogon dispar* Coquillett, 1902 Female (UCBMEP0280509): **A** dorsal view, **B** lateral view, **C** anterior view; Male (UCBMEP0280508): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Comments. Bromley (1934) states "*Saropogon dispar* is by far the most noxious species in bee-yards in the San Antonio region." See Table 1.1 for prey records. Access photographs of the holotype at http://n2t.net/ark:/65665/33098b0bf-d97f-4b92-9141-eaa52cd9f59a

Saropogon fletcheri Bromley, 1934

Figs 1.14, 1.26, 1.34

Saropogon fletcheri Bromley, 1934: 91.

References. Bromley 1934: 91 (original description); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 130 (key); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. This species is sometimes similar to *Saropogon dispar* but both sexes are reddish and the femora lack black. Scutellum has four reddish bristles; and wings are pale reddish brown. Body length 24–17 mm; wing length 11–14 mm. Flight time April – October.

Distribution. USA: Arizona, Texas

SimpleMappr: https://www.simplemappr.net/map/16984

Type material examined. UNITED STATES OF AMERICA • 1♂, holotype; Texas, Comfort; 29°58'N, 98°54'W; 19 July 1921; R. K. Fletcher; TAMUIC.

Arizona material examined. UNITED STATES OF AMERICA • 1♀; Maricopa County, Morales; 34°02’ N, 111°05’ W; 1496 m; 27 August 1913; W. D. Pierce; USNM; USNMENT01819450.

Other material examined. Supplemental material 1.1.

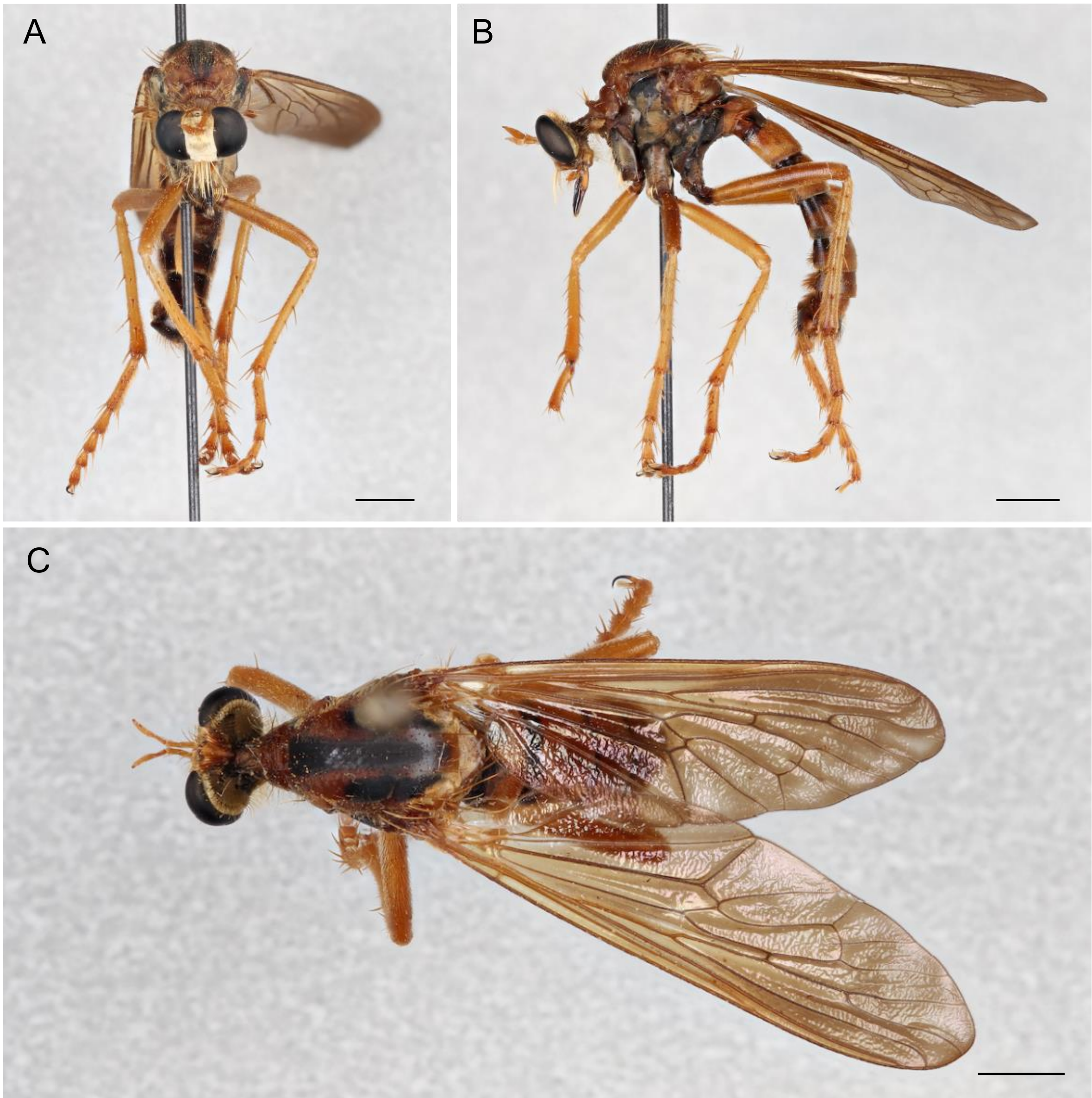

Figure 14. *Saropogon fletcheri* Bromley, 1934 Male (UCBMEP0280504): **A** anterior view, **B** lateral view, **C** dorsal view. Scale bars 2 mm.

Saropogon hyalinus Coquillett, 1904

Figs 1.15, 1.26, 1.32

Saropogon hyalinus Coquillett, 1904: 185.

References. Back 1909: 351 (key and short redescription); Curran 1930: 2 (key), 1931: 2 (key); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 129 (key); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. This species is similar to *Saropogon luteus* except the wings are pure hyaline, and the scutum is densely with yellowish pubescence, with gray pubescent median stripe and elongated sub-lateral spots, crossing the transverse suture. Body length 13–17 mm; wing length 9–11 mm. Flight time May – September.

Distribution. USA: California

SimpleMappr: https://www.simplemappr.net/map/16985

Type material examined. UNITED STATES OF AMERICA • 1 ♀, holotype; California, Los Angeles County; 34°03’N, 118°14’W; 97 m; Coquillett; USNM; USNMENT01199005.

Other material examined. Supplemental material 1.1.

Comments. You can access photographs of the holotype here: http://n2t.net/ark:/65665/308595f92-7180-42d6-a5ed-8be56e3423d4

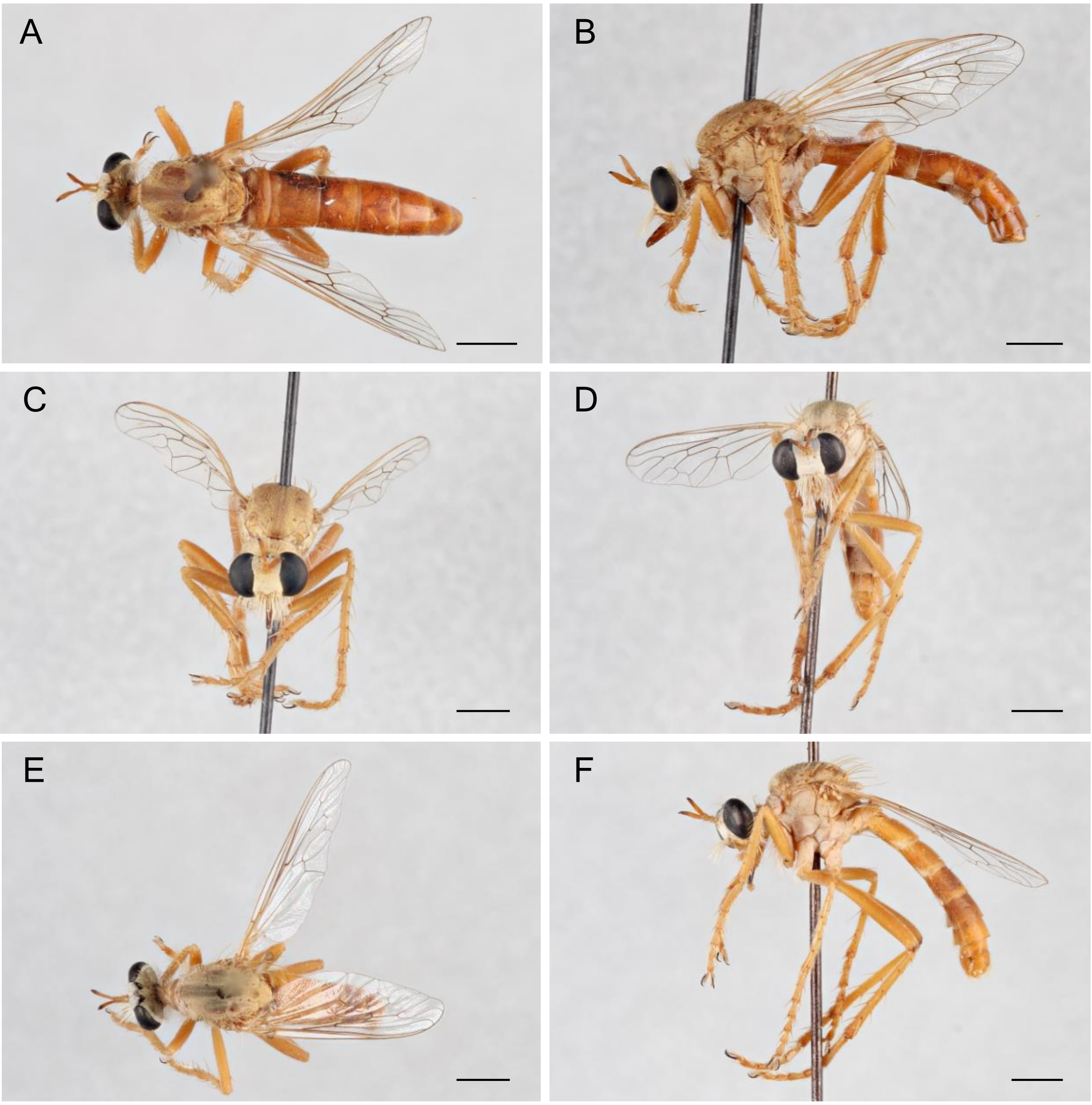

Figure 1.15. *Saropogon hyalinus* Coquillett, 1904 Female (USNMENT01830078): **A** dorsal view, **B** lateral view, **C** anterior view; Male (UCBMEP0280500): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Saropogon hypomelas (Loew, 1866)

Figs 1.5I, J, 1.16, 1.26, 1.33

Diogmites hypomelas Loew, 1866: 24 [= *Saropogon hypomelas* (Loew)].

References. Loew 1866: 24 (as *Diogmites*); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 133 (key and translation of original description); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. A large, sexually dimorphic species. Male with legs reddish, femur, sometimes tibia, black; face and frons with white pubescence; female femur proximally black or with proximal black dorsal stripe; face and frons with golden pubescence; both sexes with scutum with yellowish-gray pubescence, median stripe with brown pubescence. Body length 17–27 mm; wing length 17–18 mm. Flight time April – September.

Distribution. USA: Arizona, New Mexico, Texas; Mexico: Coahuila, Nuevo Leon

SimpleMappr: https://www.simplemappr.net/map/16986

Type material examined. UNITED STAES OF AMERICA • 1 ♀, syntype, New Mexico; 34°17’N, 106°17’W; Loew; MCZ; MCZ-ENT00012822.

Arizona material examined. UNITED STATES OF AMERICA • 1 ♀; Maricopa County, 3 mi. N. Gila Bend; 32°58’ N, 112°42’ W; 205 m; 27 July 1969; H. A. Smith; CASENT; CASENT8427317 • 1 ♀; Pima County, Madera Canyon; 31°43’ N, 110°52’ W; 1503 m; 14 July 1980; T. L. McKenzie; USNM; USNMENT01830394 • 1 ?; Pima County, Santa Rita Mtns.

Madera Canyon; 31°43’ N, 110°52’ W; 1503 m; 13 September 1964; R. H. Crandall; LACM; LACMENT579085

Other material examined. Supplemental material 1.1.

Comments. Martin and Wilcox (1965) included the name *Saropogon hypomelas* in their catalog. They did not state it as a new change, and the author who first transferred *Diogmites hypomelas* to *Saropogon*, is still unknown. Wilcox (1966) mentions receiving correspondence from Bromley in 1936 saying that after examining the type, he believed that it belonged in *Saropogon* Loew.

The syntype can be viewed at MCZBase: https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:12822. The syntypes were listed under the name *Deromyia hypomelas* but have since been changed to the current valid name.

iNaturalist lists a record of *Saropogon hypomelas* from Oklahoma (https://www.inaturalist.org/observations/90489061) This photographed specimen evidently is correctly identified and would extend the known range for this species.

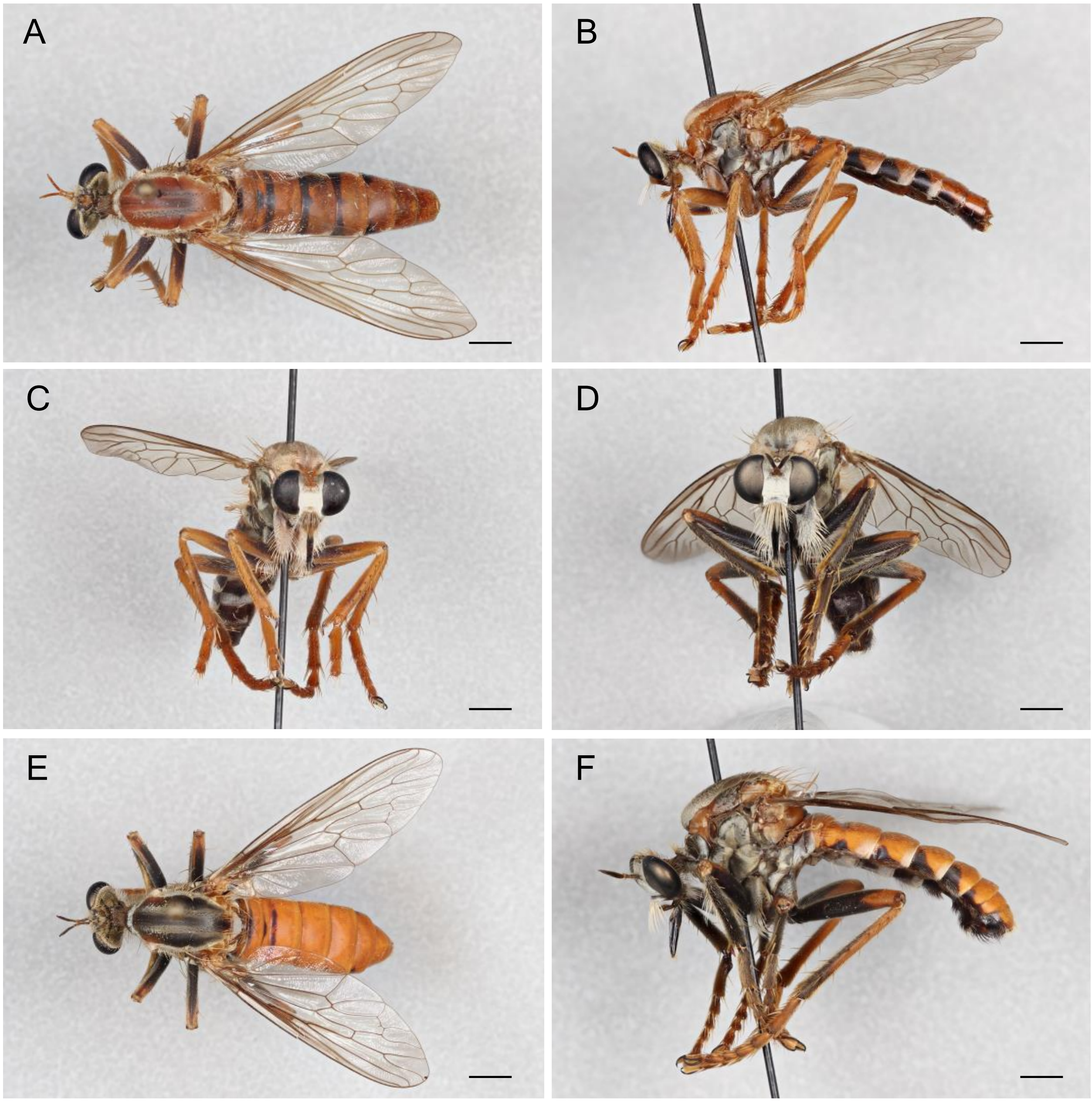

Figure 16. *Saropogon hypomelas* Loew, 1866 Female (USNMENT01830080): **A** dorsal view, **B** lateral view, **C** anterior view; Male (UCBMEP0280599): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Saropogon laparoides Bromley, 1951

Figs 1.17, 1.26, 1.32

Saropogon laparoides Bromley, 1951: 14.

References. Martin and Wilcox 1965: 383 (catalog); Wilcox 1966 (junior synonym *S. sculleni* is described and keyed); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. A small, dark species with hyaline wings and white coxal bristles. Females with mostly reddish legs with the tips of the tibiae and tarsi blackish and scutum with gray pubescence; Male femora mostly reddish, prothoracic and mesothoracic femora black dorsally, tibiae and tarsi blackish and mesonotum with yellowish gray pubescence. Male terminalia with many black setae. Body length 12–16 mm; wing length 8–9 mm. Flight time July – August.

Distribution. USA: Texas

SimpleMappr: https://www.simplemappr.net/map/16987

Type material examined. UNITED STATES OF AMERICA • 1 ♀, holotype; Texas, Presidio County, Presidio; 29°33'N, 104°22'W; 787 m; 04 Aug. 1929; AMNH • 1 ♀, paratype; Texas, Presidio County, Chinati Mtns; 29°54'N, 104°27'W; 1924 m; 04 Aug. 1924; E. R. Tinkham; USNM; USNMENT01819182

Other material examined. Supplemental material 1.1.

Comments. According to Bromley (1951), this species resembles an African Dasypogoninae genus, *Meolapharus* [sic] (= *Neolaparus*, junior synonym of the widespread genus *Pegesimallus* (Londt, 1980)).

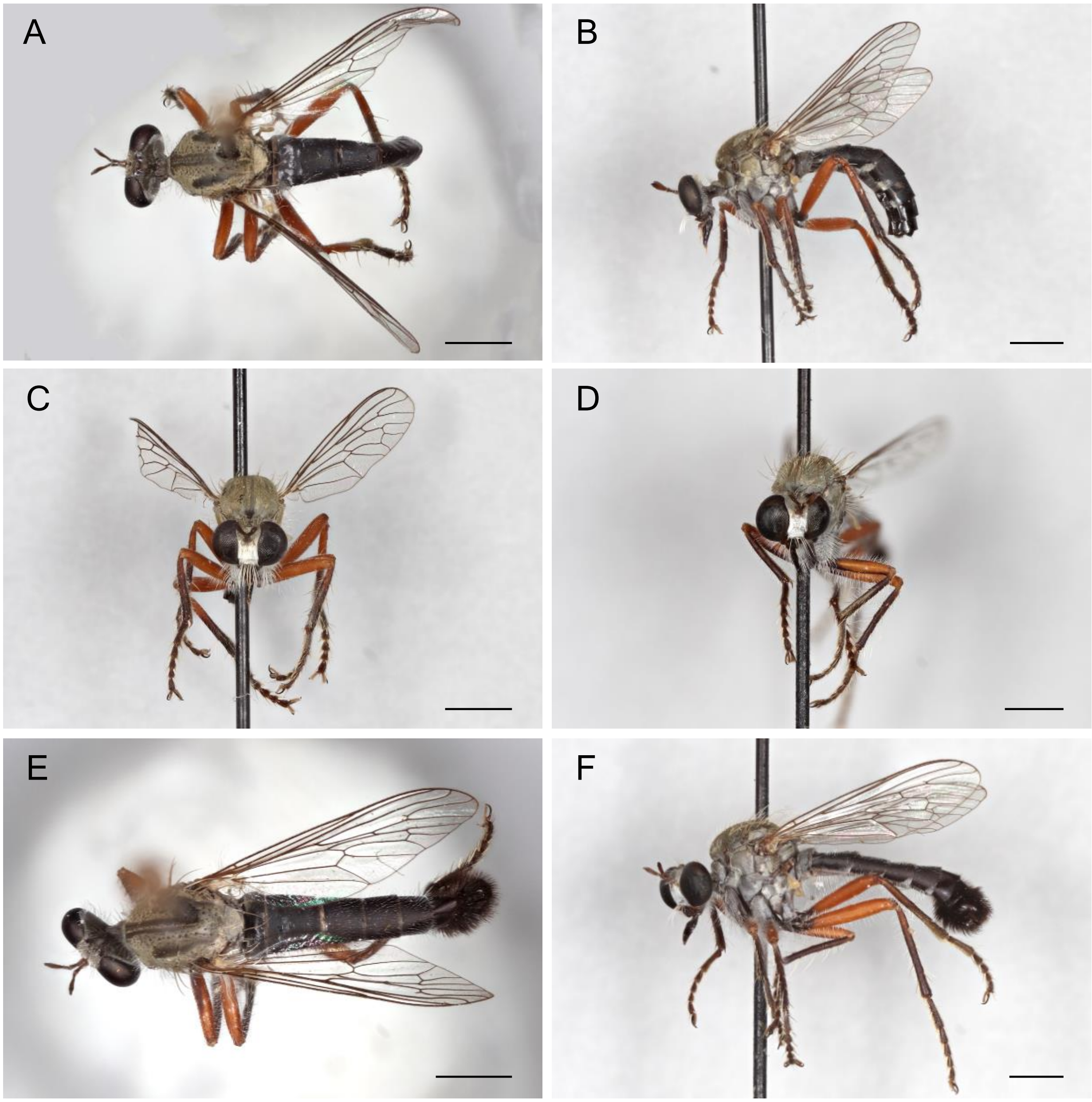

Figure 1. 17. *Saropogon laparoides* Bromley, 1951 Female (USNMENT01819592): **A** dorsal view, **B** lateral view, **C** anterior view; Male (USNMENT01819567): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Saropogon luteus Coquillett, 1904

Figs 1.5K, L, 1.18, 1.26, 1.33

Saropogon luteus Coquillett, 1904: 185.

Saropogon rufus Back 1904: 290, junior synonym.

References. Back 1909: 351 (key and redescription); Curran 1930: 2 (key); Curran 1931: 2 (key); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 130 (key); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. This species is the most likely one to be confused with *Saropogon pyrodes* sp. nov. because of its reddish color. They are easily distinguished by the entire anepisternum of *Saropogon luteus* being with gold pubescence instead of white as in *S. pyrodes* sp. nov. *Saropogon luteus* also has small, with gray pubescent spots on the posterior corners of the tergites. This species is almost exclusively found in California. Body length 11–17 mm; wing length 8–10 mm. Flight time May – September.

Distribution. USA: California; Mexico: Baja California

SimpleMappr: https://www.simplemappr.net/map/16988

Type material examined. UNITED STATES OF AMERICA • 1♀, holotype; California, Los Angeles County; 34°03’N, 118°14’W; 97 m; Coquillett; USNM; USNMENT01199100.

Other material examined. Supplemental material 1.1.

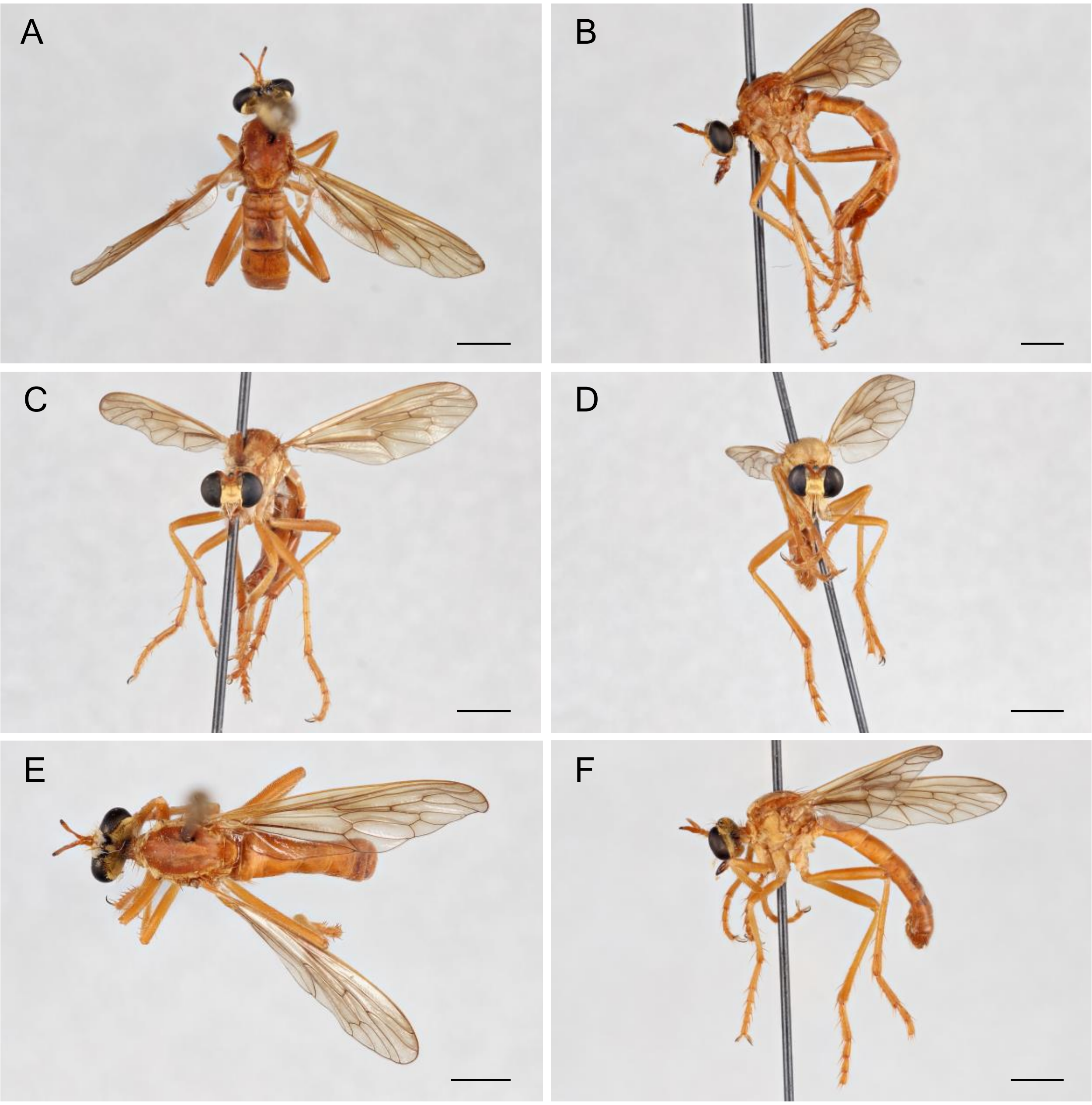

Figure 1.18. *Saropogon luteus* Coquillett, 1904 Female (UCBMEP0073792): **A** dorsal view, **B** lateral view, **C** anterior view; Male (UCBMEP0073760): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Comments. Photographs of the holotype are available here: http://n2t.net/ark:/65665/338f15b33-0872-416f-8a58-277c87bb8142. The holotype of *Saropogon* *rufus* (junior synonym to *S. luteus*) is in the Museum of Comparative Zoology at Harvard University. Photographs of this specimen are available here: https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:7583

Saropogon mohawki Wilcox, 1966

Figs 1.19, 1.26, 1.34

Saropogon mohawki Wilcox, 1966: 134.

References. Wilcox 1966: 134 (key and original description); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. Wings completely hyaline, the posterior corners of T2–4 with gray pubescence, the anterior corners of T4 and 5 (sometimes T4–6) with black spots; legs light colored in both sexes but sometimes femora blackish basally in male. This species is mostly easily confused with *Saropogon coquillettii*; the main differences are the extent of abdominal markings and the lack of wing microtrichia. Body length 10–13 mm; wing length 11–15 mm. Flight time May – October.

Distribution. USA: Arizona, California, Nevada, Utah; Mexico: Baja California, Sonora

SimpleMappr: https://www.simplemappr.net/map/16989

Type material examined. UNITED STATES OF AMERICA • 1 ♂, holotype; Arizona, Yuma County, Mohawk; 32°43’N, 113°45’W; 166 m; 16 Jul 1962; J. Wilcox; CASENT; Type No. 9279 • 1 ♀, paratype; Arizona, Yuma County, 25 mi. SE. Parker; 33°51’N, 114°3’W; 361 m; 05

Sep 1964; J. M. Davidson; USNM; USNMENT01830250 • 1 ♂, paratype; California, San Bernardino, Baker; 35°16’N, 116°4’W; 286 m; 24 Jun 1930; F. H. Wymore; BMEC; UCBMEP0003174.

Arizona material examined. UNITED STATES OF AMERICA • 1 ♀; La Paz County, Ehrenberg; 33°36’N, 114°31’W; 91 m; 27 Aug. 1938; F. H. Parker; UAIC • 1 ?; Maricopa County, 1.6 mi. SE. of Barnes Butte, near Papago Park; 33°27’ N, 111°56’ W; 378 m; 23 June 1973; M. Kolner; ASUHIC; ASUHIC0139654 • 1 ?; same collection data as for preceding; 20 July 1973; M. Kolner; ASUHIC; ASUHIC0139653 • 2 ?; same collection data as for preceding; 26 July 1973; M. Kolner; ASUHIC; ASUHIC0139655, ASUHIC0139656 • 1 ♀; Maricopa County, Cave Creek; 33°50’ N, 111°57’ W; 689 m; 08 June 1947; F. H. Parker, USNM; USNMENT01819560 • 3 ♂, 4 ♀; Maricopa County, Gila River 10 km S. Arlington; 33°13’N, 112°45’W; 200 m; 4 – 14 August 2010; M. E. Irwin; UAIC • 2 ♂; same collection data as for preceding; 14 – 21 August 2010; M. E. Irwin; UAIC • 4 ♂, 3 ♀; same collection data as for preceding; 15 – 31 July 2010; M. E. Irwin; UAIC • 1 ♂, 6 ♀; same collection data as for preceding; 1 – 7 June 2010; M. E. Irwin; UAIC • 1 ♀; same collection data as for preceding; 3 – 7 June 2010; M. E. Irwin; UAIC • 1 ?; Maricopa, S. Mtn. Park, 1.4 mi. W. of Elliot Rd. and Freeway; 33°20’ N, 112°04’ W; 539 m; 16 July 1972; M. Kolner; ASUHIC; ASUHIC0139657 • 1 ♂; Mariposa County, 6 mi. W. Gila Bend; 32°56’ N, 112°49’ W; 220 m; 09 September 1961; G. I. Stage; CASENT; CASENT8427321 • 2 ♀; Pima County, Organ Pipe Cac. N. M. Quitobaquito; 32°01’ N, 112°49’ W; 524 m; 07 April 1968; J. Gruwell; USNM; USNMENT01830276, USNMENT01830277 • 1 ♀; Pima County, Organ Pipe Cactus NM

Quitobaquito Springs; 31°56’N, 113°01’W; 326 m; 27 August 1983; Kinglsey, Bailowatz; UAIC • 1 ♀; Yuma County, 1 mi. NW Aztec; 32°50’ N, 113°27’ W; 140 m; 31 August 1979; E. M. Fisher; USNM; USNMENT01830254 • 1 ♀; Yuma County, 13 mi. W. Hope; 33°42’ N, 113°55’ W; 380 m; 30 August 1979; E. M. Fisher; USNM; USNMENT01830253 • 1 ♂, 1 ♀; Yuma County, 25 mi. SE Parker; 33°51’ N, 114°3’ W; 361 m; 05 September 1964; J. M. Davidson; USNM; USNMENT01830250 • 1 ?; Yuma County, 37 mi. S. of Quartzsite; 33°07’ N, 114°13’ W; 409 m; 26 July 1966; J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139641 • 2 ?; Yuma County, 37 mi. S. of Quartzsite; 33°07’ N, 114°13’ W; 409 m; J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139647, ASUHIC0139648 • 1 ?; Yuma County, 6 mi. SE. of Parker; 34°05’ N, 114°12’ W; 208 m; 09 July 1966; J. M. Davidson, M. A. Cazier; ASUHIC0139642 • 1 ?; Yuma County; 8 mi. SE. of Parker; 34°04’ N, 114°11’ W; 262 m; 29 May 1966; S. A. Gorodenski; ASUHIC; ASUHIC0139640 • 1 ♀; Yuma County, Mohawk; 32°43’ N, 113°45’ W; 166 m; 26 August; J. Wilcox; CASENT; CASENT8427320.

Other material examined. Supplemental material 1.1.

Comments. Photographs of the holotype can be viewed at: https://monarch.calacademy.org/taxa/index.php?tid=679456

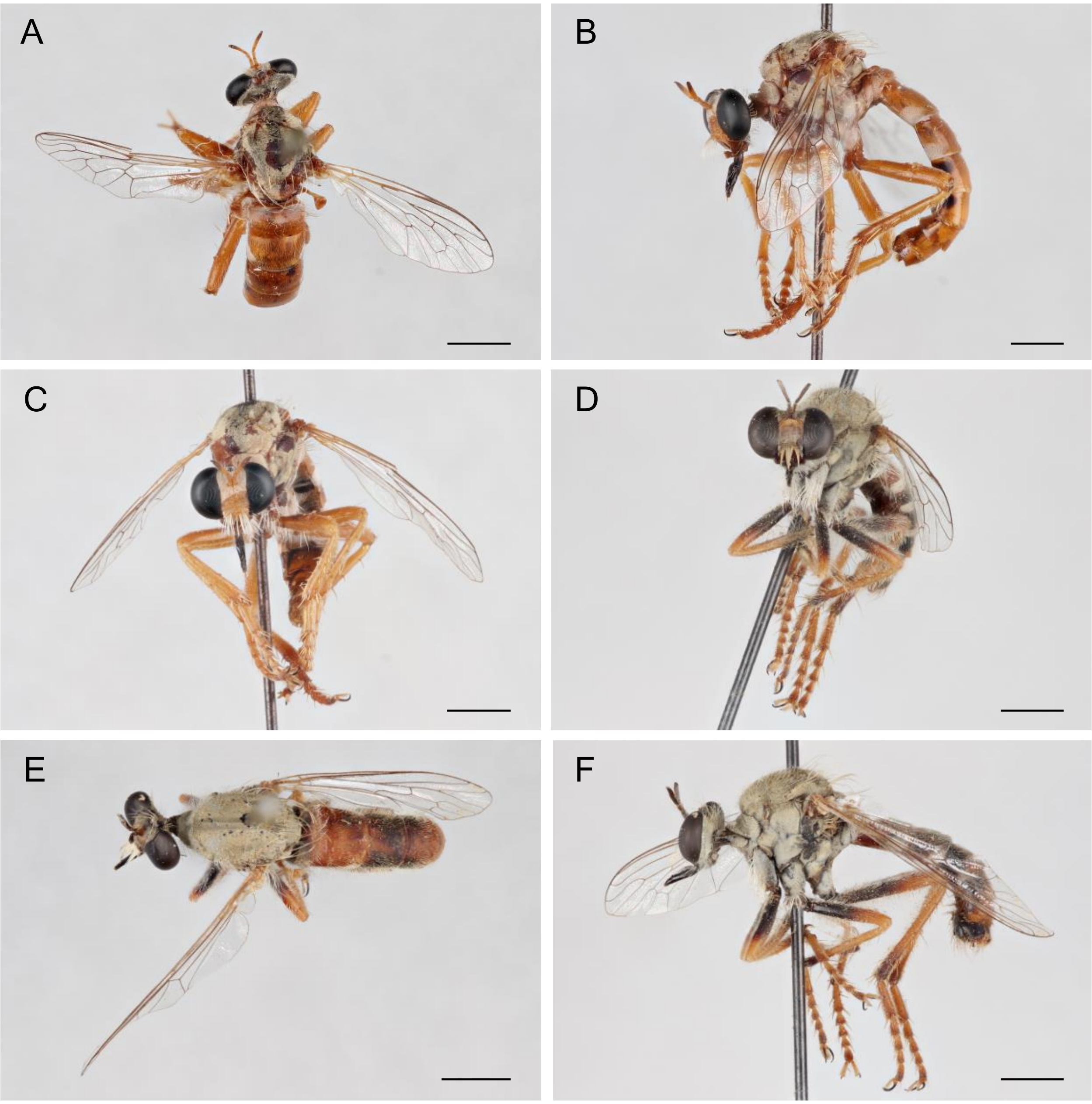

Figure 1.19. *Saropogon mohawki* Wilcox, 1966 Female paratype (UCBMEP0003173): **A** dorsal view, **B** lateral view, **C** anterior view; Male (UCBMEP0003175): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Saropogon nitidus Wilcox, 1966

Figs 1.20, 1.31

Saropogon nitidus Wilcox, 1966: 135.

References. Wilcox 1966: 135 (key and original description); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. This species can be easily distinguished from others in the region by a shining black non-pubescent spot on the anterior half of the anepisternum and katepisternum. The male has yellowish red femora with black tibiae and tarsi; the posterior corners of T2–5 (males) and T2–4 (females) are with white pubescence; legs in female are yellowish. Body length 12–14 mm; wing length 8–10 mm. Flight time May – October.

Distribution. USA: New Mexico, Texas; Mexico: Chihuahua, Coahuila

SimpleMappr: https://www.simplemappr.net/map/16990

Type material examined. UNITED STATES OF AMERICA • 1 ♂, holotype; Texas, Brewster County, Lajitas; 29°15'N, 103°46'W; 714 m; 04 Sep 1961; J. E. Gillaspy; CASENT; Type No. 9280.

Other material examined. Supplemental material 1.1.

Comments. Photographs of holotype can be found at:

https://monarch.calacademy.org/taxa/index.php?tid=679457

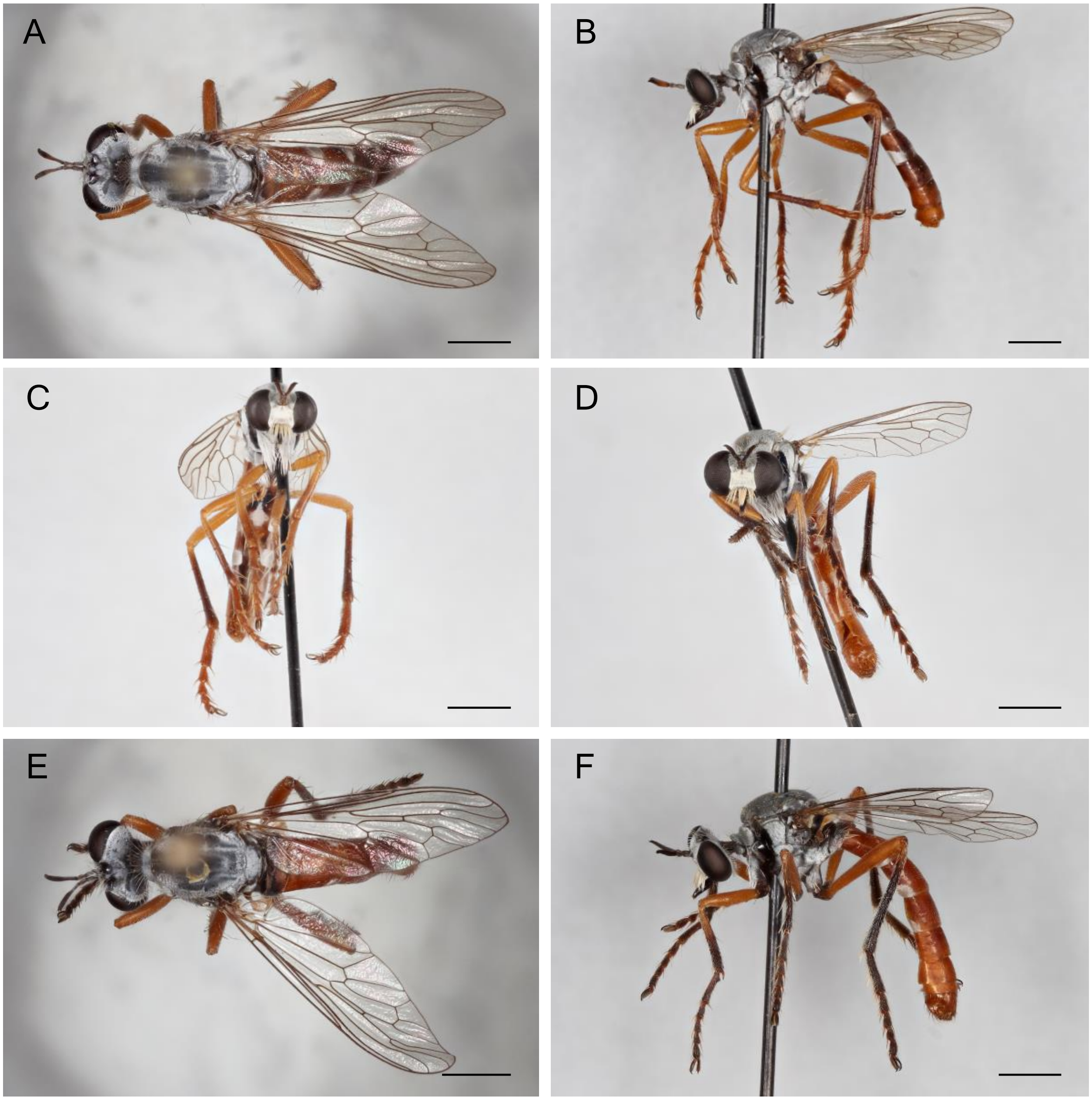

Figure 1.20. *Saropogon nitidus* Wilcox, 1966 Female (USNMENT01830081): **A** dorsal view, **B** lateral view, **C** anterior view; Male (UCBMEP0280497): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Saropogon pritchardi Bromley, 1934

Figs 1.21, 1.33

Saropogon pritchardi Bromley, 1934: 90.

References. Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 129 (key); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. This is a large species but slightly smaller and more slender than *Saropogon dispar*. The wings are proportionately longer and broader than those of *Saropogon dispar* and the legs are uniformly reddish without any dark markings. Wings and abdomen are black, the thorax with yellowish pubescence, and scutellum has two light colored bristles. Body length 20–23 mm; wing length 16–18 mm. Flight time July.

Distribution. USA: New Mexico, Oklahoma, Texas

SimpleMappr: https://www.simplemappr.net/map/16991

Type material examined. UNITED STATES OF AMERICA • 1 ♂, holotype; Texas, Mills County; 20 July 1931; R. H. Painter; SEMC; SEMC1603974 • 1 ♂, 1 ♀, metatype; Oklahoma, Cimarron County, Boise City; 36°43’N, 102°30’W; 1271 m; 10 Jul 1933; A. E. Pritchard; USNM; USNMENT01819137, USNMENT01819532.

Other material examined. Supplemental material 1.1.

Comments. The holotype is housed at SEMC and information about it can be found here: https://biodiversity.ku.edu/node/1095/.

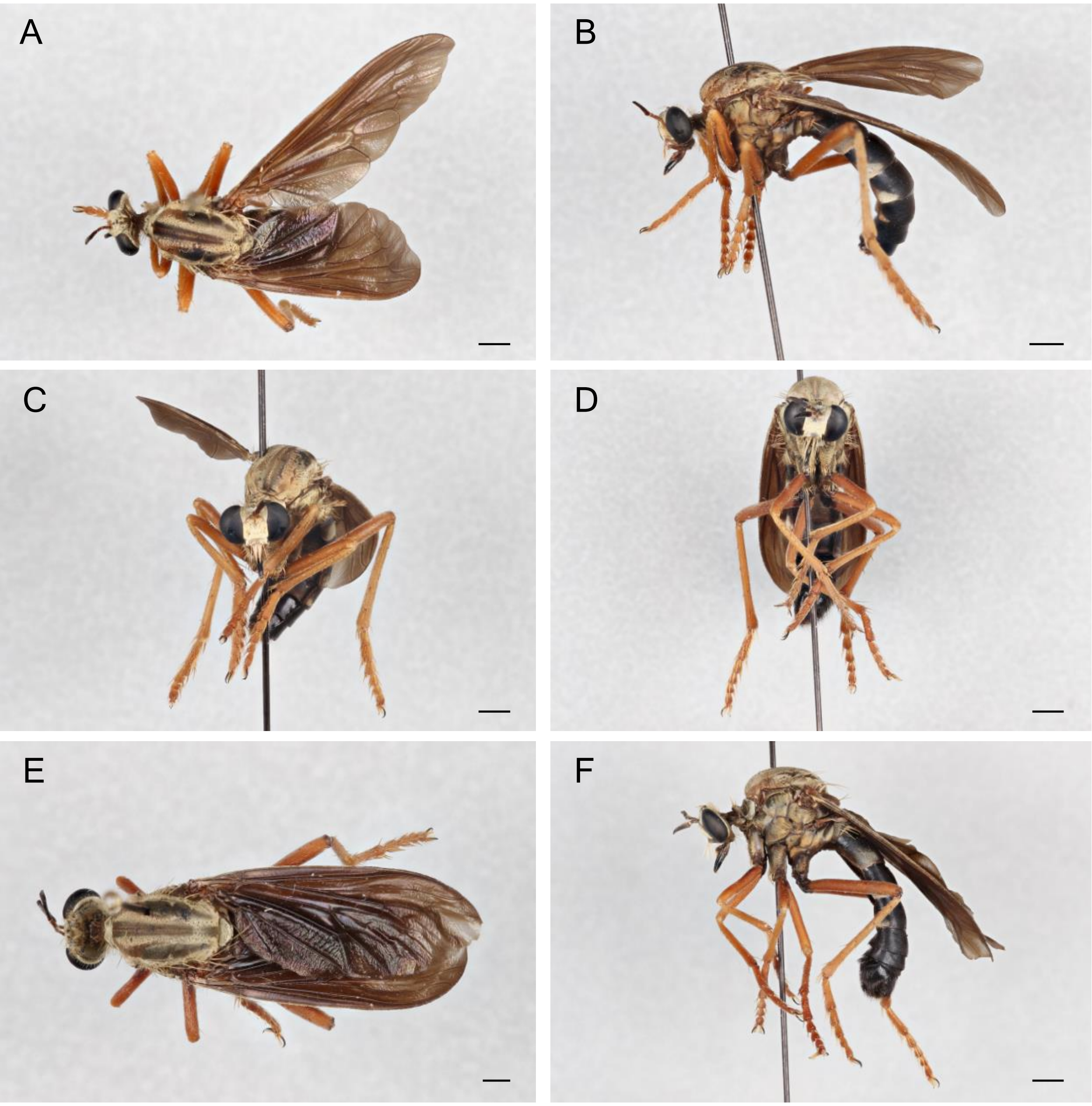

Figure 1.21. *Saropogon pritchardi* Bromley, 1934 Female (UCBMEP0280596): **A** dorsal view, **B** lateral view, **C** anterior view; Male (UCBMEP0280595): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Saropogon purus Curran, 1930
Figs 1.4E, F, 1.5M, N, 1.22, 1.26, 1.33

Saropogon purus Curran, 1930: 3.

References. Curran, 1930 (key and original description); Curran 1931: 2 (key); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 129 (key); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. The broad, brown wings easily distinguish this species from others (Fig. 5). It is a sexually dimorphic species (Fig. 4). Male abdomen and legs are black, metathoracic femora in part reddish; female abdomen and legs are mostly yellowish red, coxae densely deep with golden pubescence. Body length 11–13 mm; wing length 7–9 mm. Flight time July to August.

Distribution. USA: Arizona; Mexico: Sinaloa, Sonora
SimpleMappr: https://www.simplemappr.net/map/16992

Type material examined. UNITED STATES OF AMERICA • 1 ♂, holotype; Arizona, Pima County, Kits Peak Rincon, Baboquivari Mts.; 31°57'N, 111°33'W; 1234 m; 1–4 August 1916; F. E. Lutz; AMNH • 1♀, allotype; same collection data as holotype; AMNH.

Arizona material examined. UNITED STATES OF AMERICA • 1 ♂; Cochise County, Willcox; 32°15'N, 109°49'W; 1274 m; 13 July 1944; F. H. Parker; UAIC • 2 ♀; Gila County, Globe; 33°23'N, 110°47'W; 1074 m; 26 Jul 1987; Parker; USNM; USNMENT01819537, USNMENT01819572 • 1♀; same collection data as for preceding; 13 July 1956; F. H. Parker; UAIC • 1 ♂; same collection data as for preceding; 15 July 1943; F. H. Parker, UAIC • 1♀; same collection data as for preceding; 15 July 1948; F. H. Parker; UAIC • 1♀; same collection data as for preceding; 19 July 1947; F. H. Parker; UAIC • 1♀; same collection data as for preceding; 20 July 1956; F. H. Parker; UAIC • 2♀; same collection data as for preceding; 27 August 1955; F. H. Parker; UAIC • 1 ♂; same collection data as for preceding; 28 July 1952; F.

H. Parker; UAIC • 1 ♂; Gila County, San Carlos; 33°20’N, 110°27’W; 809 m; 11 July 1936; F. H. Parker; UAIC • 1 ?; Maricopa County, 1.5 mi. NE of Desert Vista Point, Payson Highway; 33°40’ N, 111°30’ W; 753 m; 02 August 1969; R. Wielgus; ASUHIC; ASUHIC0139662 • 1 ?; Pima County, 2.1 mi. S. of Gibbon Mountain, Santa Catalina Mountains; 32°18’ N, 110°44’ W; 1006 m; 20 Aug. 1972; O. Francke, M. Kolner; ASUHIC0139664 • 1 ♂; Pima County, Baboquivari Mts.; 31°48’ N, 111°36’ W; 1234 m; 19 July 1950; J. G. Rosen; USNM; USNMENT01830301 • 1 ♂; Pima County, Baboquivari Mts.; 31°47’N, 111°34’W; 1776 m; USNM; USNMENT01819457 • 1♀; Pima County, Box Canyon Santa Rita Mountains; 33°08’ N, 111°12’ W; 592 m; 05 August 1978; D. S. Verity; USNM; USNMENT01830083 • 1♀; Pima County, Brown Canyon; 31°28’ N, 110°17’ W; 1219 m; 27 July 1973; E. M. Fisher; USNM; USNMENT01830285 • 1♀; same collection data as for preceding; 28 July 1983; Werner, Olson; UAIC • 1♀; Pima County, Espero Canyon 10 mi. NW of Tucson; 32°18’N, 110°49’W; 844 m; 10 August 1975; B. Page; UAIC • 1♀; Pima County, Snata Rita Exp. Range; 32°50’N, 110°51’W; 1120 m; 26 July, 1971; E. Yensen; UAIC • 1 ♂; Santa Cruz County, 3 mi. W. Pina Blanca; 31°24’ N, 111°08’ W; 1476 m; 07 July 1984; A. J.. Gilbert, R. A. Clark, J. C. Ball; USNM; USNMENT01830302 • 1 ♂; Santa Cruz County, Pena Blanca Area, Vic. Atascosa Trail; 31°24’ N, 111°08’ W; 1433 m; 05 July 1972; D. G. Marqua; USNM; USNMENT01830082 • 1 ?; Yavapai County, Cordes; 34°18’ N, 112°10’ W; 1150 m; 09 August 1971; M. Kolner; ASUHIC; ASUHIC0139663.

Other material examined. Supplemental material 1.1.

Comments. Most specimens have two scutellar bristles, but Wilcox (1966) noted that some have four.

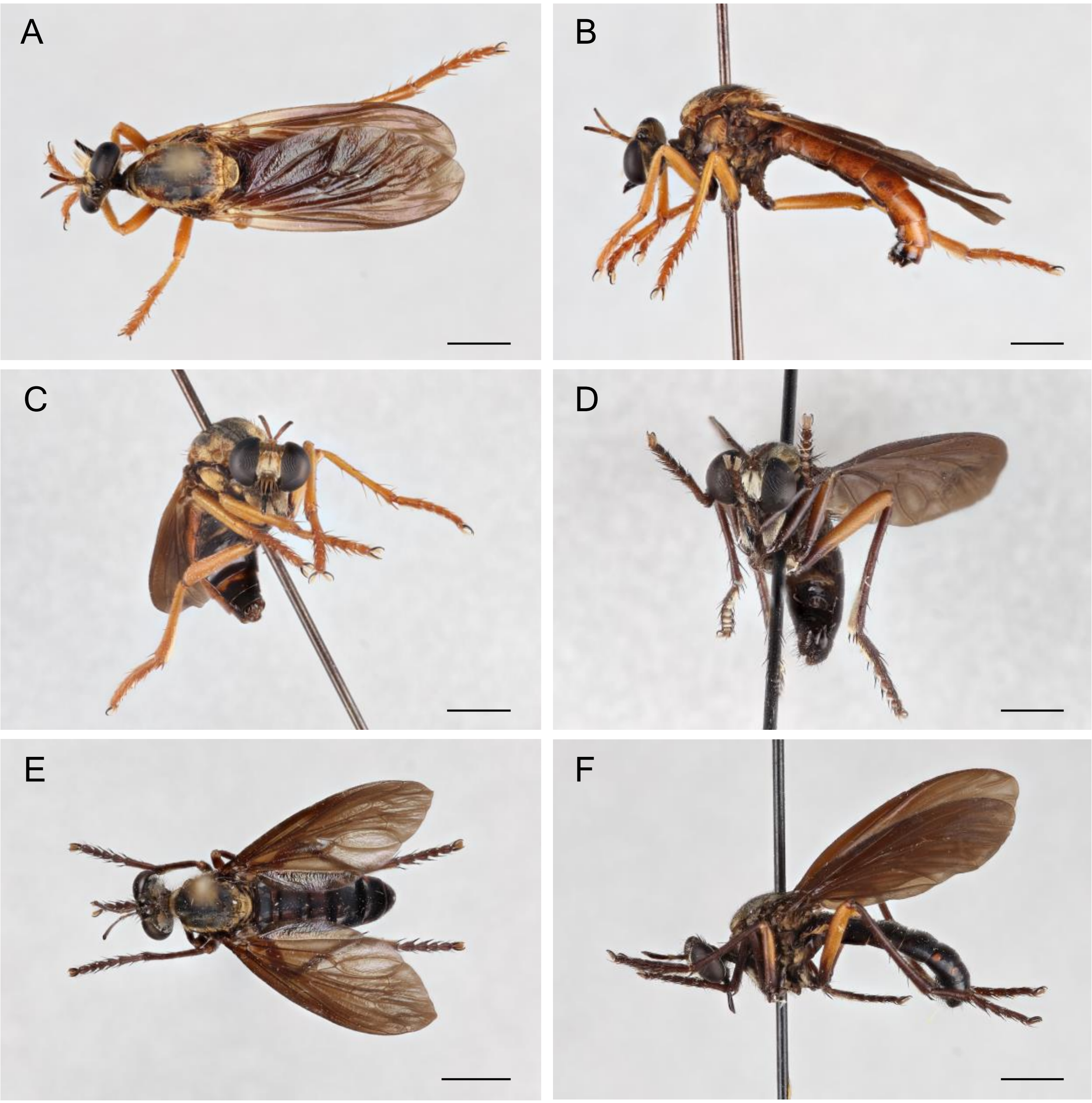

Figure 1.22. *Saropogon purus* Curran, 1930 Female (UCBMEP0280564): **A** dorsal view, **B** lateral view, **C** anterior view; Male (USNMENT01830082): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

***Saropogon pyrodes* sp. nov**.

Figs 1.1, 1.6, 1.23, 1.24, 1.25, 1.26, 1.27, 1.34

ZooBank: http://zoobank.org/3B057DFB-5B32-445D-AE22-037E7FD4C0C8

Diagnosis. The species is distinguished from congeners by its deep red color, hyaline wings, gracile body, white pubescence on the posterior margin of T1–7, and T3 is typically darker than the other tergites (Fig. 1.1).

Male. Holotype (Figs 1.6, 1.23D–F)

Head. (Fig. 1.23) Wider than high; vertex slightly depressed (less than 60^{o} angle on median margin of compound eye); facial swelling not developed and with gold pubescence; mystax 24 white macrosetae that are restricted to lower facial margin; ommatidia of different sizes, at least some median ommatidia distinctly larger; postgena with its posterior margin simple and smooth; frons with gray pubescence, white setose; ocellar tubercle with gray pubescence, with white setae and macrosetae; vertex with gray pubescence and white setae; median occiput sclerite with several white macrosetae; postocular setae slightly angled anteriorly distally, with white macrosetae; occiput predominately with gray pubescence and white setae; postocciput non-pubescent, with white and brown macrosetae.

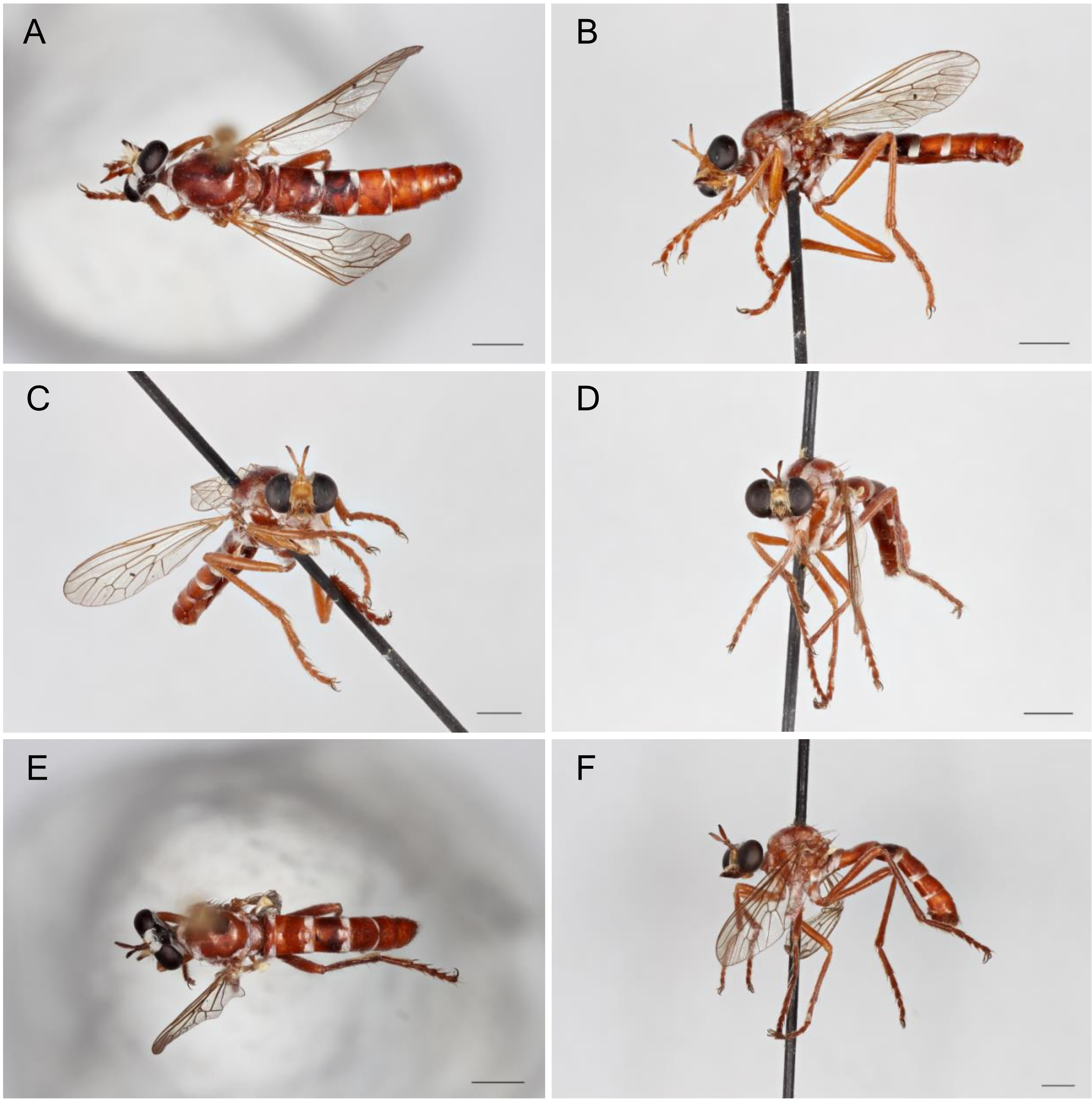

Figure 1.23. *Saropogon pyrodes* sp. nov. paratype female: **A** dorsal view, **B** lateral view, **C** anterior view; holotype male: **D** anterior view **E** dorsal view **F** lateral view. Scale bars 2 mm.

Proboscis and maxillary palpus. (Fig. 1.23) Proboscis straight, subequal in length to an eye when viewed from the front, light brown to dark brown distally; postmentum with white setae ventrally; prementum with white setae proximo-ventrally; labella reduced, apex blunt; maxillary palpus light brown to orange, with yellow setae and macrosetae, non-pubescent.

Antenna. (Fig. 1.23) Light brown to dark brown distally, with light gray pubescence; scape approximately as long as pedicel, short white setae dorsally and long white macrosetae ventrally; pedicel white and light brown setae distally; postpedicel tapering distally, medially broadest, short, approximately the same length as scape and pedicel combined, asetose; stylus composed of one element, asetose, with an apical seta-like sensory element in cavity of stylus.

Thorax. (Fig. 1.23) Light brown to orange, with white pubescence; proepisternum with gray pubescence, with white setae and macrosetae; cervical sclerite long, with white setae; antepronotum with white pubescence, with white setae and macrosetae; postpronotum with white pubescence, with white setae; postpronotal lobe setose; pleuron with white pubescence; proepimeron asetose; anepisternum asetose; anepisternum supero-posterior asetose; anterior basalare asetose, with white pubescence; posterior basalare asetose, with white pubescence; anepimeron asetose, anterior half with white pubescence, posterior half non-pubescent; katepisternum asetose, anterior half non-pubescent, posterior half with white pubescence; katepimeron asetose, non-pubescent; katergite with white setae and macrosetae, with white pubescence; meron and metanepisternum asetose, with white pubescence; metakatepisternum asetose, with white pubescence; metepimeron asetose, and with white pubescence; anatergite asetose, with white pubescence; scutum predominantly with gray pubescence; scutum brown with white setae and macrosetae; scutal setae with small sockets; two notopleural setae; one supraalar seta; one postalar seta; many (> 4) short white dorsocentral (dc) setae; many (> 4) short white acrostichal setae; many (> 4) short white medial setae on posterior scutum (between dc setae); scutellum with gray pubescence; discal scutellar setae absent; apical scutellar setae present, two long brown macrosetae.

Leg. (Fig 1.23) Light brown to orange, non-pubescent, at least some setae dorso-ventrally flattened, others circular; coxae orange, with gray pubescence, with white setae and macrosetae; prothoracic femur flattened with white setae ventrally and long white setae dorsally; prothoracic tibia with short white setae except the antero-ventral surface has short gold setae, one or two yellow macroseta on distal end of ventral side, with white macrosetae: four in a postero-dorsal row, five short ones in a postero-ventral row, one or two long macrosetae in a postero-ventral row; prothoracic tibia with sigmoid spur, originating antero-ventrally directly from tibia; mesothoracic coxa with gray pubescence, with white setae and macrosetae; mesothoracic femur ventrally asetose except for two white macrosetae on proximal end, short white macrosetae sparsely covering the rest; mesothoracic tibia with short white setae, white macrosetae: three in an antero-dorsal row, 2 in 1 antero-ventral row, four in a dorsal row, three in a postero-ventral row; metathoracic coxa with gray pubescence, with white setae and macrosetae; metathoracic femur with long white setae and macrosetae; metathoracic tibia with white macrosetae: three in a antero-dorsal row, three in an antero-ventral row, three in a dorsal row, three in a postero-ventral row, straight; tarsus with proximal pro, mes, and met tarsomeres as long as following two tarsomeres combined, with brown macrosetae; pulvilli well-developed (as long as claw); claw smoothly arched distally, pointed; empodium setiform, and well developed (as long as pulvilli).

Wing. (Fig. 1.24) 8 mm. Hyaline, withs slight microtrichia; posterior wing margin with microtrichia arranged in a single plane.

Figure 1.24. *Saropogon pyrodes* sp. nov. wing. Scale bar 2 mm.

Abdomen. (Figs 1.23, 1.25) Light brown to orange with some tergites brown dorsally; tergite sculpture smooth and setae with small sockets only; T1 white setose, laterally with long white macrosetae, predominantly with gray pubescence, medially non-pubescent, entirely sclerotized medially, dorsal surface smooth and without protuberances; T2–8 entirely sclerotized, white setose, setae short medially and longer laterally, predominantly light brown to orange, predominantly non-pubescent with gray pubescent band on posterior margin, band thinner dorso-medially; T2–8 marginal and medial macrosetae absent; S1–8 brownish orange, with short white setae, and with light gray pubescence.

Male Abdomen. (Fig. 1.25A–C) S8 simple, reduced rectangular sclerite; hypopygium rotated ~ 90° and pointing posteriorly; epandrium separated medially, joining proximally, and unfused; hypandrium well-developed and rectangular; hypandrium and epandrium approximating laterally, but not fused proximally; hypandrium and gonocoxites entirely free; gonocoxal apodeme present and short; gonostyli present and positioned distally on gonocoxites; cerci free and not fused medially; lateral ejaculatory process present and with a large cylindrical sclerite; one functional phallic prong; hypandrium with posterior margin simple with no distinct projections; sperm sac appearing weakly sclerotized; ejaculatory apodeme is a single plate.

Female Abdomen. (Fig. 1.25D–G) S7 and T7 are normally developed, without any modifications; segments eight and following comprising ovipositor; setae on T8 are directed anteriorly; T8 with anterior rectangular apodeme and entirely fused to T8; S8 plate-like with hypogynial valves extending; T9 and T10 partly fused; T10 divided into two heavily sclerotized acanthophorite plates with eight acanthophorite spurs on each plate; three equally large spermathecae, common spermathecal duct short, and not extending beyond tip of furca, individual spermathecal ducts long; spermathecal reservoir formed by coiled ducts and heavily sclerotized spermathecae contained within three most posterior segments; furca divided anteriorly into two lateral sclerites, H-shaped; furcal apodeme present, short and platelike.

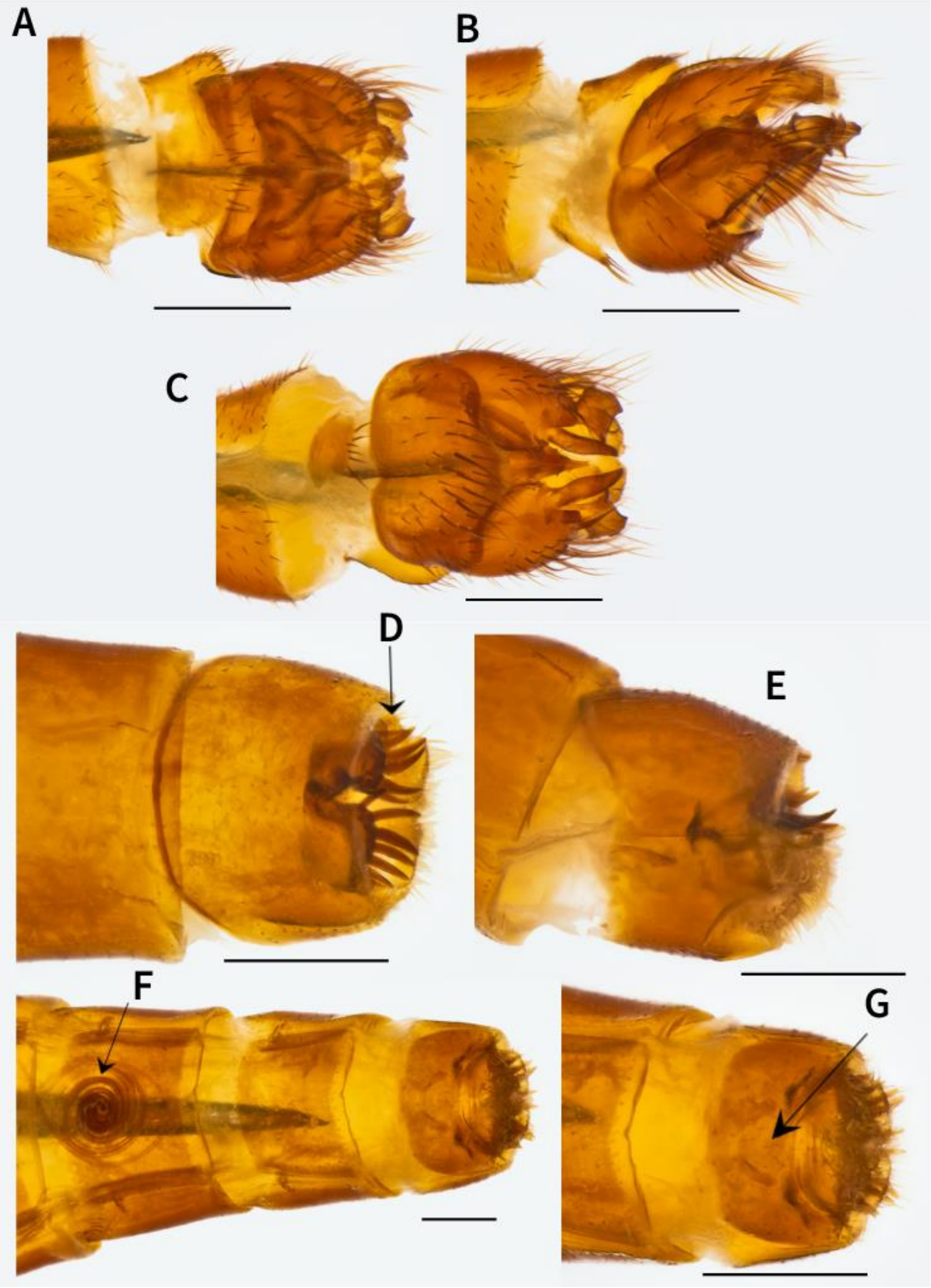

Figure 1.25. *Saropogon pyrodes* sp. nov. terminalia. Male (USNMENT01819155): **A** dorsal view 75 ×, **B** lateral view 75 ×, **C** ventral view 75 ×; female (UAIC1128818): **D** dorsal view 80 ×, arrow indicating acanthophorites (spines), **E** lateral view 95 ×, **F** ventral view of T6–9 40 ×, arrow indicating spiral spermathecal reservoir **G** ventral view of T8–9 80 ×, arrow indicating "X" shaped furca. Scale bars 1 mm.

Length. Body length 10 mm; wing length: 6 mm.

Holotype condition. The holotype is in good condition and is not missing any parts.

Type material. UNITED STATES OF AMERICA • 1♂, holotype; Arizona, Pima County, 7 mi. N. Tucson; 33°47’N, 111°34’W; 740 m; 04 Sep. 1968; D. R. Miller, J. E. Lauck; USNM; USNMENT01199000 • 1♀, 7♂, paratypes; same data as for holotype; USNM; USNMENT01819173, USNMENT01199055, USNMENT01819150, USNMENT01819585, USNMENT01819580, USNMENT01819176, USNMENT01819472 • 3♂, paratypes; same data as for holotype; CASENT; USNMENT01819175, USNMENT01819179, USNMENT01819155 • 1♂, paratype; same data as for holotype; BMEC; USNMENT01819167 • 1♂, paratype; Arizona, Pima County, 4 mi. N. Continental; 31°54’N, 110°57’W; 844 m; 11 Aug. 1964; M. E. Irwin; USNM; USNMENT01819500 • 1♀, 1♂, paratypes; Arizona, Santa Cruz County, Juan Bautista De Anza Trail Amado; 31°44’N, 11°02’W; 916 m; 31 Aug. 2018; C. W. Melton; UAIC; UAIC1128818, UAIC1128819; BugGuide: https://bugguide.net/node/view/1588371, 1588372, 1588341, 1588340, 1588338 • 1♂, paratype; same data as for proceeding; TAM; USNMENT01819495.

Other material examined. UNITED STATES OF AMERICA • 1♀; Arizona, Pima County, Green Valley; 31°50’N, 110°59’W; 943 m; 03 Sep 2016; K. Roragen; iNaturalist: https://www.inaturalist.org/observations/51920444 • 1♀; Arizona, Santa Cruz County, 0.7 km ExNE of Amado; 31°42’N, 111°03’W; 934 m; 05 Sep 2017; J. Gruber; BugGuide:

https://bugguide.net/node/view/1439519; Flickr: https://www.flickr.com/photos/7432824@N07/albums/72157701454226641.

The holotype (1♂) and several paratypes (1♀ 7♂) of the new species have recently been deposited in USNM (as a donation from Eric Fisher); the rest of the paratypes will be split between BMEC (1♂), CASENT (3♂), UAIC (1♀ 1♂), TAM (1♂).

Distribution. USA: Arizona (Fig. 1.26) https://www.simplemappr.net/map/17143

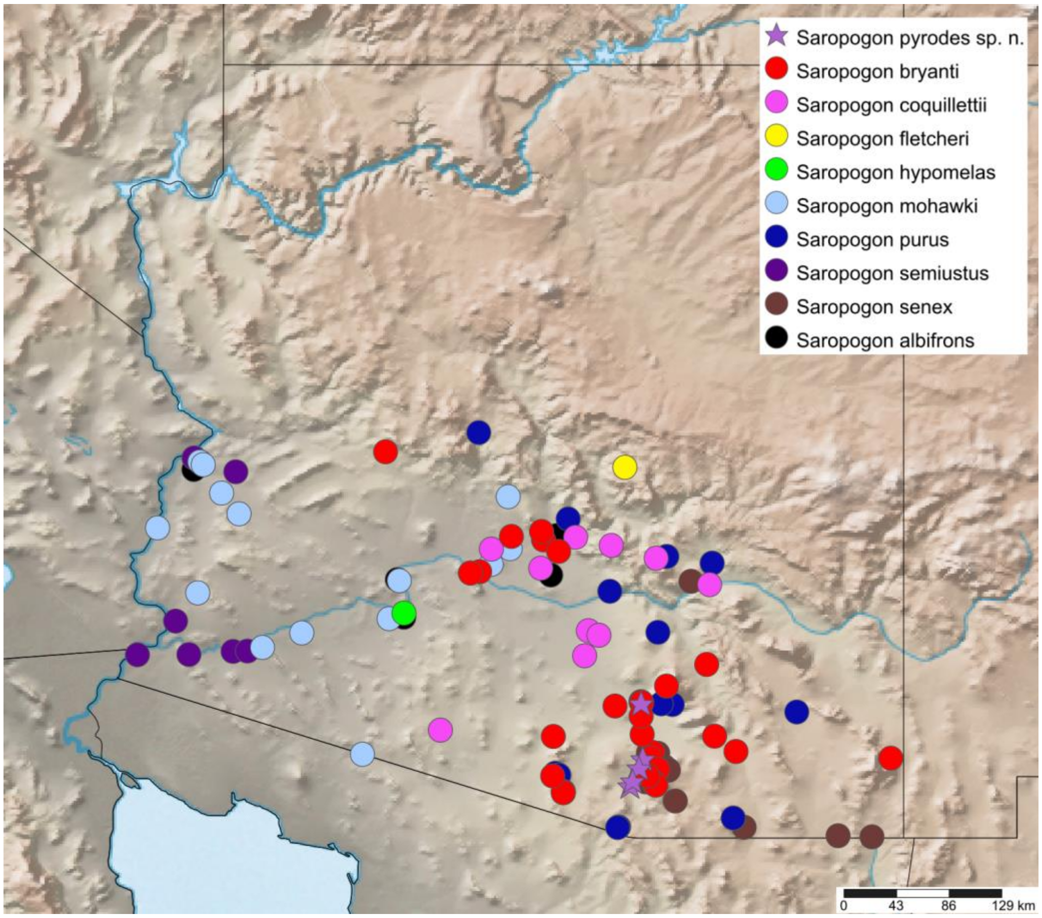

Figure 1.26. Focused map of the Arizona distribution of Nearctic *Saropogon* (Diptera: Asilidae). Map created with SimpleMappr on January 25, 2022, and available at: https://www.simplemappr.net/map/17143.

Biology. Jeff Gruber photographed specimens of *Saropogon pyrodes* sp. nov. and its habitat (Fig. 1.27A, B). *Saropogon pyrodes* sp. nov. is seen here perching/hunting on a grass, most likely *Bouteloua aristidoides* (Poaceae; Fig. 1.27C), on the edge of a sandy clearing as well as consuming its prey (Fig. 1.27D) in the typical hanging position observed in other Dasypogoninae species.

Figure 1.27. *Saropogon pyrodes* sp. nov. in natural habitat at ~ 0.7 km ENE of Amado in southern Arizona on September 5, 2017, **A** habitat overview **B** habitat detail with *S. pyrodes* included (arrow) **C** close-up of male perching **D** close-up of male consuming a bee (Hymenoptera: Apidae). Photographs by Jeff Gruber.

Jeff Gruber described some behavior (Figs 1, 1.27) on Flickr: “Found this beauty as I was walking back to my car mid-afternoon on a very warm day. It was hanging around the low grasses at the periphery of a *Pogonomyrmex* ant nest in grassland type habitat on floodplain(?) of Santa Cruz River, which at the time was a dry wash. It alternated perches between the low grasses, short dead stems poking up from the soil, and the soil surface". Original post: https://www.flickr.com/photos/7432824@N07/36417103883/in/faves-157063159@N04/

Etymology. Named for the fly's bright, fiery red color: *pyrodes* is Greek for fire-like.

Comments. In 1964, Mike Irwin collected the first record of this species, a male from four miles north of Continental, Arizona. He gave the specimen to Joseph Wilcox to identify. Then in 1968, Miller collected twelve specimens (11 ♂ and 1 ♀) from just north of Tucson, Arizona. He also donated this collection to J. Wilcox. The second author borrowed the specimens from Wilcox in approximately 1979 when he started a Ph.D. program at the University of California, Riverside. He considered describing this unique fly but never did. Finally, in 2017, beautiful photographs by Jeff Gruber (Fig. 1.27A–D) of this species appeared on BugGuide (https://bugguide.net/node/view/1439519), an online community where naturalists post and identify images of arthropods from the United States and Canada. Because of this, the second author immediately knew that this fly was long overdue for description, resulting in this manuscript.

Saropogon bryanti and *S. senex* have been collected within 10 km of the type locality of *S. pyrodes*. *Saropogon purus* and *S. coquillettii* can also be found in the area; the material examined showed specimens within 60 km of *S. pyrodes* collection sites. *Saropogon hypomelas, S. fletcheri, S. albifrons,* and *S. mohawki* are all found within 200 km (Fig. 1.26). *Saropogon* *pyrodes* typically flies later in the season (Aug. – Sep.) than *S. bryanti* and *S. senex* (Jun. – Aug.), *S. purus* (Jul.), and *S. albifrons* (Apr. – Jun.). *Saropogon coquillettii* (May – Sep.), *S. fletcheri* and *S. mohawki* (Jun – Oct.), and *S. hypomelas* (Jun. – Sep.) have longer flight seasons but are uncommon in the later months.

Saropogon semiustus Coquillett, 1904

Figs 1.26, 1.28, 1.31

Saropogon semiustus Coquillett, 1904: 186.

References. Back 1909: 351 (key and redescription); Curran 1930: 2 (key); Curran 1931: 2 (key); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 130 (key and comments); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. This species most closely resembles *Saropogon hyalinus* and *S. albifrons* but can be easily separated by its smaller size and dense grayish pubescence on the face, thorax, scutellum, and coxae. Abdomen mostly polished with sides of T1 and a spot on the posterior corner of T2–5, with gray pubescence (sometimes absent in males). Legs in male black, except red at tips of femora; legs in female are reddish. Antennae are yellowish brown. Wings hyaline. Body length 8–10 mm; wing length 7–8 mm. Flight time April – June.

Distribution. USA: Arizona, California; Mexico: Sonora

SimpleMappr: https://www.simplemappr.net/map/16994

Type material examined. UNITED STATES OF AMERICA • 1 ♂, holotype; California, San Diego County; 32°42’N, 117°09’W; 38 m; Coquillett; USNM; USNMENT01199020.

Arizona material examined. UNITED STATES OF AMERICA • 1 ♂; La Paz County, Parker, Osborn Well Road, 1.6 km E. of Route 95, white sand dunes; 34°07’ N, 114°15’ W; 150 m; 02 May 2008; T. Dikow, E. Fisher; USNM; USNMENT00870563 • 1 ♂, 1 ♀; La Paz County, Cactus Plain Wilderness Study Area, off Swansea Road near aqueduct; 34°00’ N, 113°57’ W; 365 m; 27 April 2015; T. Dikow; USNM; USNMENT01115214, USNMENT01115055 • 4 ♂, 6 ♀; La Paz County, Parker, Osborn Well Road, 1.6 km E. Route 95; 34°07’ N, 114°15’ W; 150 m; 02 May 2008; T. Dikow, E. Fisher; USNM; USNMENT01830325, USNMENT01830326, USNMENT01830327, USNMENT01830328, USNMENT01830329, USNMENT01830330, USNMENT0183031, USNMENT01830332, USNMENT01830333, USNMENT01830334 • 1 ?; Yuma County, 1 mi. W. of Tacna; 32°42’ N, 113°58’ W; 102 m; 24 April 1966; J. H. Davidson, J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139671 • 1 ?; Yuma County, 19 mi. NE of Yuma; 32°55’ N, 114°23’ W; 128 m; 09 April 1966; J. H. Davidson, J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139669 • 1 ♂; Yuma County, 5 mi. E. Tacna; 32°42’ N, 113°51’ W; 104 m; 17 June 1965; F. D. Parker; BME; BMEP0280492 • 1 ♂; same collection data as for preceding; R. M. Bohart; BME; BMEP0280493 • 3 ?; Yuma County, 6 mi. SE. of Parker; 34°05’ N, 114°12’ W; 208 m; 23 April 1966; J. H. Davidson, J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139665, ASUHIC0139666, ASUHIC0139667 • 1 ?; same collection data as for preceding; 14 May 1966; J. H. Davidson, J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139668 • 1 ?; same collection data as for preceding; 07 May 1966; J. H. Davidson, J.

M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139672 • 1 ?; Yuma County, Ligurta; 32°40’ N, 114°17’ W; 604 m; 08 April 1966; J. H. Davidson, J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139670 • 1 ♀; Yuma County, Welton; 32°40’ N, 114°40’ W; 76 m; F. H. Parker; USNM; USNMENT01819552.

Other material examined. Supplemental material 1.1.

Comments. Photographs of the holotype can be found here: http://n2t.net/ark:/65665/3648f2ac9-3f50-4efb-9719-6f3128085846.

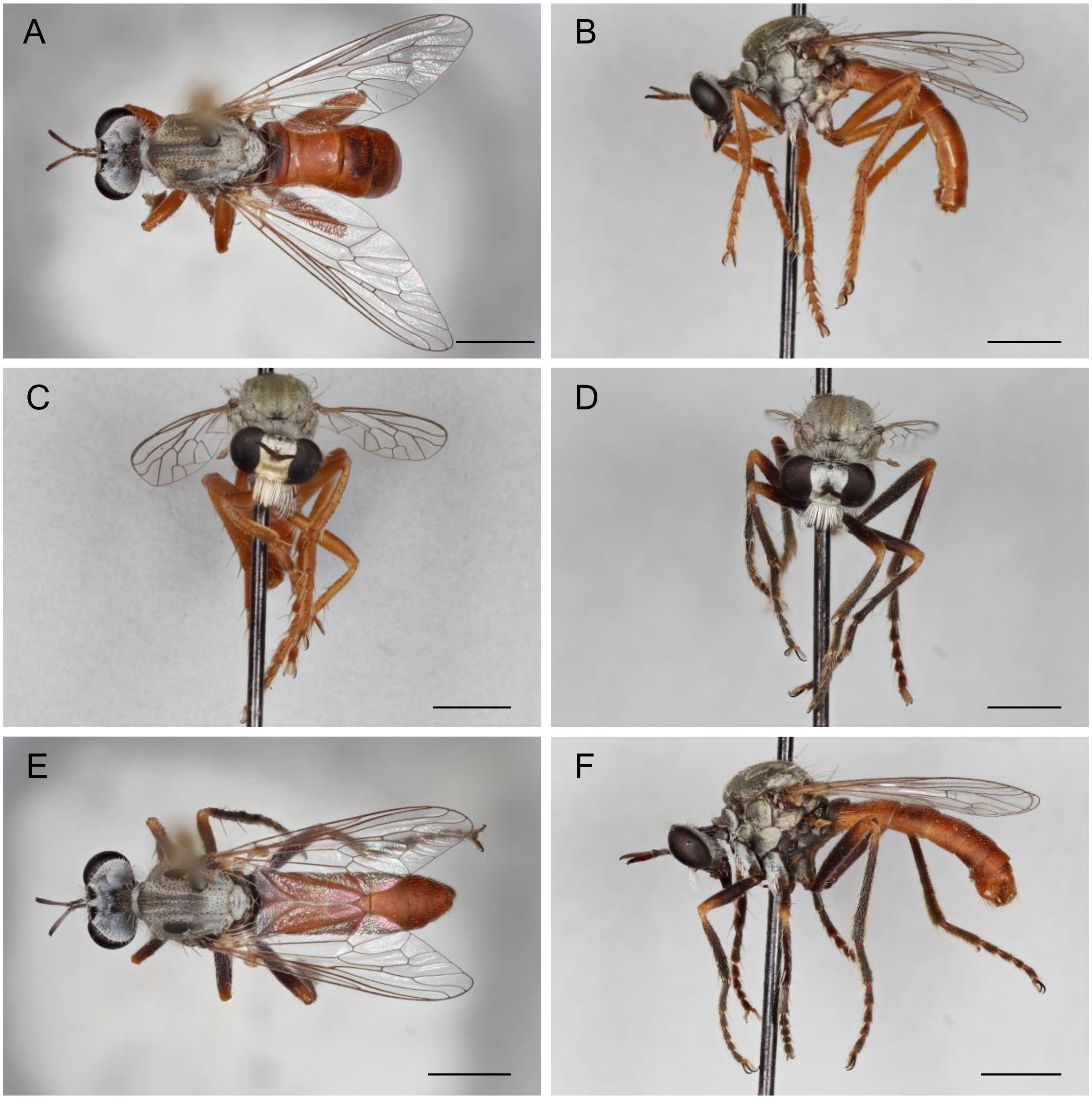

Figure 1.28. *Saropogon semiustus* Coquillett, 1904 Female (USNMENT01830085): **A** dorsal view, **B** lateral view, **C** anterior view; Male (USNMENT01830084): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Saropogon senex Osten Sacken, 1887

Figs 1.4G–H, 1.5O–P, 1.26, 1.29, 1.34

Saropogon senex Osten Sacken, 1887: 179.

Saropogon aridus Curran, 1930: 3, junior synonym.

References. Curran 1930: 2 (key, as *S. aridus*); Curran 1931: 2 (key, as *S. aridus*); Martin and Wilcox 1965: 383 (catalog); Wilcox 1966: 128 (key); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. This species is mainly black with the hind femora of the female and sometimes of the male, reddish. Discal scutellar setae absent; four short apical scutellar macrosetae; scutum, anepisternum, and scutellum with grayish pubescence. Body length 10–12 mm; wing length 7–9 mm. Flight time June – August.

Distribution. USA: Arizona; Mexico: Sinaloa, Sonora, Nayarit

SimpleMappr: https://www.simplemappr.net/map/16995.

Type material examined. MEXICO • 1 ♂, holotype; Presidio; 29°33’N, 104°22’W; Forrer; NHMUK; NHMUK013933278; Record 1427186.

Arizona material examined. UNITED STATES OF AMERICA • 1 ?; Cochise County, 1 mi. E. of Douglas; 31°20’ N, 109°31’ W; 1241 m; 26 Jul. 1962; M. A. Cazier; ASUHIC; ASUHIC0139680 • 1 ♀; Cochise County, 8920 Hereford S Bryerly Ct.; 31°24’ N, 110°13’ W; 1500 m; 24 June 2016; N. E. Woodley; USNM; USNMENT01819474 • 1 ♂; same collection data as for preceding; 25 June 2016; N. E. Woodley; USNM; USNMENT01819469 • 1 ♂, 1 ♀; same collection data as for preceding; 27 June 2017; N. E. Woodley; USNM; USNMENT01819464, USNMENT01819484 • 1 ♀; same collection data as for preceding; 10 July 2017; N. E. Woodley; USNM; USNMENT01819454 • 1 ♀; same collection data as for preceding; 14 July 2017; N. E. Woodley; USNM; USNMENT01819459 • 1 ♀; same collection data as for preceding; 09 July 2019; N. E. Woodley; USNM; USNMENT01819479 • 1 ♀; Cochise County, San Bernardino Ranch; 31°20' N, 109°16' W; 1143 m; August; F. H. Snow; USNM; USNMENT01819159 • 1 ♂; Cochise County, Texas Pass Dragon Mts; 31°59'N, 105°02'W; 1107 m; 21 July 1984; J. C. Burne; UAIC .• 2 ♀; Gila County, Globe; 33°23' N, 110°47' W; 1074 m; 03 August 1949; F. H. Parker; USNM; USNMENT01819174, USNMENT01819527 • 1 ♀; same collection data as for preceding; 27 July 1956; F. H. Parker; UAIC • 1 ♂, 1 ♀; same collection data as for preceding; 1076 m; 07 August 1970; F. H. Parker; UAIC • 2 ♀; Gila County, Hayes Mt.; 33°12'N, 110°36'W; 1517 m; 25 August, 1957; F. H. Parker; UAIC • 1 ♀; Gila County, San Carlos; 33°20'N, 110°27'W; 806 m; 29 July, 1967; F. H. Parker; UAIC • 1 ♂; Pima County, 10 mi. E. Continental; 31°51'N, 110°48'W; 1264 m; 18 July 1961; Werner, Nutting; UAIC • 1 ♂; Pima County, 10 mi. SE. Sahuarita; 31°50'N, 110°51'W; 914 m; 21 July 1977; Olson, Hetz; UAIC • 1 ♂, 1 ♀; Pima County, 3 mi. E. Sahuarita; 31°57' N, 110°55' W; 843 m; 31 July 1963; V. L. Vesterby; BME; BMEP0280477, BMEP0280478 • 1 ?; Pima County, 4 mi. N. of Madera Canyon; 31°44' N, 110°56' W; 1086 m; 25 July 1966; J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC139683 • 1 ?; Pima County 8 mi. N. of Santa Rita Exp. Sta.; 31°56' N, 110°51' W; 905 m; 17 July 1970; M. Kolner, S. Szerlip; ASUHIC; ASUHIC139684 • 2 ?; Pima County, 8 mi. NW of Santa Rita Exp. Sta.; 31°47' N, 110°57' W;

949 m; 17 July 1970; M. Kolner, S.. Szerlip; ASUHIC; ASUHIC139686, ASUHIC139687 • 1 ♂; Pima County, Brown Canyon, Baboquivari Mts; 31°28'N, 110°17'W; 1527 m; 28 July 1983; Werner, Olson; UAIC • 1 ♀; Pima County, Santa Rita Mts.; 31°49' N, 110°46' W; 1813 m; 01 August 1941; R. H. Beamer; BME; BMEP0280476 • 1 ♀; same collection data as for preceding; R. H. Beamer, C. H. Martin; BME; BMEP0280472 • 1 ♀, 1 ?; same collection data as for preceding; 09 August 1930; T. F. Winburn, R. H. Painter; CASENT; CASENT8427344, CASENT8427345 • 1 ?; Pima County, Santa Rita Range Reserve; 31°43' N, 110°52' W; 1775 m; 15 July 1970; M. Cazier, J. Bigelow, L. Welch; ASUHIC; ASUHIC0139685 • 1 ♂; Pima County, Santa Rita Mts.; 31°49' N, 110°46' W; 1814 m; 31 June 1941; F. H. Parker; USNM; USNMENT01199040 • 1 ♂; same collection data as for preceding; 31 July 1944; F. H. Parker; USNM; USNMENT01199009 • 1 ♂; Pima County, Tucson, vic. Ina/Oracle; 32°19'N, 110°58'W; 770 m; 23 July 1988; W. L. Nutting; UAIC • 1 ♀; Pima or Santa Cruz County, Santa Rita RR; 31°35' N, 110°43' W; 1308 m; 15 August 1953; F. H. Parker; USNM; USNMENT01819139 • 1 ♂; Santa Cruz County, Santa Rita Mts. Madera Canyon; 31°44' N, 110°56' W; 1086 m; 15 July 1972; D. G. Marqua; USNM:USNMENT01830378 • 1 ♀; same collection data as for preceding; 24 July 1976; D. G. Marqua; USNM; USNMENT01830379 • 4 ♂, 3 ♀; same collection data as for preceding; 07 – 09 August 1962; E. M. Fisher; USNM; USNMENT01830365, USNMENT01830366, USNMENT01830367, USNMENT01830368, USNMENT01830369, USNMENT01830370, USNMENT01830371 • 1 ♂; same collection data as for preceding; 12 – 14 July 1961; E. M. Fisher; USNM; USNMENT01830372 • 2 ?; same collection data as for preceding; 25 July 1966; J. M. Davidson, M. A. Cazier; ASUHIC; ASUHIC0139681, ASUHIC0139682 • 1 ?; same collection data as for preceding; 26 August

1964; R. H. Crandall; LACM; LACMENT579126 • 2 ?; same collection data as for preceding; 01 – 06 August 1965; R. H. Crandall; LACM; LACMENT579128, LACMENT579129 • 1 ?; same collection data as for preceding; 06 August 1965; R. H. Crandall; LACM; LACMENT579127 • 2 ♂, 2♀; same collection data as for preceding; 13 July, 1958; R. M. Bohart, USNM, USNMENT01830374, USNMENT01830375, USNMENT01830376 • 2 ♂, 7♀; same collection data as for preceding; 31 July 1958; R. M. Bohart; BME; BMEP0280479, BMEP0280480, BMEP0280481, BMEP0280482, BMEP0280483, BMEP0280484, BMEP0280485, BMEP0280486; USNM; USNMENT01830373 • 1 ♀; same collection data as for preceding; 28 July 1979; S. Mannweiler; USNM; USNMENT01830377 • 1 ♀; same collection data as for preceding; 01 August 1960; S.. L. Wood, J. B. Karren, H. Shurtleff; BYU; BYUC215820 • 1 ?; Yavapai County, Badger Spring exit, 3.5 mi. NNE of Bumble Bee; 34°15' N, 112°06' W; 975 m; 04 August 1973; O. Francke, M. Kolner; ASUHIC; ASUHIC0139688.

Other material examined. Supplemental material 1.1.

Comments. Information about the holotype can be found here: https://data.nhm.ac.uk/record/bb909597-dedf-427d-8c04-4c02b3a24db3/1427186/1656374400000. At time of publication, there were no publicly available photographs of the specimen; however, pictures are scheduled to be posted to this link in the near future.

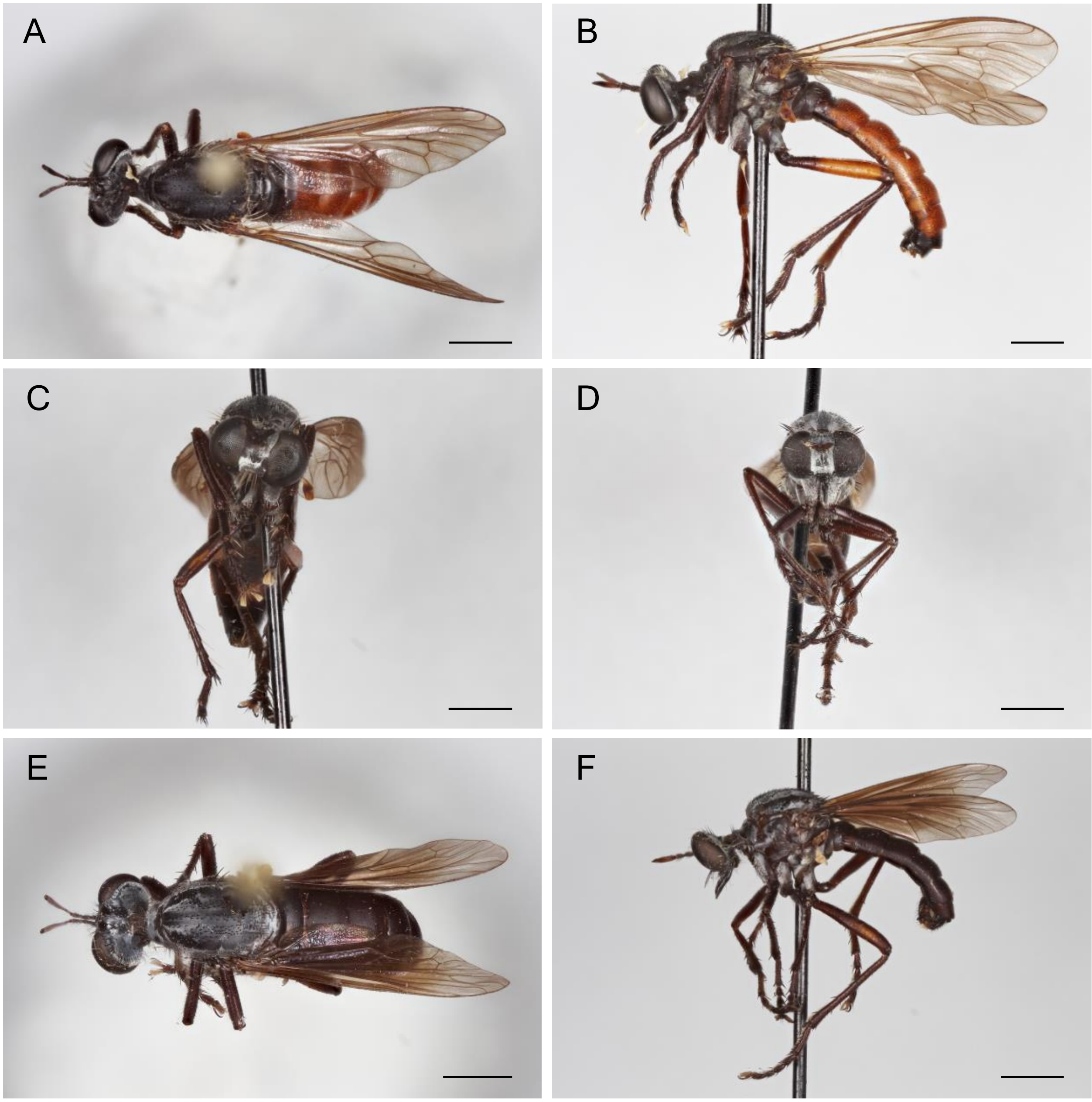

Figure 1.29. *Saropogon senex* Osten Sacken, 1887 Female (UCBMEP0280483): **A** dorsal view, **B** lateral view, **C** anterior view; Male (UCBMEP0280489): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2 mm.

Saropogon solus Bromley, 1951

Figs 1.30, 1.31

Saropogon solus Bromley, 1951: 15.

References. Martin and Wilcox 1965: 383 (catalog); Wilcox, 1966: 128 (key); Fisher and Wilcox 1997: 4 (catalog).

Diagnosis. This species is distinguishable from all other North American species by its lack of apical scutellar bristles. Wings are yellow tinged with gray tips; legs are reddish yellow. Body length 12 mm; wing length 8 mm. Flight time June – Aug.

Distribution. USA: Texas; Mexico: Tamaulipas

SimpleMappr: https://www.simplemappr.net/map/16996.

Type material examined. UNITED STATES OF AMERICA • 1 ♂, holotype; Texas, Hildago County; 26°27’N, 98°13’W; 39 m; 16 Jun 1933; S. W. Bromley; USNM; USNMENT01199013.

Other material examined. Supplemental material 1.1.

Comments. Photographs of the holotype are available at; http://n2t.net/ark:/65665/320c061d2-3a39-4baf-9836-909bdf168a64.

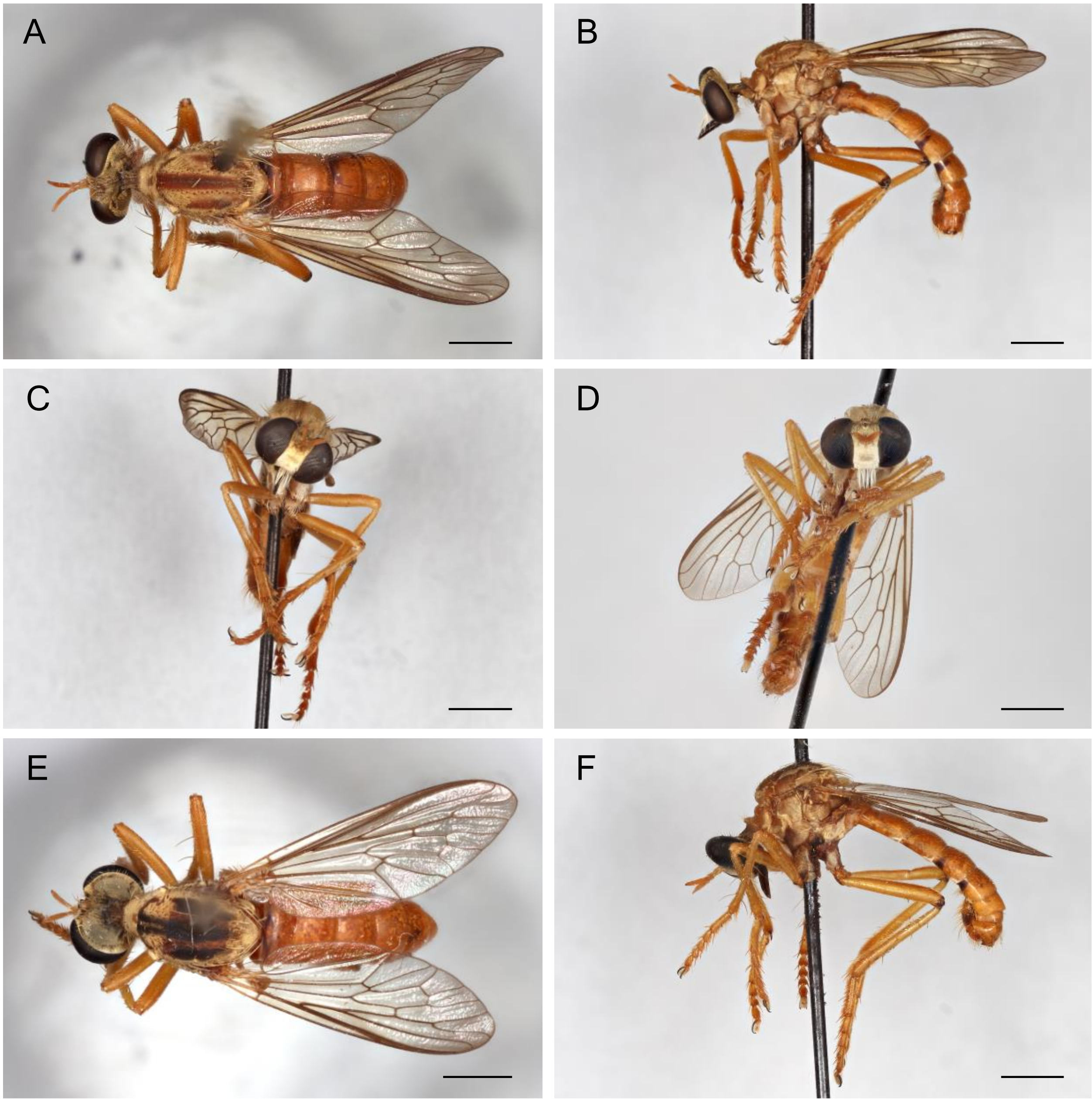

Figure 1.30. *Saropogon solus* Bromley, 1951 Female (USNMENT01819178): **A** dorsal view, **B** lateral view, **C** anterior view; Male (USNMENT01819132): **D** anterior view, **E** dorsal view, **F** lateral view. Scale bars 2mm.

Discussion

The description of the unique species of *Saropogon pyrodes* sp. nov. with the summary of our knowledge of the Nearctic *Saropogon* north of Mexico in the present study is an initial contribution to understanding the diversity of this genus. A future, more detailed revision of all Nearctic species including those occurring in Mexico, would be a natural extension of this project. Multiple new species from Sinaloa, Sonora, Durango, and Jalisco have been accumulating in the collection of the second author (recently donated to the USNM). Combined with specimens housed in Mexican natural history collection, these will provide the foundation for a comprehensive revision of the entire Nearctic fauna. With the description of *Saropogon pyrodes* sp. nov. there are now 20 species known from the USA, and *Saropogon* is now the third most speciose genus of Dasypogoninae after *Cophura* (~ 34 spp.) and *Diogmites* with (~ 25 spp.) in the Nearctic north of Mexico (see Fisher and Wilcox 1997). In terms of the entire Asilidae fauna of the Nearctic, *Saropogon* is the 14th most species-rich genus (Fisher and Wilcox 1997; Geller-Grimm 2004).

There are a few morphological characters not previously mentioned that may prove useful for future species diagnosis and delimitation. The most apparent are the pubescence patterns on the dorso-median occiput (part or all of the median occipital sclerite). Of the species examined, *Saropogon albifrons, S. bryanti*, *S. coquillettii*, and *S. dispar* have minimal to no patterning with solid pubescence. *Saropogon hyalinus, S. luteus, S. mohawki, S. nitidus, S. purus, S. semiustus, S. senex, and S. pyrodes* sp. nov. have two non-pubescent spots directly adjacent to slightly posterior to, the ocellar tubercle. Particularly distinct patterns occur in *Saropogon mohawki* where the cuticle showing through the two non-pubescent spots is light brown instead of black as in the other species examined; *S. purus* has one large non-pubescent spot behind the ocellar tubercle, and *S. pyrodes* sp. nov. has two non-pubescent spots, but they appear much rounder and larger than in the other material examined. These are far from concrete descriptions, but it shows further observation may be warranted. Another character we would like to reexamine in future studies is the dependence on the number of apical scutellar setae in the identification of *Saropogon*. This character has been heavily relied upon in past identification keys despite it being known for being inconsistent within species. Our key attempts to replace this character with other more dependable characters and only rely on apical scutellar setae where necessary (e.g., *S. mohawki* and *S. hyalinus*).

Platforms like iNaturalist and BugGuide have greatly facilitated communication between community and professional entomologists. *Saropogon pyrodes* sp. nov. is an excellent example of how community involvement can assist in the discovery and, ultimately, the description of new species. These community-based websites are a relatively new resource that scientists are learning to utilize in their research, and we hope to encourage future participation on both sides of the professional plane.

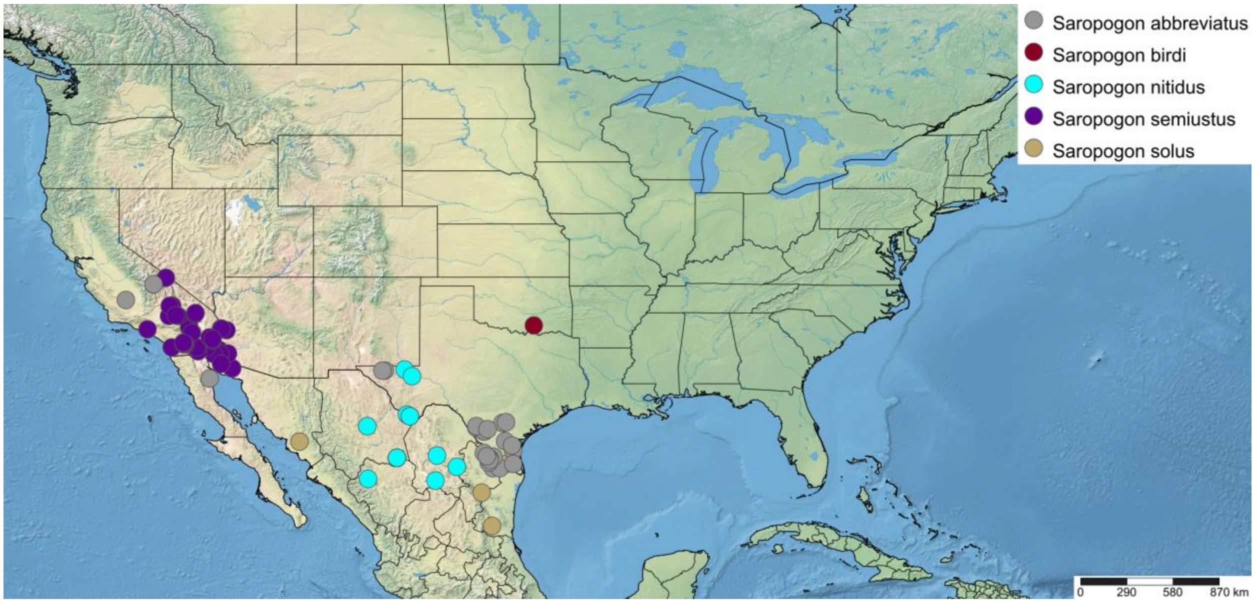

Figure 1.31. Distribution of *Saropogon* (Diptera: Asilidae) specimens studied for *S. abbreviatus, S. birdi, S. nitidus, S. semiustus,* and *S. solus*. Map created with SimpleMappr on July 25, 2022, and available at: https://www.simplemappr.net/map/18363

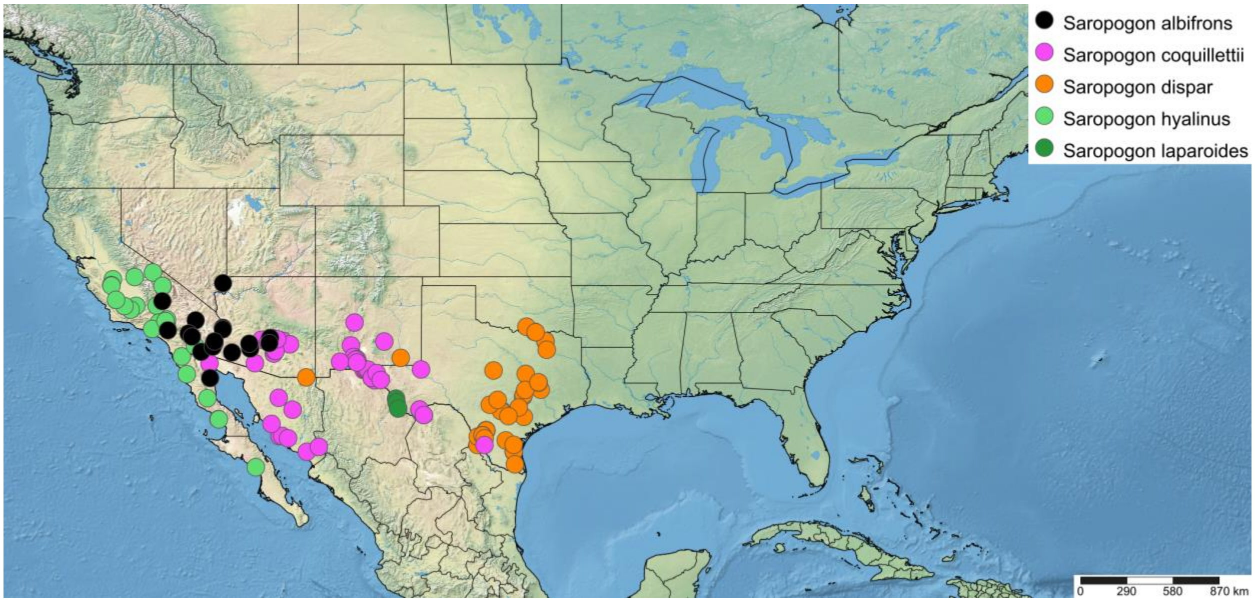

Figure 1.32. Distribution of *Saropogon* (Diptera: Asilidae) specimens studied for *S. albifrons*, *S. coquillettii*, *S. dispar*, *S. hyalinus*, and *S. laparoides*. Map created with SimpleMappr on July 25, 2022, and available at: https://www.simplemappr.net/map/18317

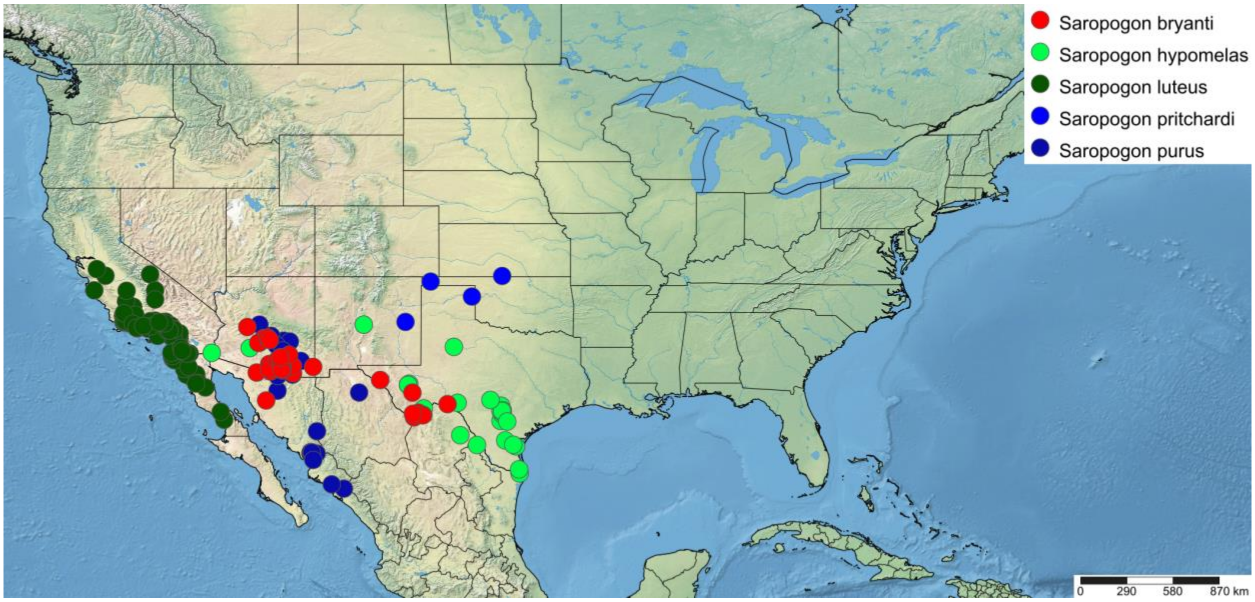

Figure 1.33. Distribution of *Saropogon* (Diptera: Asilidae) specimens studied for *S. bryanti*, *S. hypomelas*, *S. luteus*, *S. pritchardi*, and *S. purus*. Map created with SimpleMappr on July 25, 2022, and available at: https://www.simplemappr.net/map/18318

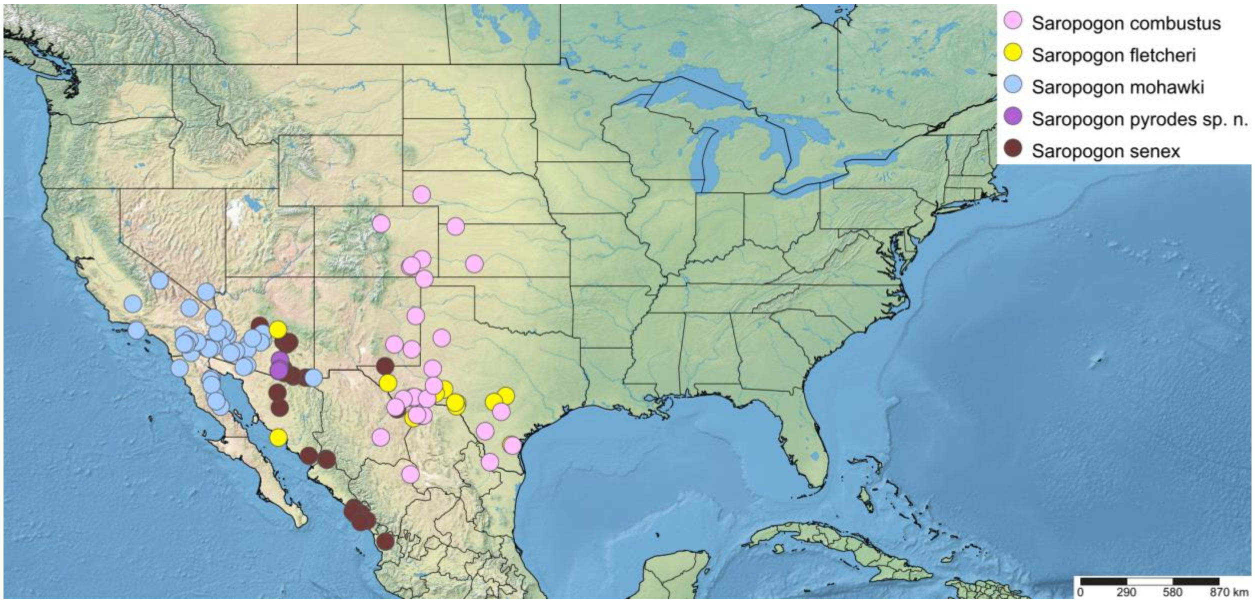

Figure 1.34. Distribution of *Saropogon* (Diptera: Asilidae) specimens studied for *S. combustus, S. fletcheri, S. mohawki, S. pyrodes sp. nov.,* and *S. senex*. Map created with SimpleMappr on July 25, 2022, and available at: https://www.simplemappr.net/map/18362

Acknowledgements

First, we would like to thank the community scientists who helped inspire us to make this publication a priority, especially Jeff Gruber and Charles W. Melton for posting photographs of the new species to BugGuide, Flickr, and iNaturalist. We would like to thank Chris Grinter for allowing the first author to visit the CASENT collection, Helen Vessels for access to the NMSU Arthropod Collection, and Karen Wright for help visiting TAMUIC and photographs of *S. fletcheri*. We would like to thank Torsten Dikow with his help editing the manuscript, imaging resources, and access to USNM specimens, and Lynn Kimsey for access to BMEC, workspace, and imaging resources. We would like to thank Shawn Clark and Riley Nelson for loaning specimens from the BYU collection, and Gene Hall, Tristan McKnight, and Wendy Moore for allowing access to the collection and loaning specimens from UAIC. We would like to thank Melissa Aja for giving us access to photographs of *Saropogon combustus, S. rufus (luteus), S. abbreviatus, S. adustus* (*combustus*) and *S. bicolor* (*abbreviatus*) holotypes at the MCZ, Zachary Falin for photographs of *S. albifrons* and *S. pritchardi* holotypes from the SEMC collection, David Grimaldi, Christine Johnson, Agnieszka Pierwola, and Courtney Richenbacher for sending photographs of *S. birdi, S. laparoides,* and *S. purus* holotypes at the AMNH, Erica McAlister and Nigel Wyatt for photographs of the *S. senex* holotype from the NHMUK collection, and Nicole Gunter for taking and sending pictures of a very confusing Ohio *Saropogon,* which turned out to be *Diogmites*. We would like to thank Ellen Dean for help with habitat and plant identification, Emma Cluff for help with databasing and organizing specimens, Brennen Dyer for help taking pictures using the complicated GIGAmacro imaging system and tracking down elusive specimens, and Jessica Gillung for helping organize the manuscript. A special thanks to Keely Davies for making an incredible illustration of this *S. pyrodes* sp. nov., and Martin Hauser and the reviewers for giving us great advice on how to improve this manuscript. Finally, we would like to thank George Alberts and family for their love and support while the first author chased flies around the world. The authors have no funding to report and have declared that no competing interest exist.

References

Artigas JN, Papavero N (1988) The American genera of Asilidae (Diptera): keys for identification with an atlas of female spermathecae and other morphological details. II. Subfamily Dasypogoninae Macquart, with descriptions of new genera and species and new synonymies. Gayana Zoologia 52(3–4): 199–260. https://biostor.org/reference/100813

Back EA (1904) New species of North American Asilidae. The Canadian Entomologist 36(10): 298–293. https://doi.org/10.4039/Ent36289-10

Back EA (1909) The Robber-flies of America, north of Mexico, belonging to the subfamilies Leptogastrinae and Dasypogoninae. Transactions of the American Entomological Society 35(1): 137–400. https://doi.org/10.5962/bhl.title.9381

Bellamy CL (2002) Coleoptera: Buprestoidea. In: Houston WWK (Ed.) Zoological Catalogue of Australia. CSIRO Publishing, Collingwood, Australia, 492 pp. ISBN: 0643069003

Bromley SW (1934) The Robber Flies of Texas (Diptera, Asilidae) Annals Entomological Society of America 27: 74–113. https://doi.org/10.1093/aesa/27.1.74

Bromley SW (1951) Asilid notes (Diptera), with descriptions of thirty-two new species. American Museum Novitates 1532: 1–36. https://hdl.handle.net/2246/2377

Cohen CM, Noble K, Cole TJ, Brewer MS (2021) The phylogeny of robber flies (Asilidae) inferred from ultraconserved elements. Systematic Entomology: 1–15. https://doi.org/10.1111/syen.12490

Coquillett DW (1902) New Orthorrhaphous Diptera from Mexico and Texas. Journal New York Entomological Society 10: 136–141. https://www.jstor.org/stable/25002994

Coquillett DW (1904) New North American Diptera. Proceedings of the Entomological Society of Washington 6: 166–192. https://www.biodiversitylibrary.org/page/2345832

Cumming JM, Wood DM (2017) Adult morphology and terminology In: Brown B V, Borkent A, Cumming JM, Wood DM, Woodley NE, Zumbabo MA (Eds) Manual of Central American Diptera. Vol. 1. National Research Council Research Press, Ottawa, Ontario, 714 pp. ISBN: 0660198339.

Curran CH (1930) New American Asilidae (Diptera). The American Museum of Natural History, American Museum Novitates 425: 1–21. http://hdl.handle.net/2246/2113

Curran CH (1931) New American Asilidae (Diptera). II. The American Museum of Natural History, American Museum Novitates 487: 1–25. https://hdl.handle.net/2246/3035

Dikow T (2009a) Phylogeny of Asilidae inferred from morphological characters of imagines (Insects: Diptera: Brachycera: Asiloidea). Bulletin American Museum of Natural History 319: 1–175. https://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 and Evolution 9: 165–188. https://doi.org/10.1016/j.ode.2009.02.004

Dikow T (2018) Asiloid flies: deciphering their diversity and evolutionary history. Asilidae generic classification *sensu* Dikow 2009. Available from: https://asiloidflies.si.edu/ [Accessed Oct 2, 2021].

Fisher EM, Wilcox J (1997) Catalog of the robber flies (Diptera: Asilidae) of the Nearctic region. [distributed as unpublished document to Asilidae workers, widely used in community; new version underway with Cunnings, R. – to be published].

GBIF.org (2022): GBIF Registry of Scientific Collections. Available from: https://www.gbif.org/grscicoll

Geller-Grimm F (2004) A world catalogue of the genera of the family Asilidae (Diptera). Studia dipterologica 10(2): 473–526. https://doi.org/10.5281/zenodo.14704

Google Earth Pro (2021) Version 7.3.4.8248 Available through: https://www.google.com/earth/versions/ [Accessed 3 October 2021].

Hardy GH (1926) A new classification of Australian robberflies belonging to the subfamily Dasypogoninae (Diptera, Asilidae). Proceedings of the Linnean Society of New South Wales 51: 305–312. https://biostor.org/reference/105137

Hull FM (1956) Some Asilidae (Diptera). Entomological News 67: 131–135. https://doi.org/10..1080/00222935608655832

Hull FM (1962) Robber flies of the world: the genera of the family Asilidae. In: Smithsonian Institution, United States National Museum. Bulletin 224. Part 2. Smithsonian Institution, United States National Museum, Washington, DC, 431– 906. https://doi.org/10.5479/si.03629236.224

Hurd PD (1952) Revision of the Nearctic species of the pompilid genus *Pepsis* (Hymenoptera: Pompilidae). Bulletin of the American Museum of Natural History 98: 257–334. http://hdl.handlenet/2246/1025.

Hurd PD, Linsley EG (1975) Some insects other than bees associated with Larrea tridentata in the southwestern United States. Proceedings of the Entomological Society of Washington 77: 100–120. ISSN: 0013-8797.

Johnson CW (1903) A new genus and four new species of Asilidae. Psyche 10: 111–114. https://doi.org/10.1155/1903/25137

Lehr PA (1988) Family Asilidae, In: Soos, A. (Ed.) and Papp, L. (Ed.), Catalogue of Palaearctic Diptera, Budapest, 197–326 pp. ISBN: 9780444996022

Linsley EG (1960) Ethology of some bee-and wasp killing robber flies of southeastern Arizona and Western New Mexico (Diptera: Asilidae). *In:* Linsley, EG, Smith RF, Steinhaus EA, and Usinger RL (Eds.) University of California Publications in Entomology, University of California Press, Berkeley and Los Angeles, 16(7): 357–392.

Loew H (1847) Ueber die europäischen Raubfliegen (Diptera Asilica). Linnaea Entomologica 2: 384–568. https://doi.org/10.5962/bhl.title.11475

Loew H (1874) Neue nordamerikanische Dasypogonina. Berliner Entomologische Zeitschrift 18: 353–377. https://doi.org/10.1002/mmnd.18740180322

Londt JGH (1997) Afrotropical Asilidae (Diptera) 29. A review of the genus *Saropogon* Loew, 1847 (Dasypogoninae). Annals of the Natal Museum 38: 137–157. https://hdl.handle.net/10520/AJA03040798_167

Londt JGH (1980) Afrotropical Asilidae (Diptera) 4. The genus *Pegesimallus* Loew, 1858 (=Lagodias Loew, 1858; Neolaparus Williston, 1889), including species from other zoogeographical regions and the descriptions of the two new genera, *Brevirostrum* and *Caroncoma*. Annals of the Natal Museum 24: 233–347. https://hdl.handle.net/10520/AJA03040798_563

Martin CH, Papavero N (1970) A catalogue of the diptera of the Americas south of the United States 35b Family Asilidae. Museu de Zoologia, Universidade de São Paulo 35b.1–35b.139. https://doi.org/10.5962/bhl.title.110114

Martin CH, Wilcox J (1965) Family Asilidae, *In*: Stone A, Sabrosky CW, Wirth WW, Foote RH, and Coulson JR. A catalog of the diptera of America north of Mexico. U. S. Government Printing Office, Washington D.C. 360–1116 pp. https://handle.nal.usda.gov/10113/CAT87208336

Mesaglio T, Soh A, Kurniawidjaja S, Sexton C (2021) First known photographs of living specimens': the power of iNaturalist for recording rare tropical butterflies. Journal of Insect Conservation 25: 905–911. https://doi.org/10.1007/s10841-021-00350-7

Nelson RC (1987) Robber flies of Utah (Diptera: Asilidae). Great Basin Naturalist 47:1(6) 38–90. https://scholarsarchive.byu.edu/gbn/vol47/iss1/6

Nichols (1989) Torre-Bueno glossary of entomology. New York Entomological Society, New York, USA, 840 pp. ISBN: 0913424137.

Oldroyd H (1975) Family Asilidae, *In:* Delfinado M D and Hardy D Elmo (Eds.), A catalog of the Diptera of the Oriental region, The University Press of Hawaii, Honolulu, 99–156 pp. ISBN: 9780824803469

Osten Sacken CR (1887) Fam. Asilidae. Biologia Centrali-Americana 1: 167–213. https://doi.org/10.5962/bhl.title.730

Papavero N (1973) Studies of Asilidae (Diptera) systematics and evolution. I. A preliminary classification in subfamilies. Arquivos de Zoologia 23(3) 217–274. https://doi.org/10.11606/issn.2176-7793.v23i3p217-274

Pollock DA (2021) Robber flies (Diptera: Asilidae) as predators of harvester ant workers (Hymenoptera: Formicidae: *Pogonomyrmex*) in Eastern New Mexico and West Texas. The Southwestern Naturalist 65(1): 19–27. https://doi.org/10.1894/0038-4909-65.1.3

Sakhvon VV (2020) Review of the genus *Saropogon* Loew, 1847 (Diptera: Asilidae) from Russia, Transcaucasia and central Asia, with description of three new species. Zootaxa 4860(4): 577–591.https://doi.org/10.11646/zootaxa.4860.4.7

Saropogon Loew, 1847 in GBIF Secretariat (2021). GBIF Backbone Taxonomy. Checklist dataset Available from https://www.GBIF.org [Accessed 4 October 2021]. https://doi.org/10.15468/39omei

Shorthouse, David P (2010) SimpleMappr, an online tool to produce publication-quality point maps. Available from https://www.simplemappr.net [Accessed 24 November 2020].

Sweetman H (1958) The principles of biological control. W. C. Brown, Dubuque, 560pp.

Thorp RW (1973) Prey records for robber flies of the Lake Texoma region Oklahoma (Diptera: Asilidae). Pan-Pacific Entomologist 49(1): 89–90.

VanDyk J ed. (2021) BugGuide.Net: Identification, images, and information for insects, spiders and their kin for the United States and Canada. Iowa State University Available from https://bugguide.net/ [Accessed 4 October 2021].

Wilcox J (1936) Asilidae, new and otherwise, from the south-west, with a key to the genus Stichopogon. The Pan-Pacific Entomologist 13(1–2): 37–45. https://www.biodiversitylibrary.org/page/53411556

Wilcox J (1966) New species and a key to the species of *Saropogon* Loew (Diptera: Asilidae). The Pan-Pacific Entomologist 42(2): 127–136. https://www.biodiversitylibrary.org/page/53621647

Winterton S L, Guek HP, Brooks SJ (2012) A charismatic new species of green lacewing discovered in Malaysia (Neuroptera, Chrysopidae): the confluence of citizen scientist, online

image database and cybertaxonomy. ZooKeys 214: 1–11.
https://doi.org/10.3897/zookeys.214.3220

Over 3,400 predator-prey records for assassin flies (Insecta: Diptera: Asilidae) compiled from United States entomological collections

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Abstract

More than 3,400 Asilidae specimens with their associated prey have been specimen-level databased, by examining 15 natural history collections in the USA. The orders of arthropods preyed upon are, in order of representation, Hymenoptera, Diptera, Coleoptera, Orthoptera, Blattodea, Odonata, Araneae, Neuroptera, Thysanoptera, Siphonaptera, and Trichoptera. Asilidae genera with sufficient data to warrant special attention are: Asilinae (*Efferia, Mallophora, Megaphorus, Proctacanthus, Promachus,* and *Triorla*), Brachyrhopalinae (*Ceraturus, Cyrtopogon, Heteropogon, Holopogon,* and *Nicocles*), Dasypogoninae (*Diogmites* and *Saropogon*), Dioctriinae (*Dioctria*), Laphriinae (*Atomosia* and *Laphria*), Leptogastrinae (*Leptogaster*), Ommatiinae (*Ommatius*), Stenopogoninae (*Callinicus, Microstylum, Ospriocerus, Scleropogon,* and *Stenopogon*), Stichopogoninae (*Stichopogon*), and Trigonomiminae (*Holcocephala*). Most Asilidae prefer a generalist or polyphagous diet consisting of only arthropod prey. However, several genera appear oligophagous – *Ceraturgus* on Coleoptera, *Diogmites* on Hymenoptera, *Laphria* on Lampyridae, *Mallophora* on Apidae, *Megaphorus* on Hymenoptera, *Nicocles* on Diptera, *Ospriocerus* on Meloidae, *Promachus* on Apidae, *Saropogon* on Hymenoptera, and *Stichopogon* on Diptera. This dataset also supports previous findings that female asilid predators outnumbered males in a 1.5 to 1 ratio.

Keywords

natural history collections, ecology, entomology, insect predation, prey analysis

Introduction

Entomological collections preserved in natural history museums are of immense value to science and society (Bakker et al. 2020, Winston 2007). They are a catalog of the Earth's past and allow us to study not only taxonomy but biological characteristics, such as predator-prey associations as well.

Assassin flies or robber flies (Diptera: Asilidae) are unique and essential arthropod predators present in all zoogeographical regions. Asilids are the third most speciose family of Diptera, with over 7,500 species in more than 550 genera (Pape et al. 2011). Assassin flies are mainly found in warm regions with exceptionally high diversity in the tropics, arid, and semi-arid environments (Londt and Dikow 2017). Many species are considered economically important in their role as predators of other insects (Fattig 1945, Bromley 1950, Londt 1993) and indicative of environmental health (Londt and Dikow 2017, Wagner et al. 2021). Asilid larvae feed on other larvae in the soil and dead wood, especially beetle larvae. Some Laphriinae larvae feed on white grub worms, which include the invasive European chafer (*Rhizotrogus majalis*) and Japanese beetle (*Popillia japonica*) (Fattig 1945, Bromley 1945). While other species, such as *Diogmites angustipenis*, *Diogmites symmachus*, and *Saropogon dispar* are known for preferring honeybees and are considered destructive to apiaries causing economic losses in Florida and Texas (Fattig 1945, Bromley 1948a, 1950). Bromley (1948b) lists Asilidae as important natural control agents of mosquitoes. Asilid adults generally feed on a broad range of arthropod prey, primarily caught in flight but sometimes actively searching for resting or grounded prey (Farr 1962, Cannings 2014, Lavigne 2016). Both Asilidae sexes prey on other arthropods as adults and larvae, making them unique among the Diptera. Although asilids are known to be predatory, many aspects of Asilidae predation and biology remain unanswered, such as why adult females are more often recorded with prey than males or how asilids evolved to become predators and how it has affected the diversity of the family. Are asilids mostly generalists, or are there specialist species that prefer a particular prey type, and does their biology reflect this specialization?

Asilidae are typically well represented in entomological collections and are often pinned with prey in association (Fig. 2.1). This may be because the predator tends to perch on exposed surfaces such as leaves or logs to consume captured prey. The assassin can then be easily captured with the associated prey. Predator-prey interactions are often referenced in Asilidae literature, and researchers have tried to organize these references into databases to provide insight into asilid prey selection (e.g., Lavigne 2016). Though incredibly interesting and helpful in suggesting trends, this information is often difficult to verify and analyze. Therefore, more specific information can be gained by studying these predator-prey interactions in entomological collections where voucher specimens can be cataloged, providing a solid foundation for subsequent studies.

This data paper includes information about sex and prey associations from more than 3,400 Asilidae specimens housed in 15 entomological collections in the USA. Though this data paper provides some interpretation of the results, its primary function is to make these records publicly available for future scientific investigation, including analysis in an evolutionary context (Alberts in prep). A similar collection-based dataset of Asilidae predator-prey specimens was published by Londt (2006).

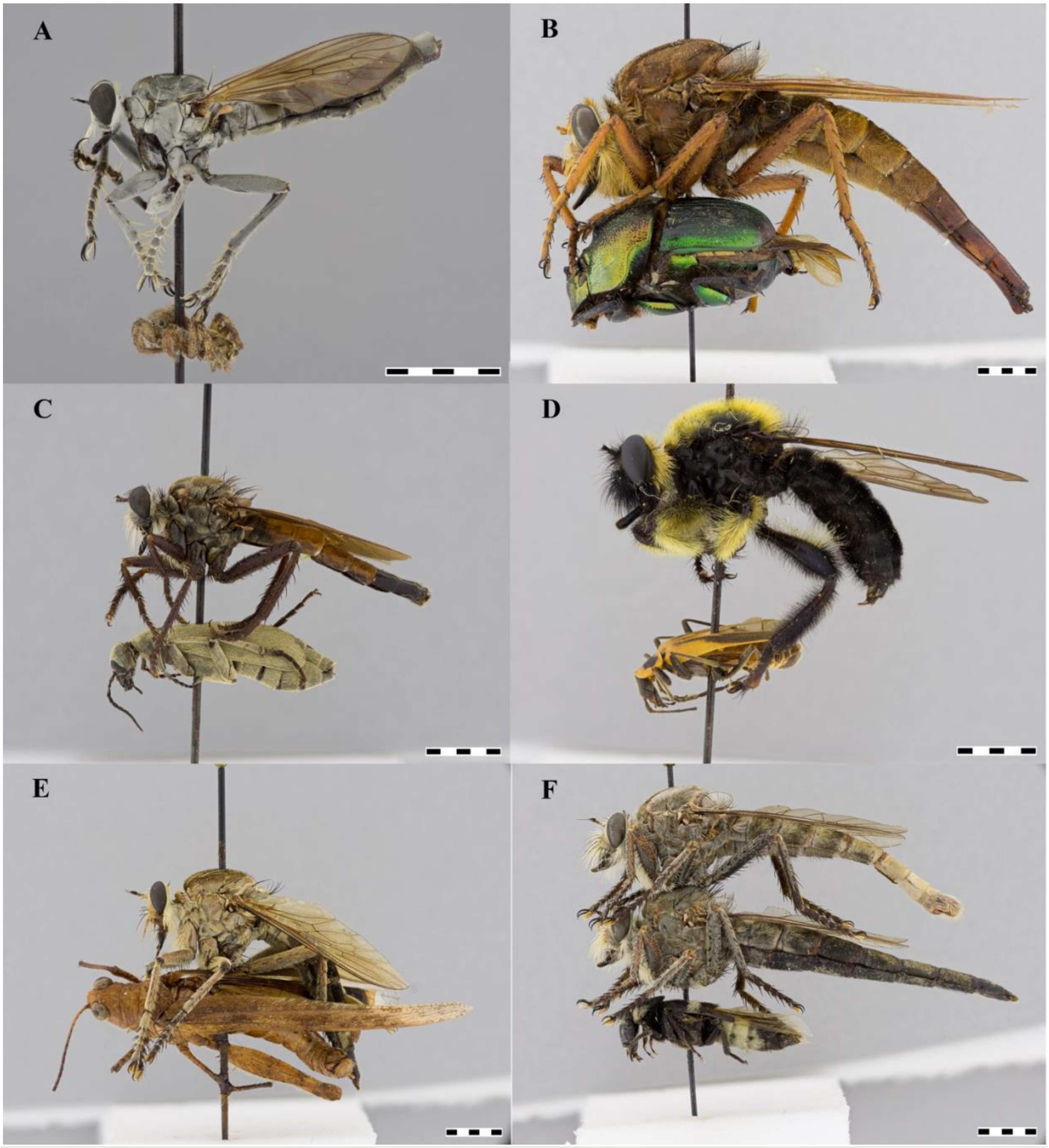


Figure 2.1.

Pinned Asilidae predator-prey specimens in the USNM. **A.** *Stichopogon trifasciatus* with Salticidae prey (USNMENT01115407) **B.** *Proctacanthus heros* with Scarabaeidae prey (USNMENT01172973) **C.** *Stenopogon aeacidinus* with Meloidae prey (USNMENT01265858) **D.** *Laphria affinis* with Lampyridae prey (USNMENT01172234) **E.** *Triorla interrupta* with Acrididae prey (USNMENT01163822) **F.** Mated pair of *Proctacanthus occidentalis* with Staphylinidae prey (USNMENT01163860). Photographs by C. H. E. Alberts. Scale lines = 5 mm.

Methods

Collections and Specimen Examination

This study is based on examined specimens from the following institutions and collections I visited or had material loaned:

ASUHIC – The Hasbrouck Insect Collection, Arizona State University, Tempe, Arizona, U.S.A.

BMEC – The Bohart Museum of Entomology, University of California, Davis, U.S.A.

BYU – Brigham Young University, Provo, Utah, U.S.A.

CASENT – California Academy of Sciences Entomological Collection, San Francisco, California, U.S.A.

CSCA – California Department of Food and Agriculture, Sacramento, California, U.S.A.

EMEC – Essig Museum of Entomology, University of California, Berkeley, U.S.A.

JWSU – M. T. James Entomological Collection, Washington State University, Pullman, Washington, U.S.A.

LACM ENT – Natural History Museum of Los Angeles County Entomological Collection, Los Angeles, California, U.S.A.

NMSU – New Mexico State University Arthropod Collection, Las Cruces, New Mexico, U.S.A.

SDC – The personal collection of Dr. Steve Dennis, donated to the USNM in 2022, in Washington, D.C., U.S.A.

TAMUIC - Texas A&M University Insect Collection, College Station, Texas, U.S.A.

UAIC – The University of Arizona Insect Collection, Tucson, Arizona, U.S.A.

UCR – Entomology Research Museum, University of California, Riverside, U.S.A.

UMNH – Natural History Museum of Utah, Salt Lake City, Utah, U.S.A.

USNM – Smithsonian National Museum of Natural History, Washington, D.C., U.S.A.

WFBM – W. F. Barr Entomology Collection, University of Idaho, Moscow, Idaho, U.S.A

The author visited JWSU, LACM ENT, NMSU, TAMUIC, UAIC, UCR, UMNH, and WFBM during the Summer of 2017 in search of Asilidae associated with prey. BMEC, CASENT, CSCA, EMEC, and USNM were visited multiple times in 2016–2022 and often for extended periods to collect data. The USNM collection consists of many donated personal collections, such as Dr. Steve Dennis's, donated in 2022, and Dr. Eric Fisher's, which is currently being donated. ASUHIC and BYU loaned material for this or other projects included in the Asilidae prey database. Many other western U.S. entomological collections were contacted but unavailable, or the estimated number of Asilidae associated with prey was too few to warrant a visit (<30). There are currently 3,421 prey records in this dataset. Collection abbreviations are from the 2022 GBIF Registry of Scientific Collections, with some additions of preferred names from the collection's website or personal communication.

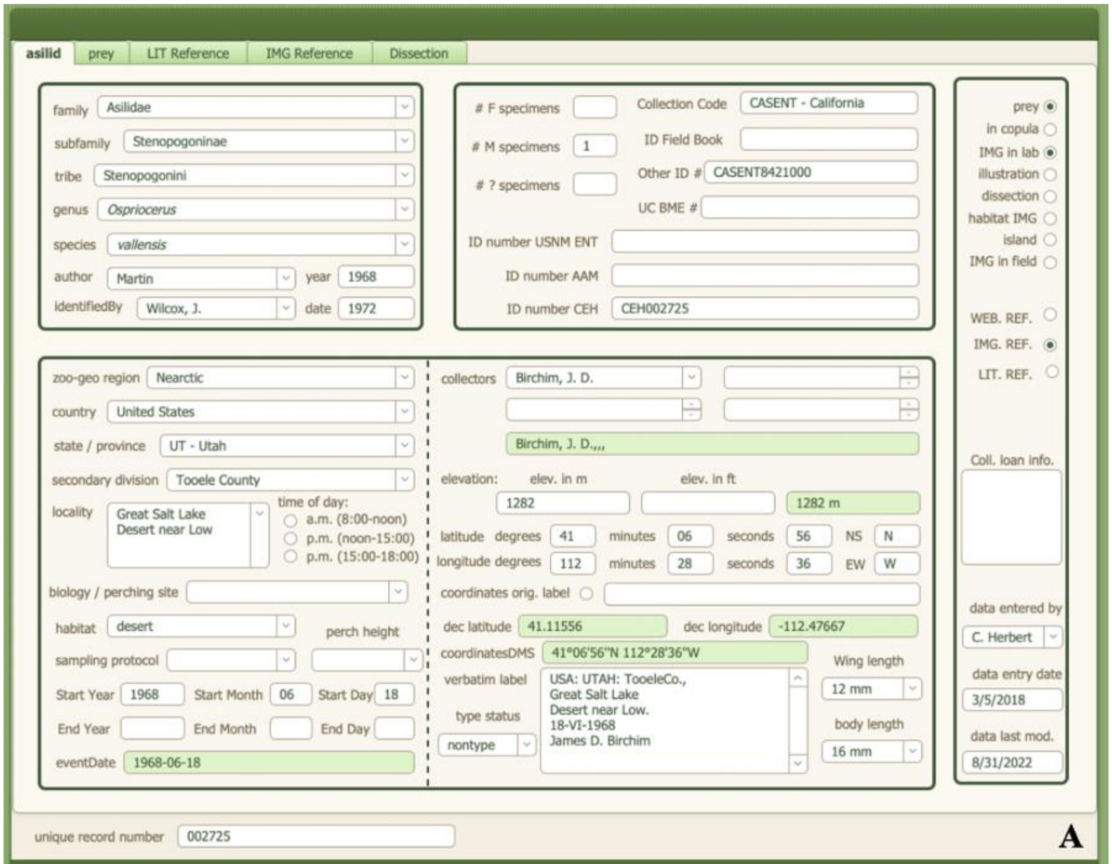
Prey record determination

Prey items were mainly pinned together with the individual predators on the same pin with the prey underneath (Fig. 2.1); however, prey items were pinned separately, in some cases. Large prey was usually pinned underneath or on a separate pin next to the predator. If the prey was pinned separately, it would have identical identification numbers and references to the predator indicated on the label. Small prey items were often point mounted, double mounted on a minute pin, or placed in a cellulose pill capsule and pinned below the predator. Some prey collections, such as Dr. Steve Dennis's, were accumulated systematically by capturing the predator with its prey, identifying the predator in the field, releasing the predator, and retaining the prey record for reference. In this case, each prey specimen had the predator identification clearly labeled with the prey. Records were only included in this dataset if the predator and prey were clearly indicated. All prey items were identified to Order and Family level, with a few exceptions. A more precise identification was attempted when a prey species seemed to be particularly favored (> 30% of records). The author identified the majority of prey specimens, and primarily only to the family level.

Database

Records are locally stored in a custom FileMaker Pro database (Fig. 2.2A-C). The author developed this database to capture information and images of the predator and prey found in the collections. Due to this personal database being used for many years and different projects, there are some irrelevant fields to this study, so the author made a Microsoft Excel worksheet of only the relevant data (Table 2.1, Supplemental material 2.1). Data from the Excel worksheet is publicly available through the publishing of this manuscript, as well as stored in FigShare in CSV format for future study.

In all instances, specimens were dry-mounted on pins. Morphological features were examined with a stereo microscope provided by the hosting museum. Label information was entered into the database, and a unique record number (catalogNumber) was either recorded or provided by the custodial institution. The catalogNumbers provided reference the unique record number from the database (CEH######). In most cases, the labels, and specimens were photographed using an iPhone SE or iPhone 13 for confirmed identification after the initial visit. For the USNM collection, the labels and specimens were not photographed because they were entered into the database before the author started taking pictures for this project. The predator and prey specimens in the USNM collection have been meticulously curated and separated from the primary collection for ease of access in case verification is needed.



family: Asilidae
subfamily: Stenopogoninae
tribe: Stenopogonini
genus: *Ospriocerus*
species: *vallensis*
author: Martin
year: 1968
identifiedBy: Wilcox, J.
date: 1972

\# F specimens:
\# M specimens: 1
\# ? specimens:
Collection Code: CASENT - California
ID Field Book:
Other ID #: CASENT8421000
UC BME #:
ID number USNM ENT:
ID number AAM:
ID number CEH: CEH002725

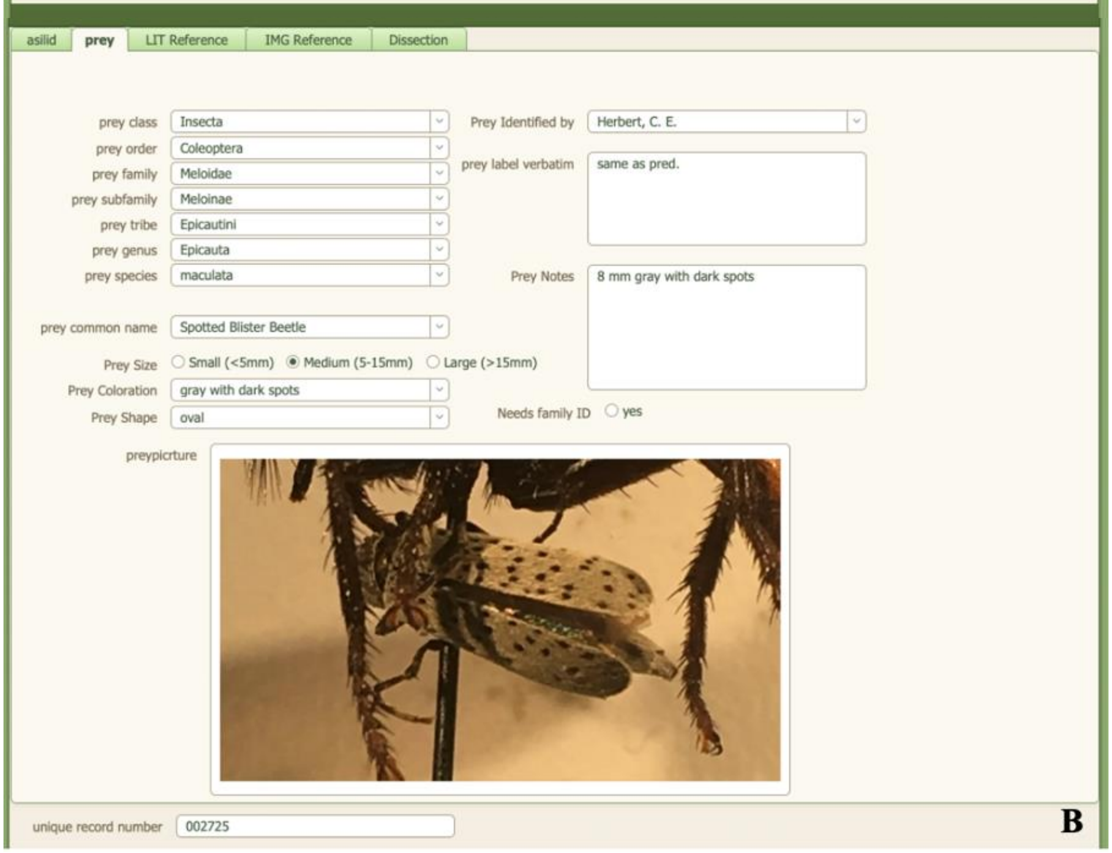
prey ●
in copula ○
IMG in lab ●
illustration ○
dissection ○
habitat IMG ○
island ○
IMG in field ○
WEB. REF. ○
IMG. REF. ●
LIT. REF. ○

zoo-geo region: Nearctic
country: United States
state / province: UT - Utah
secondary division: Tooele County
locality: Great Salt Lake Desert near Low
time of day:
○ a.m. (8:00-noon)
○ p.m. (noon-15:00)
○ p.m. (15:00-18:00)
biology / perching site:
habitat: desert
perch height:
sampling protocol:
Start Year: 1968
Start Month: 06
Start Day: 18
End Year:
End Month:
End Day:
eventDate: 1968-06-18

collectors: Birchim, J. D.
Birchim, J. D.,,,
elevation: elev. in m: 1282
elev. in ft:
1282 m
latitude degrees: 41 minutes: 06 seconds: 56 NS: N
longitude degrees: 112 minutes: 28 seconds: 36 EW: W
coordinates orig. label ○
dec latitude: 41.11556
dec longitude: -112.47667
coordinatesDMS: 41°06'56"N 112°28'36"W
verbatim label:
USA: UTAH: TooeleCo.,
Great Salt Lake
Desert near Low.
18-VI-1968
James D. Birchim
type status: nontype
Wing length: 12 mm
body length: 16 mm

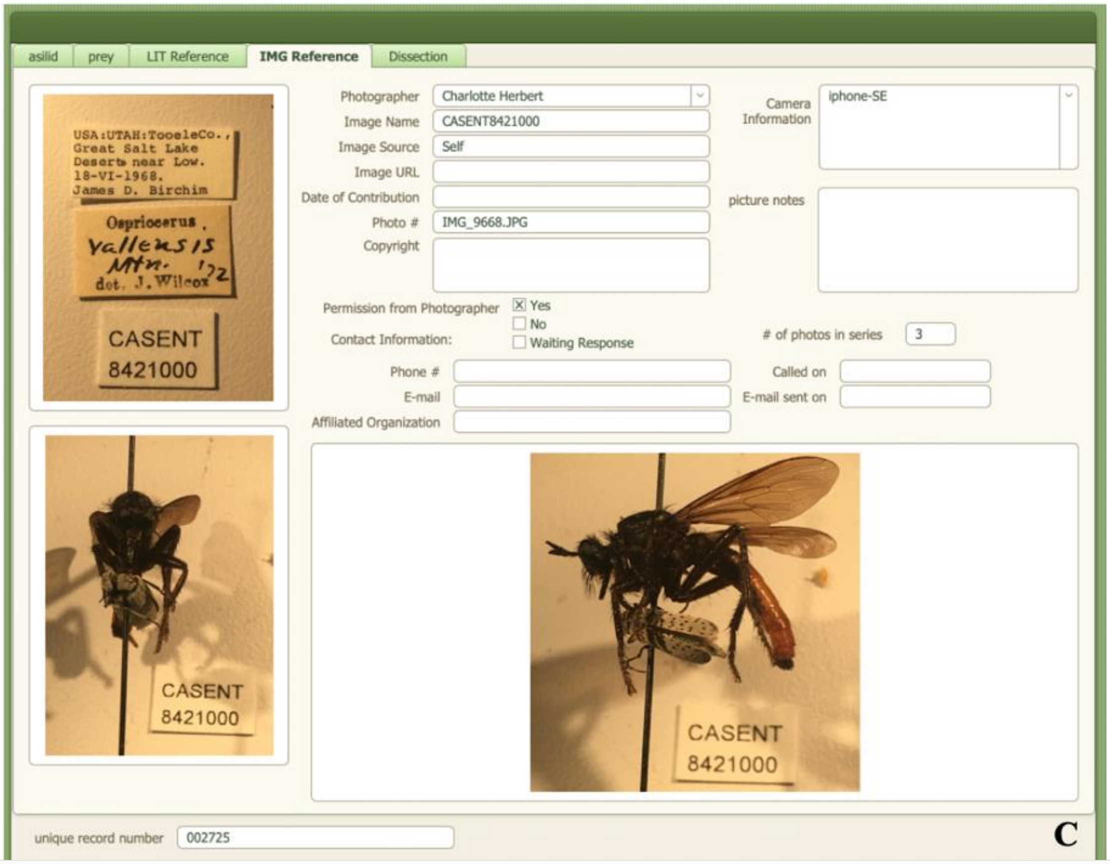
Coll. loan info.:
data entered by: C. Herbert
data entry date: 3/5/2018
data last mod.: 8/31/2022

unique record number: 002725



prey class: Insecta
prey order: Coleoptera
prey family: Meloidae
prey subfamily: Meloinae
prey tribe: Epicautini
prey genus: Epicauta
prey species: maculata
prey common name: Spotted Blister Beetle
Prey Size: ○ Small (<5mm) ● Medium (5-15mm) ○ Large (>15mm)
Prey Coloration: gray with dark spots
Prey Shape: oval
Prey Identified by: Herbert, C. E.
prey label verbatim: same as pred.
Prey Notes: 8 mm gray with dark spots
Needs family ID ○ yes
preypicrture

unique record number: 002725



Photographer: Charlotte Herbert
Image Name: CASENT8421000
Image Source: Self
Image URL:
Date of Contribution:
Photo #: IMG_9668.JPG
Copyright:
Camera Information: iphone-SE
picture notes:
Permission from Photographer: ☒ Yes ☐ No ☐ Waiting Response
Contact Information:
\# of photos in series: 3
Phone #:
E-mail:
Affiliated Organization:
Called on:
E-mail sent on:
unique record number: 002725

Figure 2.2.

Screenshot of the original FileMaker Pro Asilidae predator and prey database used to capture specimen identification for predator and prey, label data, collection information, and photograph reference.
A: Asilid tab for predator and data label information
B: Prey tab for prey identification and information
C: Image tab for photographs and information

Placing specimen information into the database

Many fields in the database match the Darwin Core Standards to facilitate the sharing of biological diversity (Wieczorek et al. 2012). However, some fields were modified to fit this project's scope, such as preyFamily. The nomenclature fields with current and valid names follow the standards of Dikow 2009. If the name was changed, the verbatim name on the label was retained in the "previousIdentifications" field. Empty fields indicate missing data on labels.

All localities and elevations not stated explicitly on the original label were estimated using Google Earth Pro version 7.3.4.8248 (Google Earth Pro 2021) and noted as estimates in the specimen record datasheet. SimpleMappr was used to generate the distribution map of specimens recorded in the United States of America (Shorthouse 2010).

Table 2.1.

The thirty-six data entry fields in the Microsoft Excel spreadsheet (Supplemental Material 2.1). Fields are paired down from the original FileMaker database to only relevant data.

DATA ENTRY FIELD	DEFINITION
catalogNumber	A unique identifier for the record. Preferable from custodial institution.
institutionCode	The acronym in use by the institution having custody of the object(s) or information referred to in the record
family	The full scientific name of the family in which the predator is classified.
subfamily	The full scientific name of the subfamily in which the predator is classified.
tribe	The full scientific name of the tribe in which the predator is classified. If unplaced, notes included on if the genus was included for study in Dikow 2009 the most current classification for the family.
genericName	The full scientific name of the genus (without authorship) in which the predator is classified.
specificEpithet	The name of the species epithet in which the predator is identified as.
scientificNameAuthorship	The authorship information for the predator’s scientific name formatted to the applicable nomenclatural code.
sex	The sex of the predator represented in the occurrence.
higherGeorgraphyID	Zoogeographical region within in which the event occurred.
country	The name of the country or major administrative unit in which the event occurred.
stateProvince	The name of the first order administrative region within the country in which the event occurred.
county	The name of the smaller administrative region than stateProvince in which the event occurred.
locality	Municipality and specific locality in which the event occurred.
verbatimCoordinates	The verbatim original spatial coordinates of the location on the labels.

coordinatesDMS	The geographic location both latitude and longitude (in degrees, minutes, and seconds) estimated using Google Earth Pro.
decimalLatitude	The geographic latitude (in decimal degrees) using Google Earth Pro.
decimalLongitude	The geographic longitude (in decimal degrees) using Google Earth Pro.
elevationInMeters	Estimated elevation in meters. The digital elevation model (DEM) was used to calculate estimated elevation.
elevationVerbatim	The original elevation found on specimen label.
eventDate	The date or interval during which the event occurred. Following the Darwin Core format of Year-Month-Day. If the event occurred over an interval, it is indicated with /.
recordedBy	List of collector(s) or organization(s) associated with the record. Formatted with full last name first, followed by initials when available.
verbatimLabel	The original text found on specimen label.
preyClass	The full scientific name of the class in which the prey is classified.
preyOrder	The full scientific name of the order in which the prey is classified.
preyFamily	The full scientific name of the family in which the prey is classified.
preySubfamily	The full scientific name of the subfamily in which the prey is classified.
preyTribe	The full scientific name of the tribe in which the prey is classified.
preyGenericName	The full scientific name of the genus (without authorship) in which the prey is classified.
preySpecificEpithet	The name of the species epithet in which the prey is identified as.
preyIdentifiedBy	The name of the person who assigned the identification to the prey.
preyCommonName	The common name associated with the prey identification
preyNotes	Comments or notes about the prey
typeStatus	The nomenclatural type applied to the predator
previousIdentifications	A list of previous assignments of names to the organism.
eventRemarks	Comments or notes about the Event

Incorporation of Lavigne (2016) database

Dr. Lavigne created a publicly available predator-prey database (https://www.geller-grimm.de/catalog/lavigne.htm), mainly compiled from Asilidae literature. The database, as of 2016, has 14,387 records and is updated on a semi-regular basis. Some predator-prey records within the database are unpublished and based on specimens collected in the field. Because there is no specimen-specific data for each record, it is not easy to know whether some overlap with this dataset. If errors or duplications are found in this dataset, the author would greatly appreciate them reported to ceherb11@gmail.com.

Results

Geographical coverage

The data support the broad distribution of species in Asilidae across the Americas and Asia. Specifically, specimens were recorded from the following countries: Argentina (2), Australia (7), Bahamas (1), Brazil (3), British Guiana (2), Canada (7), Chile (3), Costa Rica (20), Cuba (2), Dominican Republic (3), Honduras (1), Malaysia (1), Mexico (18), Mozambique (1), Namibia (3), Panama (4), South Africa (3), Thailand (1), United States of America (3332), Uruguay (1), Venezuela (1), Zimbabwe (4), and Unknown (1). Coverage was best for the continental United States because all the collections visited reside there (Fig. 2.3). Coastal United States was particularly well represented by collection visiting. This most likely has more to do with the individual location of more extensive collections such as CASENT and USNM. If collections held worldwide could be surveyed, the number of records in other countries is expected to expand.

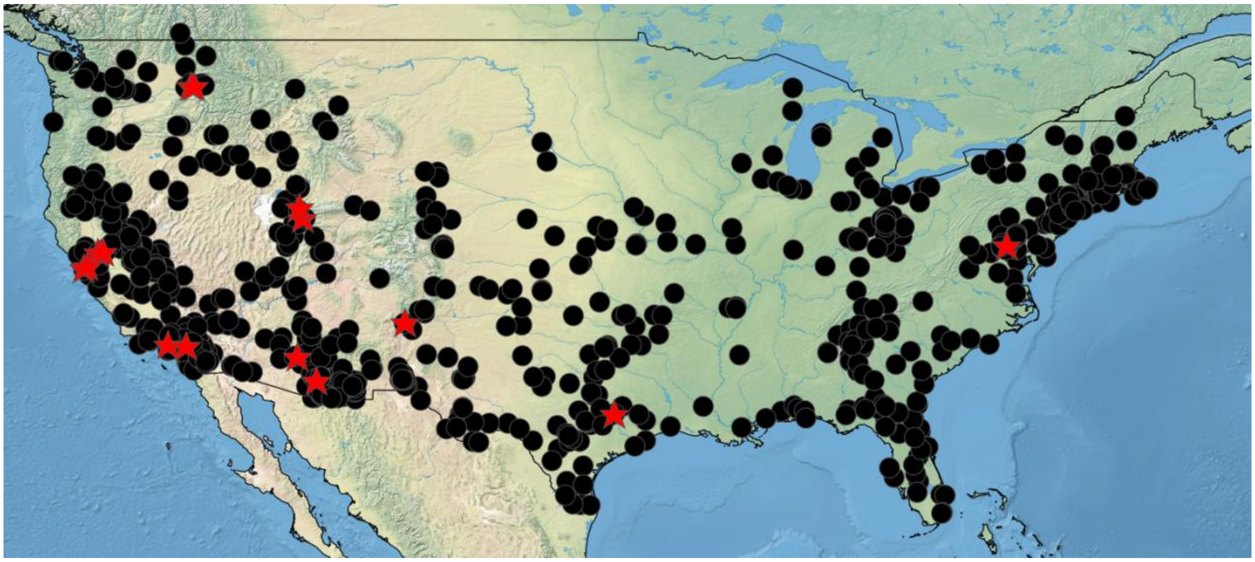


Figure 2.3.

Distribution of Asilidae prey records within the continental United States of America. Black circles represent 3,332 records from sixteen U.S. entomological collections (red stars).

Representation

Twelve of the 14 currently recognized subfamilies are represented within this dataset. The subfamilies with the most records (number in brackets) in decreasing order are: Asilinae (1,775), Dasypogoninae (528), Brachyrhopalinae (267), Trigonomiminae (267), Stenopogoninae (265), Laphriinae (151), Stichopogoninae (138), Dioctriinae (14), Ommatiinae (8), Leptogastrinae (6), Bathypogoninae (1), and Willistonininae (1). The missing subfamilies are: Phellinae and Tillobromatinae, which are relatively small subfamilies with ten and fifty-four valid species/subspecies recognized. A complete list of Taxa included is shown in Table 2.2. The number of prey items recorded for each subfamily is shown in Table 2.3, as well as the percentage of their prey represented by each arthropod order. The exceptionally high number of prey records for Asilinae probably relates to the abundance of individuals. The genera

Promachus (418), *Efferia* (332), and *Proctacanthus* (374) make up over 60% of Asilinae, with excellent representation in this dataset. Dasypogoninae also shows this trend with the large and charismatic genus, *Diogmites* (468), which accounts for over 88% of the subfamily's representation. Bathypogoninae and Willistonininae both only have one prey record, which is not surprising because Bathypogoninae is mainly an Australasian subfamily, and this zoogeographical region is generally poorly represented in U.S. collections. Willistonininae are found in the Afrotropical, Nearctic, and Palaearctic regions. However, of the two genera found in the U.S. (*Ablautus* and *Willistonina*), *Ablautus* tend to be small, fast-flying, and like desert habitat, which may reflect why they are not well represented in this sampling. The collector may not have been able to see the small prey associated with the collecting event. *Willistonina* is only known from a single species and is rarely collected. Though common in the U.S., Leptogastrinae may have a low prey number because of their small and gracile bodies. They are often caught while net sweeping grassy fields and not actually seen feeding.

Table 2.2.

Assassin fly (Diptera: Asilidae) taxa included in dataset found in Supplemental Material 2.1. Classification follows Dikow 2009a. Asterisk indicates specimens from this study, at least partially, residing outside the U.S.A.

Subfamily	**Tribe**	**Scientific Name**
Asilinae	Apocleini	*Megaphorus acrus* (Curran, 1931)
Asilinae	Apocleini	*Megaphorus clausicellus* (Macquart, 1850)
Asilinae	Apocleini	*Megaphorus frusta flavida* (Cole, 1964)
Asilinae	Apocleini	*Megaphorus frusta frusta* (Pritchard, 1935)
Asilinae	Apocleini	*Megaphorus laphroides* (Wiedemann, 1828)
Asilinae	Apocleini	*Megaphorus minutus* (Macquart, 1935)
Asilinae	Apocleini	*Megaphorus prudens* (Pritchard, 1935)
Asilinae	Apocleini	*Megaphorus pulcher* (Pritchard, 1935)
Asilinae	Apocleini	*Megaphorus willistoni* (Cole, 1964)
Asilinae	Apocleini	*Promachus albifacies* Williston, 1885
Asilinae	Apocleini	*Promachus aldrichii* Hine, 1911
Asilinae	Apocleini	*Promachus bastardii* (Macquart, 1838)

Asilinae	Apocleini	*Promachus fitchii* (Osten Sacken, 1878)
Asilinae	Apocleini	*Promachus giganteus* Hine, 1911
Asilinae	Apocleini	*Promachus hinei* Bromley, 1931
Asilinae	Apocleini	*Promachus magnus* Bellardi, 1861
Asilinae	Apocleini	*Promachus minusculus* Hine, 1911
Asilinae	Apocleini	*Promachus nigrialbus* Martin, 1970
Asilinae	Apocleini	*Promachus oklahomensis* Pritchard, 1935
Asilinae	Apocleini	*Promachus princeps* Williston, 1885
Asilinae	Apocleini	*Promachus rufipes* (Fabricius, 1775) *
Asilinae	Apocleini	*Promachus sackeni* Hine, 1911
Asilinae	Apocleini	*Promachus smithi* Parui & Joseph, 1994
Asilinae	Apocleini	*Promachus texanus* Bromley, 1934
Asilinae	Apocleini	*Promachus truquii* Bellardi, 1861
Asilinae	Apocleini	*Promachus vertebratus* (Say, 1828)
Asilinae	Asilini	*Asilus sericeus* Say, 1823
Asilinae	Efferia group	*Efferia aestuans* (Linnaeus, 1763)
Asilinae	Efferia group	*Efferia albibarbis* (Macquart, 1838) *
Asilinae	Efferia group	*Efferia anomala* (Bellardi, 1861) *
Asilinae	Efferia group	*Efferia apicalis* (Wiedemann, 1821)
Asilinae	Efferia group	*Efferia argentifrons* (Hine, 1911)
Asilinae	Efferia group	*Efferia argyrosoma* (Hine, 1911)
Asilinae	Efferia group	*Efferia arida* (Williston, 1893)
Asilinae	Efferia group	*Efferia armata* (Hine, 1918)
Asilinae	Efferia group	*Efferia basingeri* Wilcox, 1966
Asilinae	Efferia group	*Efferia benedicti* (Bromley, 1940)
Asilinae	Efferia group	*Efferia bicaudate* (Hine, 1919)
Asilinae	Efferia group	*Efferia bimaculata* (Bellardi, 1861) *
Asilinae	Efferia group	*Efferia californica* (Schaeffer, 1916)
Asilinae	Efferia group	*Efferia cana* (Hine, 1916)
Asilinae	Efferia group	*Efferia candida* Coquillett, 1893
Asilinae	Efferia group	*Efferia canella* (Bromley, 1934)
Asilinae	Efferia group	*Efferia femorata* (Macquart, 1838)
Asilinae	Efferia group	*Efferia frewingi* Wilcox, 1966
Asilinae	Efferia group	*Efferia grandis* (Hine, 1919)
Asilinae	Efferia group	*Efferia harveyi* (Hine, 1919)
Asilinae	Efferia group	*Efferia helenae* (Bromley, 1951)
Asilinae	Efferia group	*Efferia inflata* (Hine, 1919)
Asilinae	Efferia group	*Efferia kansensis* (Hine, 1919)
Asilinae	Efferia group	*Efferia luna* Wilcox, 1966
Asilinae	Efferia group	*Efferia nemotalis* Hine, 1911
Asilinae	Efferia group	*Efferia neosimilis* Forbes, 1987
Asilinae	Efferia group	*Efferia rapax* (Osten Sacken, 1887)
Asilinae	Efferia group	*Efferia tabescens* (Banks, 1919)
Asilinae	Efferia group	*Efferia texana* (Banks, 1919) *
Asilinae	Efferia group	*Efferia tolandi* Wilcox, 1966

Asilinae	Efferia group	*Efferia tricella* (Bromley, 1951)
Asilinae	Efferia group	*Efferia triton* (Osten Sacken, 1887) *
Asilinae	Efferia group	*Efferia truncate* (Hine, 1911)
Asilinae	Machimini	*Machimus comans* Oldroyd, 1940
Asilinae	Machimini	*Machimus erythocnemius* (Hine, 1909)
Asilinae	Machimini	*Machimus notatus* (Wiedemann, 1828)
Asilinae	Machimini	*Machimus novaescotiae* (Macquart, 1847)
Asilinae	Machimini	*Machimus occidentalis* (Hine, 1909)
Asilinae	Machimini	*Machimus paropus* (Walker, 1849)
Asilinae	Machimini	*Machimus sadyates* (Walker, 1849)
Asilinae	Unplaced	*Amblyonychus trapezoidalis* (Bellardi, 1861) *
Asilinae	Unplaced	*Eccritosia rubriventris* (Macquart, 1850) *
Asilinae	Unplaced	*Eccritosia zamon* (Townsend, 1895)
Asilinae	Unplaced	*Glaphyropyga dryas* Fisher & Hespenheide, 1982 *
Asilinae	Unplaced	*Mallophora bomboides* (Wiedemann, 1821)
Asilinae	Unplaced	*Mallophora fautrix* Osten Sacken, 1887 *
Asilinae	Unplaced	*Mallophora leschenaultia* Macquart, 1838
Asilinae	Unplaced	*Mallophora macquarti* Rondani, 1850 *
Asilinae	Unplaced	*Mallophora minos* (Wiedemann, 1824) *
Asilinae	Unplaced	*Mallophora orcina* (Wiedemann, 1828)
Asilinae	Unplaced	*Neoitamus brevicomus* (Hine, 1909) *
Asilinae	Unplaced	*Neoitamus flavofemoratus* (Hine, 1909)
Asilinae	Unplaced	*Neoitamus orphne* (Walker, 1849)
Asilinae	Unplaced	*Nevadasilus auriannulatus* (Hine, 1906) *
Asilinae	Unplaced	*Polacantha composita* (Hine, 1918)
Asilinae	Unplaced	*Proctacanthella cacopiloga* (Hine, 1909)
Asilinae	Unplaced	*Proctacanthella exquisite* (Osten Sacken, 1887)
Asilinae	Unplaced	*Proctacanthella leucopogon* (Williston, 1893)
Asilinae	Unplaced	*Proctacanthella willistoni* Fisher & Wilcox, 1987
Asilinae	Unplaced	*Triorla interrupta* (Macquart, 1834)
Asilinae	Unplaced	*Wyliea mydas* (Brauer, 1885)
Asilinae	Unplaced	*Negasilus astutus* (Williston, 1893)
Asilinae	Unplaced	*Proctacanthus brevipennis* (Wiedemann, 1828)
Asilinae	Unplaced	*Proctacanthus coquillettii* Hine, 1911
Asilinae	Unplaced	*Proctacanthus darlingtonia* Curran, 1951 *
Asilinae	Unplaced	*Proctacanthus dominicanus* Curran, 1951 *
Asilinae	Unplaced	*Proctacanthus duryi* Hine, 1911
Asilinae	Unplaced	*Proctacanthus fulviventris* Macquart, 1850
Asilinae	Unplaced	*Proctacanthus gracilis* Bromley, 1928
Asilinae	Unplaced	*Proctacanthus heros* (Wiedemann, 1828)
Asilinae	Unplaced	*Proctacanthus hinei* Bromley, 1928
Asilinae	Unplaced	*Proctacanthus lerneri* Curran, 1951 *
Asilinae	Unplaced	*Proctacanthus longus* (Wiedemann, 1821)
Asilinae	Unplaced	*Proctacanthus micans* Schiner, 1867
Asilinae	Unplaced	*Proctacanthus milbertii* Macquart, 1838

Asilinae	Unplaced	*Proctacanthus nearno* Martin, 1962 *
Asilinae	Unplaced	*Proctacanthus nigriventris* Macquart, 1838
Asilinae	Unplaced	*Proctacanthus nigrofemoratus* Hine, 1911
Asilinae	Unplaced	*Proctacanthus occidentalis* Hine, 1911
Asilinae	Unplaced	*Proctacanthus philadelphicus* Macquart, 1838
Asilinae	Unplaced	*Proctacanthus rodecki* James, 1933
Asilinae	Unplaced	*Proctacanthus rufus* Williston, 1885
Bathypogoninae	Bathypogonini	*Bathypogon spp.*
Brachyrhopalinae	Brachyrhopalini	*Austrosaropogon claviger* Hardy, 1926 *
Brachyrhopalinae	Ceraturgini	*Ceraturgus cruciatus* (Say, 1823)
Brachyrhopalinae	Ceraturgini	*Ceraturgus fasciatus* Walker, 1849
Brachyrhopalinae	Chrysopogonini	*Chrysopogon albopunctatus* (Macquart, 1846) *
Brachyrhopalinae	Chrysopogonini	*Chrysopogon crabroniformis* Roeder, 1881 *
Brachyrhopalinae	Cyrtopogonini	*Cyrtopogon curtistylus* Curran, 1923
Brachyrhopalinae	Cyrtopogonini	*Cyrtopogon falto* (Walker, 1849)
Brachyrhopalinae	Cyrtopogonini	*Cyrtopogon inversus* Curran, 1923
Brachyrhopalinae	Cyrtopogonini	*Cyrtopogon marginalist* Loew, 1866
Brachyrhopalinae	Cyrtopogonini	*Cyrtopogon montanus montanus* Loew, 1874
Brachyrhopalinae	Cyrtopogonini	*Cyrtopogon pulcher* Back 1909
Brachyrhopalinae	Cyrtopogonini	*Cyrtopogon willistoni* Curran, 1922
Brachyrhopalinae	Unplaced	*Cophura getzendaneri* Wilcox, 1959
Brachyrhopalinae	Unplaced	*Cophura pollinose* Curran, 1930
Brachyrhopalinae	Unplaced	*Heteropogon johnsoni* (Back, 1904)
Brachyrhopalinae	Unplaced	*Heteropogon martini* Wilcox, 1965
Brachyrhopalinae	Unplaced	*Heteropogon rubrifasciatus* Bromley, 1931
Brachyrhopalinae	Unplaced	*Heteropogon spatulatus* Pritchard, 1935
Brachyrhopalinae	Unplaced	*Holopogon guttulus* (Wiedemann, 1821)
Brachyrhopalinae	Unplaced	*Holopogon phaeonotus* Loew, 1874
Brachyrhopalinae	Unplaced	*Holopogon snowi* Back 1909
Brachyrhopalinae	Unplaced	*Nicocles pictus* (Loew, 1866)
Brachyrhopalinae	Unplaced	*Nicocles politus* (Say, 1823)
Dasypogoninae	Blepharepiini	*Blepharepium annulatum* (Bigot, 1857) *
Dasypogoninae	Blepharepiini	*Blepharepium cajennense coarctatum* (Perty, 1833)
Dasypogoninae	Blepharepiini	*Blepharepium sonorense* Papavero & Bernardi, 1973 *
Dasypogoninae	Megapodini	*Deromyia fuscipennis* (Blanchard, 1852) *
Dasypogoninae	Megapodini	*Neolaparus spp.**
Dasypogoninae	Saropogonini	*Saropogon abbreviatus* Johnson, 1903
Dasypogoninae	Saropogonini	*Saropogon albifrons* Back, 1904
Dasypogoninae	Saropogonini	*Saropogon bryanti* Wilcox, 1966
Dasypogoninae	Saropogonini	*Saropogon combustus* Loew, 1874
Dasypogoninae	Saropogonini	*Saropogon coquillettii* Back, 1909
Dasypogoninae	Saropogonini	*Saropogon dispar* Coquillett, 1902
Dasypogoninae	Saropogonini	*Saropogon fletcheri* Bromley, 1934
Dasypogoninae	Saropogonini	*Saropogon hypomelas* (Loew, 1966)
Dasypogoninae	Saropogonini	*Saropogon luteus* Coquillett, 1904

Dasypogoninae	Saropogonini	*Saropogon senex* Osten Sacken, 1887 *
Dasypogoninae	Unplaced	*Allopogon spp.**
Dasypogoninae	Unplaced	*Diogmites aberrans* (Wiedemann, 1821) *
Dasypogoninae	Unplaced	*Diogmites angustipennis* Loew, 1866
Dasypogoninae	Unplaced	*Diogmites basalis* (Walker, 1851)
Dasypogoninae	Unplaced	*Diogmites bilobatus* Barnes, 2010
Dasypogoninae	Unplaced	*Diogmites coloradensis* (James, 1933)
Dasypogoninae	Unplaced	*Diogmites contortus* Bromley, 1936
Dasypogoninae	Unplaced	*Diogmites crudelis* Bromley, 1936
Dasypogoninae	Unplaced	*Diogmites discolor* Loew, 1866
Dasypogoninae	Unplaced	*Diogmites esuriens* Bromley, 1936
Dasypogoninae	Unplaced	*Diogmites fragilis* Bromley, 1936
Dasypogoninae	Unplaced	*Diogmites misellus* Loew, 1866
Dasypogoninae	Unplaced	*Diogmites missouriensis* Bromley, 1951
Dasypogoninae	Unplaced	*Diogmites neoternatus* (Bromley, 1931)
Dasypogoninae	Unplaced	*Diogmites nigripennis* (Macquart, 1847) *
Dasypogoninae	Unplaced	*Diogmites platypterus* Loew, 1866
Dasypogoninae	Unplaced	*Diogmites properans* Bromley, 1936
Dasypogoninae	Unplaced	*Diogmites sallei* (Bellardi, 1861)
Dasypogoninae	Unplaced	*Diogmites salutans* Bromley, 1936
Dasypogoninae	Unplaced	*Diogmites texanus* Bromley, 1934
Dasypogoninae	Unplaced	*Hodophylax basingeri* Pritchard, 1938
Dasypogoninae	Unplaced	*Omninablautus spp.*
Dasypogoninae	Unplaced	*Theromyia murina* (Philippi, 1865) *
Dioctriinae	Dioctriini	*Eudioctria doanei* (Melander, 1924)
Dioctriinae	Dioctriini	*Dioctria hyalipennis* (Fabricius, 1794)
Dioctriinae	Unplaced	*Myelaphus labicornis* (Osten Sacken, 1877)
Laphriinae	Andrenosomatini	*Andrenosoma fulvicaudum* (Say, 1823)
Laphriinae	Andrenosomatini	*Andrenosoma rubidium* (Williston, 1901)
Laphriinae	Andrenosomatini	*Dasyllis spp.**
Laphriinae	Andrenosomatini	*Pilica formidolosa* Walker, 1860 *
Laphriinae	Atomosiini	*Atomosia puella* (Wiedemann, 1828)
Laphriinae	Atomosiini	*Atomosia tenuis* Curran, 1930 *
Laphriinae	Atomosiini	*Atomosia tibialis* Macquart, 1846 *
Laphriinae	Atomosiini	*Cerotainia albipilosa* Curran, 1930
Laphriinae	Atomosiini	*Cerotainia ornatipes* James, 1953 *
Laphriinae	Atomosiini	*Smeringolaphria spp.* *
Laphriinae	Hoplistomerini	*Trichardis picta* Hermann, 1906 *
Laphriinae	Laphriini	*Lampria bicolor* (Wiedemann, 1828)
Laphriinae	Laphriini	*Laphria affinis* Macquart, 1855
Laphriinae	Laphriini	*Laphria apila* (Bromley, 1951)
Laphriinae	Laphriini	*Laphria astur* Osten Sacken, 1887 *
Laphriinae	Laphriini	*Laphria champlainii* (Walton, 1910)
Laphriinae	Laphriini	*Laphria columbica* Walker, 1866
Laphriinae	Laphriini	*Laphria divisor* (Banks, 1917)

Laphriinae	Laphriini	*Laphria fernaldi* (Back, 1904)
Laphriinae	Laphriini	*Laphria flavicollis* Say, 1824
Laphriinae	Laphriini	*Laphria floridensis* (Bromley, 1950)
Laphriinae	Laphriini	*Laphria grossa* (Fabricius, 1775)
Laphriinae	Laphriini	*Laphria posticata* Say, 1824 *
Laphriinae	Laphriini	*Laphria royalensis* (Bromley, 1950)
Laphriinae	Laphriini	*Laphria saffrana* Fabricius, 1805
Laphriinae	Laphriini	*Laphria sicula* McAttee, 1919
Laphriinae	Laphriini	*Laphria thoracica* Fabricius, 1805
Laphriinae	Laphriini	*Laphria virginica* (Banks, 1917)
Laphriinae	Laphriini	*Laphria vorax* (Bromley, 1929)
Laphriinae	Unplaced	*Psilocurus nudiusculus* Loew, 1874
Leptogastrinae	Leptogastrini	*Beameromyia bifida* (Hardy, 1942)
Leptogastrinae	Leptogastrini	*Beameromyia lunula* Martin, 1957
Leptogastrinae	Leptogastrini	*Leptogaster arida* Cole, 1919
Leptogastrinae	Leptogastrini	*Leptogaster incisuralis* Loew, 1862
Ommatiinae	Ommatiini	*Ommatius floridensis* Bullington & Lavigne, 1984
Ommatiinae	Ommatiini	*Ommatius tibialis* (Say, 1823)
Stenopogoninae	Cyrtopogonini	*Callinicus calcaneus* Loew, 1872
Stenopogoninae	Cyrtopogonini	*Callinicus pictitarsis* (Bigot, 1878)
Stenopogoninae	Cyrtopogonini	*Callinicus pollenius* (Cole, 1919)
Stenopogoninae	Cyrtopogonini	*Callinicus vittatus* Wilcox, 1936
Stenopogoninae	Cyrtopogonini	*Eucyrtopogon maculosus* (Coquillett, 1904)
Stenopogoninae	Cyrtopogonini	*Itolia maculata* Wilcox, 1936
Stenopogoninae	Enigmomorphini	*Microstylum galactodes* Loew, 1866
Stenopogoninae	Enigmomorphini	*Microstylum morosum* Loew, 1872
Stenopogoninae	Enigmomorphini	*Prolepsis tristis* (Walker, 1851)
Stenopogoninae	Stenopogonini	*Gonioscelis bykanistes* Londt, 2004 *
Stenopogoninae	Stenopogonini	*Ospriocerus aeacus* (Wiedemann, 1828)
Stenopogoninae	Stenopogonini	*Ospriocerus latipennis* (Loew, 1866)
Stenopogoninae	Stenopogonini	*Ospriocerus nitens* (Coquillett, 1904)
Stenopogoninae	Stenopogonini	*Ospriocerus tenebrosus* (Coquillett, 1904)
Stenopogoninae	Stenopogonini	*Ospriocerus vallensis* Martin, 1968
Stenopogoninae	Stenopogonini	*Scleropogon bradleyi* (Bromley, 1937)
Stenopogoninae	Stenopogonini	*Scleropogon coyote* (Bromley, 1931) *
Stenopogoninae	Stenopogonini	*Scleropogon dispar* (Bromley, 1937)
Stenopogoninae	Stenopogonini	*Scleropogon indistinctus* (Bromley, 1937)
Stenopogoninae	Stenopogonini	*Scleropogon neglectus* (Bromley, 1931)
Stenopogoninae	Stenopogonini	*Scleropogon picticornis* Loew, 1866
Stenopogoninae	Stenopogonini	*Scleropogon subulatus* (Wiedemann, 1828)
Stenopogoninae	Stenopogonini	*Stenopogon breviusculoides* Bromley, 1937
Stenopogoninae	Stenopogonini	*Stenopogon breviusculus* Loew, 1872
Stenopogoninae	Stenopogonini	*Stenopogon californiae* (Walker, 1849)
Stenopogoninae	Stenopogonini	*Stenopogon cazieri* Brookman, 1941
Stenopogoninae	Stenopogonini	*Stenopogon engelhardti* Bromley, 1937

Stenopogoninae	Stenopogonini	*Stenopogon gratus* Loew, 1872
Stenopogoninae	Stenopogonini	*Stenopogon inquinatus* Loew, 1866 *
Stenopogoninae	Stenopogonini	*Stenopogon inyae* Wilcox, 1971
Stenopogoninae	Stenopogonini	*Stenopogon jubatoides* Bromley, 1937
Stenopogoninae	Stenopogonini	*Stenopogon jubatus* (Coquillett, 1904)
Stenopogoninae	Stenopogonini	*Stenopogon macswaini* Wilcox, 1971
Stenopogoninae	Stenopogonini	*Stenopogon martini* Bromley, 1937
Stenopogoninae	Stenopogonini	*Stenopogon neojubatus* Wilcox & Martin, 1945
Stenopogoninae	Stenopogonini	*Stenopogon obscuriventris* Loew, 1872
Stenopogoninae	Stenopogonini	*Stenopogon rufibarbis* Bromley, 1931
Stenopogoninae	Stenopogonini	*Stenopogon wilcoxi* Bromley, 1937
Stenopogoninae	Unplaced	*Remotomyia spp.* *
Stenopogoninae	Unplaced	*Neoscleropogon spp.* *
Stichopogoninae	Stichopogonini	*Stichopogon argenteus* (Say, 1823)
Stichopogoninae	Stichopogonini	*Stichopogon trifasciatus* (Say, 1823)
Stichopogoninae	Unplaced	*Lasiopogon tetragrammus* Loew, 1847
Trigonomiminae	Trigonomimini	*Holcocephala abdominalis* Say, 1823
Trigonomiminae	Trigonomimini	*Holcocephala calva* (Loew, 1872)
Trigonomiminae	Trigonomimini	*Holcocephala fusca* Bromley, 1951
Trigonomiminae	Xenomyzini	*Damalis spp.* *
Willistonininae	Sisyrnodytini	*Ablautus mimus mimus* Osten Sacken, 1877

Table 2.3.

The arthropod prey of 3,412 Asilidae housed in 16 studied entomological collections in the USA. Abbreviations: Asi = Asilinae, Bat = Bathypogoninae, Bra = Brachyrhopalinae, Das = Dasypogoninae, Dio = Dioctriinae, Lap = Laphriinae, Lep = Leptogastrinae, Omm = Ommatiinae, Ste = Stenopogoninae, Sti = Stichopogoninae, Tri = Trigonomiminae, Wil = Willistonininae. Dominant data are presented in bold face.

Prey Order	**Total #**	**Asilidae Subfamily**											
	%	Asi	Bat	Bra	Das	Dio	Lap	Lep	Omm	Ste	Sti	Tri	Wil
Araneae	20	2	0	2	2	2	1	1	0	0	7	3	0
	0.6%	0.1%	0%	0.7%	0.4%	14.3%	0.7%	16.7%	0%	0%	5.1%	1.1%	0%
Blattodea	58	2	0	44	0	0	1	0	0	0	0	11	0
	1.7%	0.1%	0%	16.5%	0%	0%	0.7%	0%	0.0%	0%	0%	4.1%	0%
Coleoptera	304	141	0	17	29	2	**49**	0	2	39	1	24	0
	8.9%	8.0%	0%	6.4%	5.5%	14.3%	**32.5%**	0%	25.0%	14.7%	0.7%	9.0%	0%
Diptera	745	345	1	**88**	63	4	19	1	1	39	**90**	**93**	1
	21.8%	19.5%	100%	**33.0%**	11.9%	28.6%	12.6%	16.7%	12.5%	14.7%	**65.2%**	**34.8%**	100%
Hemiptera	248	105	0	47	30	1	13	0	**4**	23	2	23	0
	7.3%	5.9%	0%	17.6%	5.7%	7.1%	8.6%	0%	**50.0%**	8.7%	1.4%	8.6%	0%
Hymenoptera	**1583**	**832**	0	60	**384**	**5**	**65**	**3**	1	**123**	4	**106**	0
	46.4%	**47.1%**	0%	22.5%	**72.7%**	**35.7%**	**43.0%**	**50.0%**	12.5%	**46.4%**	2.9%	**39.7%**	0%
Lepidoptera	177	144	0	0	10	0	3	1	0	14	0	5	0
	5.2%	8.2%	0%	0%	1.9%	0%	2.0%	16.7%	0%	5.3%	0%	1.9%	0.0%
Neuroptera	18	12	0	2	3	0	0	0	0	1	0	0	0
	0.5%	0.7%	0%	0.7%	0.6%	0%	0%	0%	0%	0.4%	0%	0%	0%
Odonata	27	21	0	0	3	0	0	0	0	3	0	0	0
	0.8%	1.2%	0%	0%	0.6%	0%	0%	0%	0%	1.1%	0%	0%	0%
Orthoptera	222	162	0	0	4	0	0	0	0	23	33	0	0
	6.5%	9.2%	0%	0%	0.8%	0%	0%	0%	0%	8.7%	23.9%	0%	0%
Siphonaptera	1	0	0	0	0	0	0	0	0	0	0	1	0
	0.0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0.4%	0%
Thysanoptera	8	0	0	7	0	0	0	0	0	0	0	1	0
	0.2%	0%	0%	2.6%	0%	0%	0%	0%	0%	0%	0%	0.4%	0%
Trichoptera	1	0	0	0	0	0	0	0	0	0	1	0	0
	0.0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0.7%	0%	0%
Total #	3412	1766	1	267	528	14	151	6	8	265	138	267	1

Prey composition

Thirteen different arthropod orders have been recorded as prey. Over 99% of records are insects, with <1% of spiders as prey. Five insect orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, and Orthoptera) comprise over 90% of the prey records, with 3,102 specimens. Hymenoptera prey dominates the majority (8) of the Asilidae subfamilies. For each subfamily, a detailed analysis of prey records is provided below. Details are available in Supplemental Material 2.1 and Table 2.3.

Asilinae

The subfamily Asilinae has the largest number of prey records in this dataset, with 1,766. Two orders, Diptera and Hymenoptera, together make up 67% of their prey. At a subfamily level, Asilinae appears to be polyphagous. 112 species in 19 genera are represented in this dataset. An analysis of the six genera with over 100 records (*Efferia, Mallophora, Megaphorus, Proctacanthus, Promachus,* and *Triorla*) is shown below in alphabetical order.

Efferia Coquillett, 1893 (332 records; Fig. 2.4): Diptera (149), Hymenoptera (62), Lepidoptera (38), Orthoptera (29), Hemiptera (23), Coleoptera (15), Neuroptera (7) Odonata (7), Araneae (1), Blattodea (1). This genus generally seems polyphagous. However, there is a slight preference for Diptera, with 45% of its prey represented in this order. The dominant prey families making up 61% of the prey are the Bombyliidae (28), Asilidae (19: 6 congeneric, 2 conspecifics), Muscidae (18), Syrphidae (14), and Calliphoridae (12).

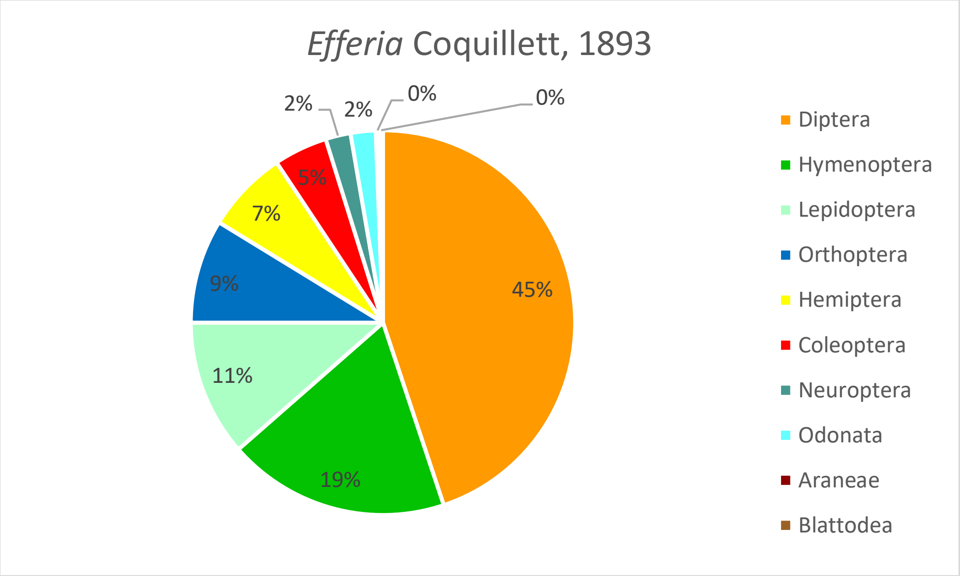


Figure 2.4.

Prey of *Efferia* Coquillett species represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 332)

These findings seem generally supported by the literature. For example, Bromley (1948b) lists many different species of *Efferia* as predators of mosquitoes. Bromley (1934) found that *E. (Erax) texanus* (Banks, 1919) is commonly found around apiaries, feeding on bees, and *E.* (*Nerax*) *aestuans* (Linnaeus, 1763) often feed on house flies. Moreover, O'Neill and Seibert (1996) record *E. staminea* (Williston, 1885) as having a polyphagous diet comprising of 10 insect orders and spiders.

Mallophora Macquart, 1838 (191 records; Fig. 2.5): Hymenoptera (179), Diptera (5), Coleoptera (4), Orthoptera (2), Hemiptera (1). The data indicate that *Mallophora* is oligophagous in its prey. Though it sometimes consumes other orders, Hymenoptera is preferred. The prey family Apidae makes up 61% of the Hymenoptera prey, with honeybees making up 83% of the represented Apidae.

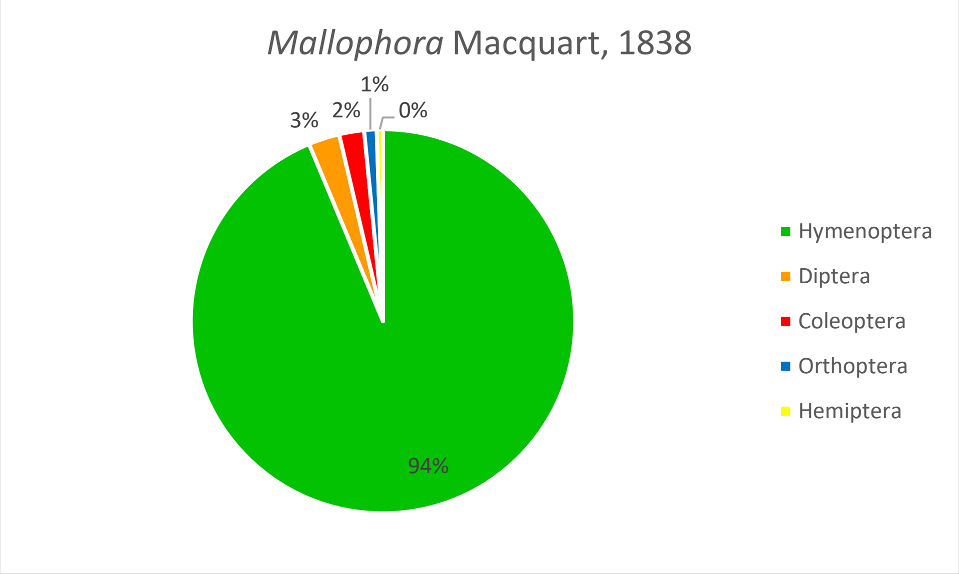


Figure 2.5.

Prey of *Mallophora* Macquart (Diptera: Asilidae) represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 191)

Bromley (1934, 1946) also found that *M. orcina* (Wiedemann, 1828) “feeds almost entirely on aculeate Hymenoptera.” *Mallophora* has been shown to prefer Hymenoptera, specifically honeybees. So much that *M. orcina*. and *M. bomboides* (Wiedemann, 1821), are considered harmful to Florida and Texas apiaries and have caused significant economic loss (Bromley 1950).

Megaphorus Bigot, 1857 (149 records; Fig. 2.6): Hymenoptera (103), Coleoptera (16), Diptera (14), Hemiptera (14), Lepidoptera (2). *Megaphorus* seems to prefer Hymenoptera, with 69% of its prey. The dominant family is Apidae (22). *Megaphorus* does not seem to be very selective beyond just preferring Hymenoptera.

The Lavigne (2016) database also shows a preference for Hymenoptera, with the prey order making up 68% of their prey. O'Neill and Seibert (1996) state that *M. willistoni* (Cole, 1964) tend to prey upon what is abundant in their environment at the time, but the prey is nearly always Hymenoptera.

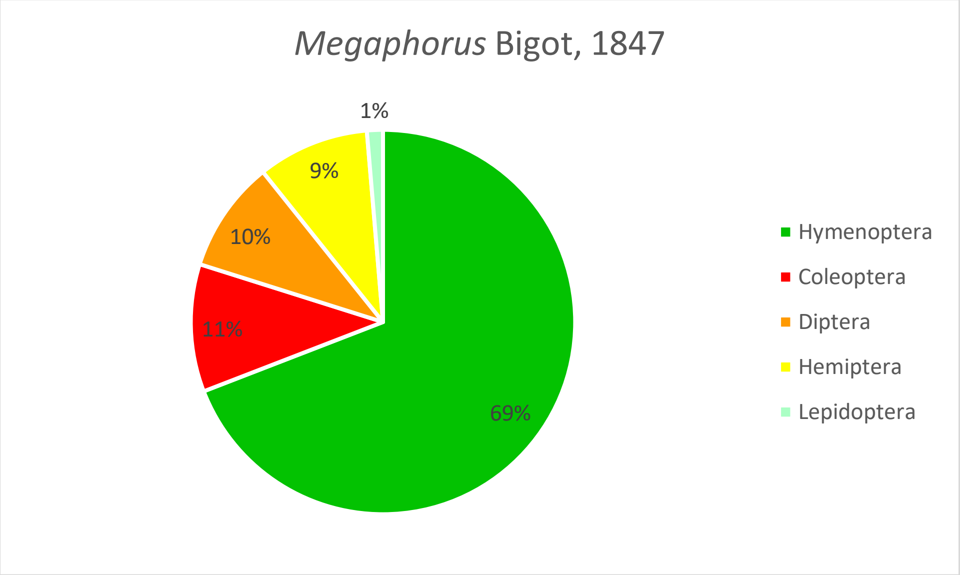


Figure 2.6.

Prey of *Megaphorus* Bigot (Diptera: Asilidae) represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 149)

Proctacanthus Macquart, 1838 (374 records; Fig. 2.7): Hymenoptera (167), Coleoptera (57), Diptera (50), Orthoptera (46), Lepidoptera (37), Hemiptera (8), Odonata (7), Blattodea (1), Neuroptera (1). Hymenoptera makes up 45% of their prey, with 50% of the order dominated by

Apidae. *Proctacanthus*, at the generic level, generally seems to have a polyphagous diet with nine orders represented. However, there seems to be more prey selectivity when broken down to the species level.

Coleoptera and Hymenoptera comprise over 56% of *Proctacanthus brevipennis* (Wiedemann, 1828) (105) prey. Hymenoptera and Orthoptera comprise 59% of *P. milbertii* Macquart, 1838 (63) prey, and Lepidoptera makes up 22% of their prey. Bromley (1949) also found that *P. milbertii* prefers Lepidoptera and Orthoptera and comprises 75% of its prey, which is misleading because *P. milbertii* is known as the "Missouri Bee-Killer." *P. rufus* Williston, 1885 (21) only had Hymenoptera as prey, which aligns with Bromley's (1934) conclusion of *P. rufus* preferring aculeate Hymenoptera. The prey of *P. longus* (Wiedemann, 1821) (22) is dominated by Diptera 59%, which contrasts with Bromley (1934), who found them to feed mainly on grasshoppers. *P. nearno* Martin, 1962 (23), *P. occidentalis* Hine, 1911 (24), and *P. philadelphicus* Macquart, 1838 (31) all showed a strong preference for Hymenoptera, with 83%, 63%, and 77% of their prey, respectively.

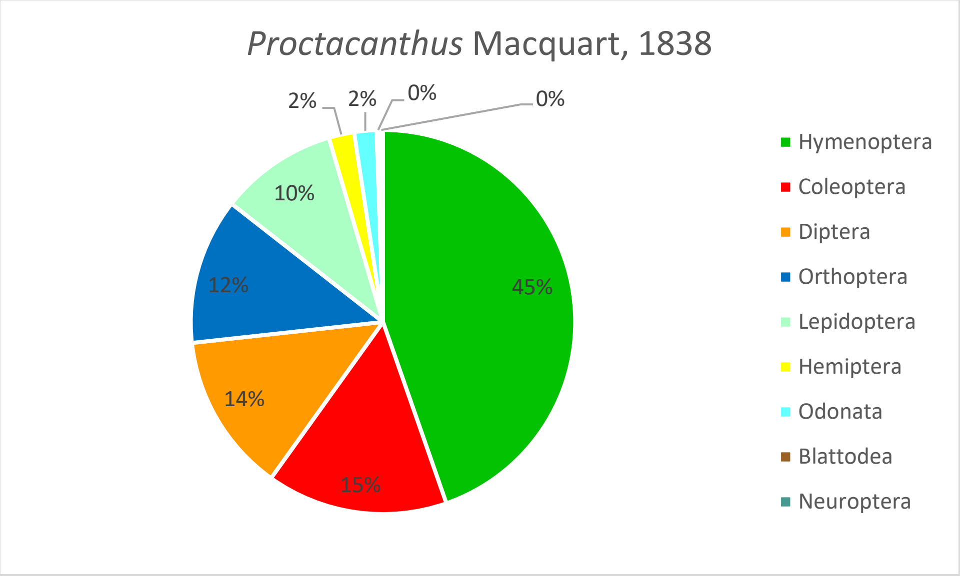


Figure 2.7.

Prey of *Proctacanthus* Macquart represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 374)

Promachus Loew, 1848 (418 records; Fig. 8): Hymenoptera (273), Diptera (48), Hemiptera (39), Coleoptera (27), Orthoptera (18), Lepidoptera (10), Odonata (2), Neuroptera (1). 57% of Hymenoptera belong to the family Apidae. Unlike *Proctacanthus, Promachus* seems consistent across species in preferring Hymenoptera prey.

Bromley (1934, 1948a) mentions that *Promachus bastardii* (Macquart, 1838), the "False Nebraska Bee Killer," is common around apiaries and kills many honeybees. Moreover, *P. fitchii* Osten Sacken, 1878 is considered the "Nebraska Bee Killer" and a distinct enemy of the honeybee. Dennis (2016) also found that *P. bastardii* prey was also dominated by Hymenoptera (59%).

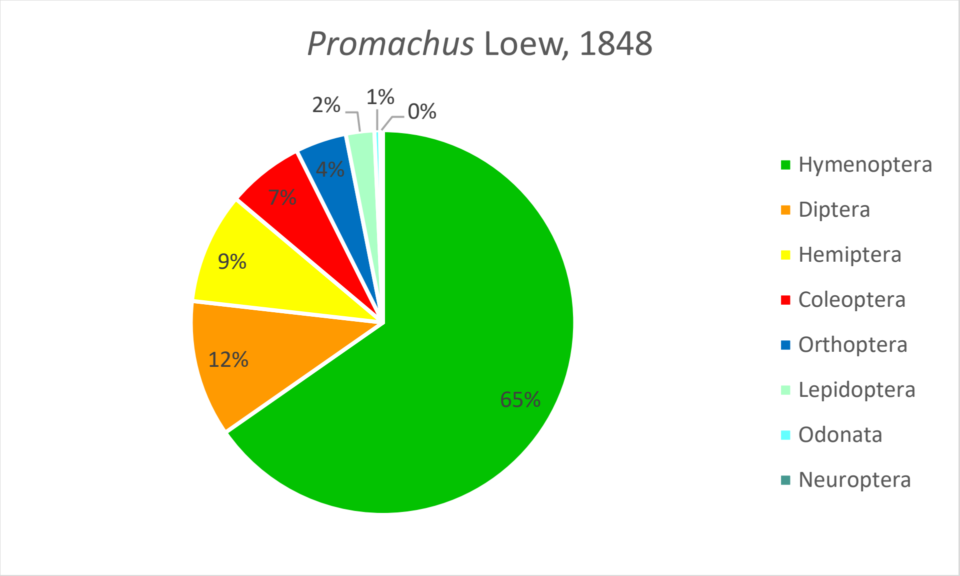


Figure 2.8.

Prey of *Promachus* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 418)

Triorla Parks, 1968 (188 records; Fig. 2.9): Orthoptera (65), Diptera (47), Lepidoptera (38), Hymenoptera (16), Hemiptera (10), Odonata (5), Coleoptera (4), Neuroptera (2), Araneae (1). *Triorla* seems to prefer Orthoptera more than most other genera of Asilidae, with 35% of their prey, the exception being *Scleropogon* with 59% and *Stichopogon* with 38%, which is supported by what Bromley (1934) found that *T. (Asilus) interrupta* (Macquart, 1834) feeds primarily on grasshoppers. Lavigne (1979) found that *T. (Efferia) argyrogaster* (Macquart, 1846) preferred Hymenoptera.

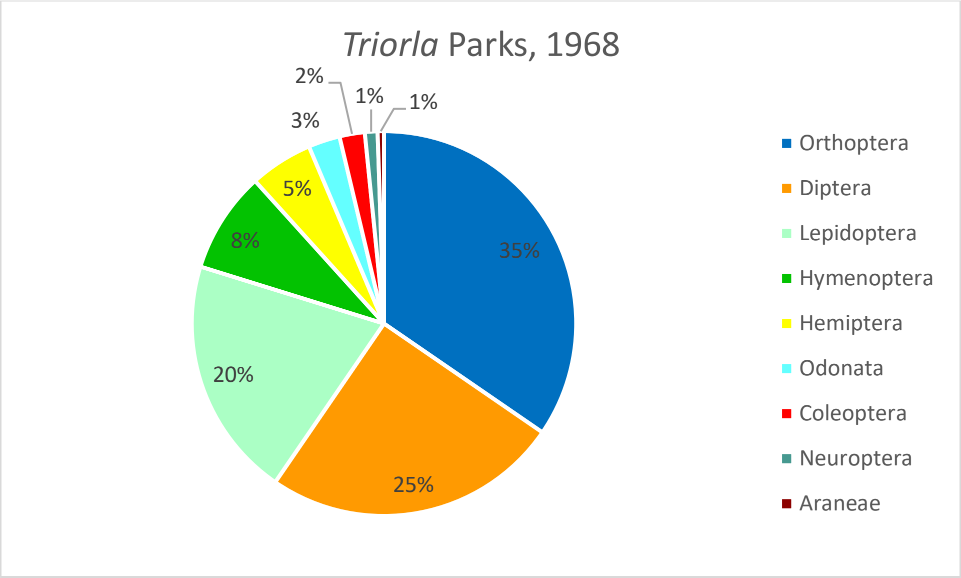


Figure 2.9.

Prey of *Triorla* Parks represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 188)

Bathypogoninae

With only one prey record for this subfamily, data is insufficient to allow meaningful comment currently (Table 2.3). The one record is of *Bathypogon* Loew, 1851, preying on Diptera in Western Australia.

Brachyrhopalinae

There are 267 prey records representing 23 species in eight genera. At a subfamily level, Diptera is the most common prey choice, with 33%, followed by Hymenoptera (22%), Hemiptera (17.6%), and Blattodea (16.5%) (Table 2.3). This dataset's five best-represented genera are

Ceraturgus, *Cyrtopogon*, *Heteropogon*, *Holopogon*, and *Nicocles*. Further analysis of their generic level prey preference is below in alphabetical order.

Ceraturgus Wiedemann, 1824 (9 records; Fig. 2.10): Coleoptera (8), Hymenoptera (1). Though there are only nine prey records in this dataset for *Ceraturgus* it is important to note that all but one record is Coleoptera. The Lavigne (2016) database also had a relatively high representation of Coleoptera (42%) in the prey of *Ceraturgus*, though not as high as in this one. Barnes (2008) also found that the majority of *Ceraturgus* prey is dominated by Coleoptera, especially in the family Scarabaeidae.

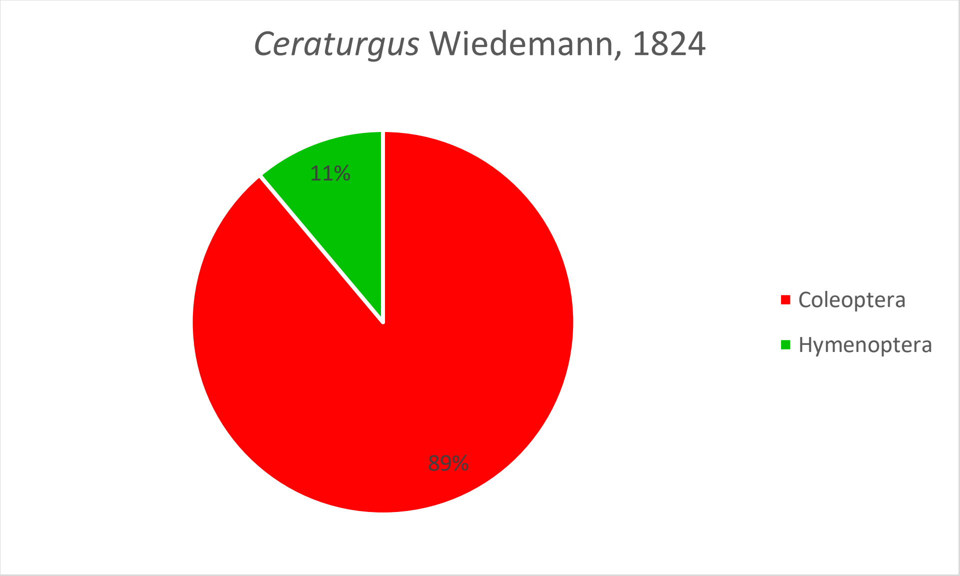


Figure 2.10.

Prey of *Ceraturgus* Wiedemann represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 9)

Cyrtopogon Loew, 1847 (32 records; Fig. 2.11): Diptera (14), Hymenoptera (13), Coleoptera (4), Neuroptera (1). *Cyrtopogon* seems to consistently prefer Diptera and Hymenoptera, which make up 84% of their prey. Bullington and Lavigne (1992) found that *C. montanus wilcoxi* James, 1942 prey on six orders represented and dominated by Diptera, followed by Hymenoptera. The Lavigne (2016) database also confirms this trend, with Diptera being 48% and Hymenoptera 22% of their prey.

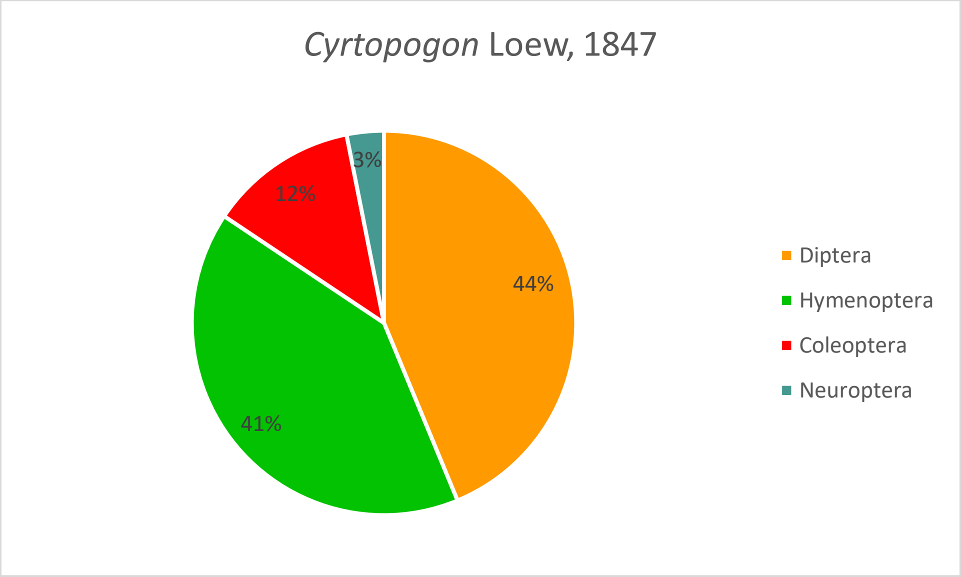


Figure 2.11.

Prey of *Cyrtopogon* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 32)

Heteropogon Loew, 1847 (15 records; Fig. 2.12): Hemiptera (7), Hymenoptera (4), Coleoptera (2), Diptera (2). The data shows a slight preference for Hemiptera, but there are not enough records to make a meaningful comment at this time. However, when compared to other literature, similar trends seem to arise.

The Lavigne (2016) database has 131 prey records for *Heteropogon*, which break down to 30% Coleoptera, 26% Hemiptera (Heteroptera and Homoptera), and 21% Hymenoptera. Lavigne (1970) found that *H. maculinervis* James, 1937 specialized on Hemiptera (Homoptera) and Hymenoptera. Lavigne and Bullington (1999) found a similar trend in *H. paurosomus* Pritchard, 1935 consuming prey of a wide variety of arthropod orders, with Diptera and Hemiptera (Heteroptera and Homoptera) predominating. Overall, *Heteropogon* seems to have a polyphagous diet.

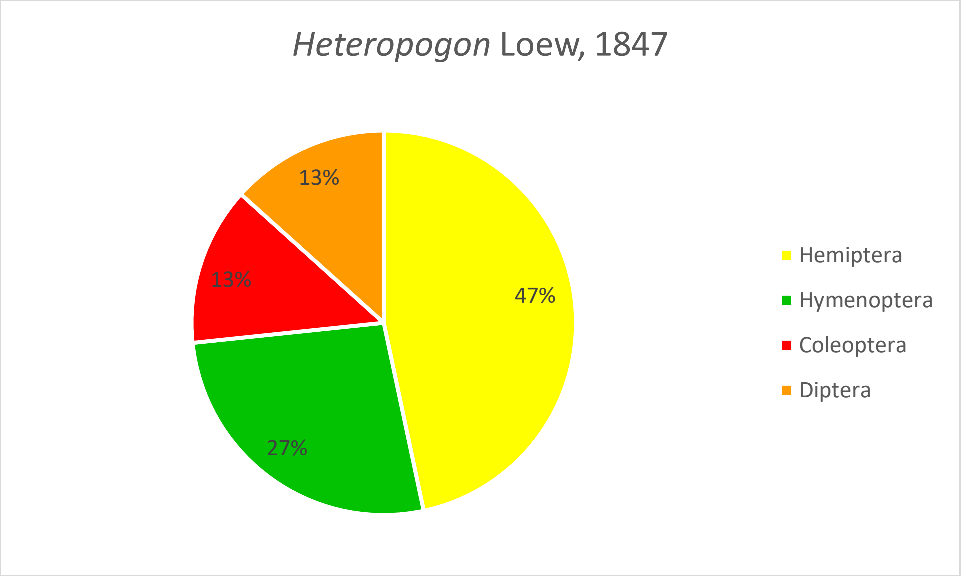


Figure 2.12.

Prey of *Heteropogon* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 15)

Holopogon Loew, 1847 (166 records; Fig. 2.13): Diptera (48), Blattodea (42), Hemiptera (34), Hymenoptera (31), Thysanoptera (7), Araneae (2), Coleoptera (2). The data show a polyphagous arthropod diet. A point of interest is the high representation of Blattodea (25%) in *Holopogon* prey. More than 50% of these records are booklice (Psocoptera) collected by Dr. Steve Dennis in north-eastern Florida. This high representation may be due to the thoroughness of the collecting in an area that may have a high proportion of these prey available or the ability of the collector to collect such small predators and prey regularly. Smaller families of prey are most likely under-recorded as prey because of their difficulty to see and collect.

The Lavigne (2016) database has prey records for *Holopogon* from nine orders, with the dominant orders being 40% Hemiptera (Heteroptera and Homoptera) and 30% Diptera. Lavigne et al. (1993) show similar results for *H. seniculus* Loew, 1866, with Diptera and Hemiptera (Homoptera) comprising 92.7% of the total prey taken. Dennis (2018) found that *H. snowi* Back, 1909 prey is dominated by Hemiptera (26.4%) and Thysanoptera (27.5%), and in a 2014 study, Dennis found that *H. phaeonotus* Loew, 1874 prey comprised mostly of Diptera (33%) and Psocoptera (23%).

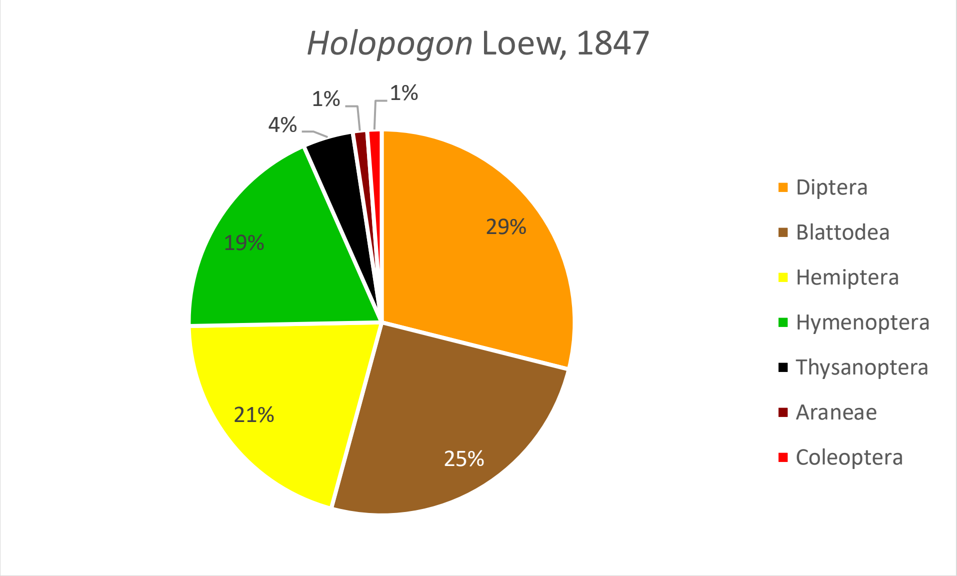


Figure 2.13.

Prey of *Holopogon* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 166)

Nicocles Jaennicke, 1867 (40 records; Fig. 2.14): Diptera (24), Hymenoptera (7), Hemiptera (5), Blattodea (2), Coleoptera (1), Neuroptera (1). This data suggests that *Nicocles* is oligophagous, with 60% of its prey being Diptera. The Lavigne (2016) database only has three records for *Nicocles*, which reflects the amount of literature on the genus. Very little is known about the ethology and predation of *Nicocles*. Most of the prey records were collected by Dr. Steve Dennis in St. Augustine, FL, and are new to science.

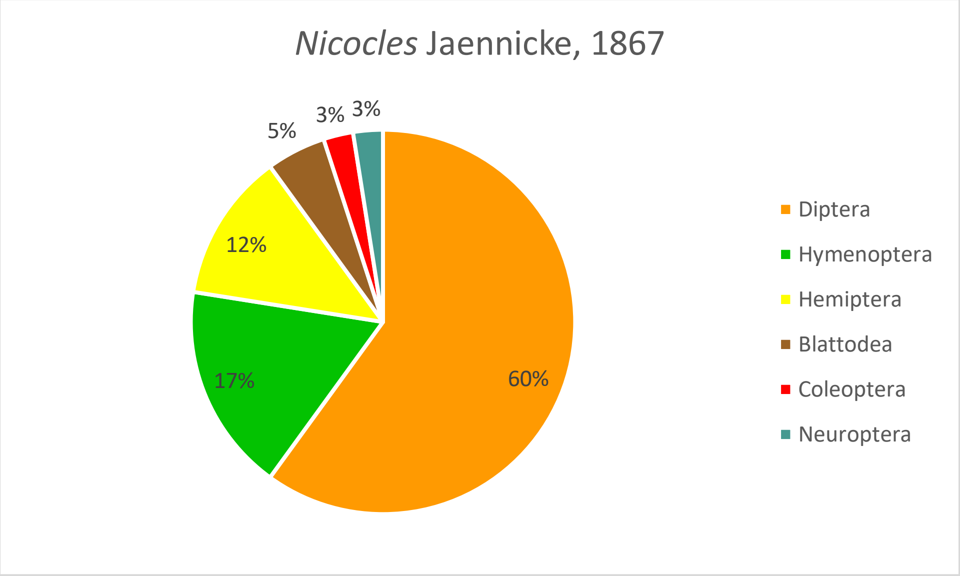


Figure 2.14.

Prey of *Nicocles* Jaennicke represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 40)

Dasypogoninae

The subfamily *Dasypogoninae* has the second-largest number of prey records (528) after Asilinae. The dataset includes 37 species representing nine genera. The subfamily seems to significantly prefer Hymenoptera which dominates the data with almost 73% of the prey records, the highest percentage of one prey order represented at the subfamily level. Further examination and analysis of results for the two best-represented genera (*Diogmites* and *Saropogon*) are below.

Diogmites Loew, 1866 (468 records; Fig. 2.15): Hymenoptera (335), Diptera (59), Hemiptera (29), Coleoptera (25), Lepidoptera (9), Orthoptera (4), Odonata (3), Araneae (2), Neuroptera (2). *Diogmites* strongly prefer Hymenoptera, which constitutes 72% of its prey, 42% of which belongs to the family Apidae.

Bromley (1934) states that *Diogmites angustipennis* Loew, 1866 is “cannibalistic to a high degree,” where females often kill courting males. Contrarily, in this dataset *D. angustipennis* (117) has only 9% of its prey as Diptera, half of the records were Asilidae, and only one was potentially cannibalism. *D. angustipennis* is considered one of the most abundant “bee-catchers” and favors apiaries with a strong preference for Hymenoptera which is similarly reflected in this dataset.

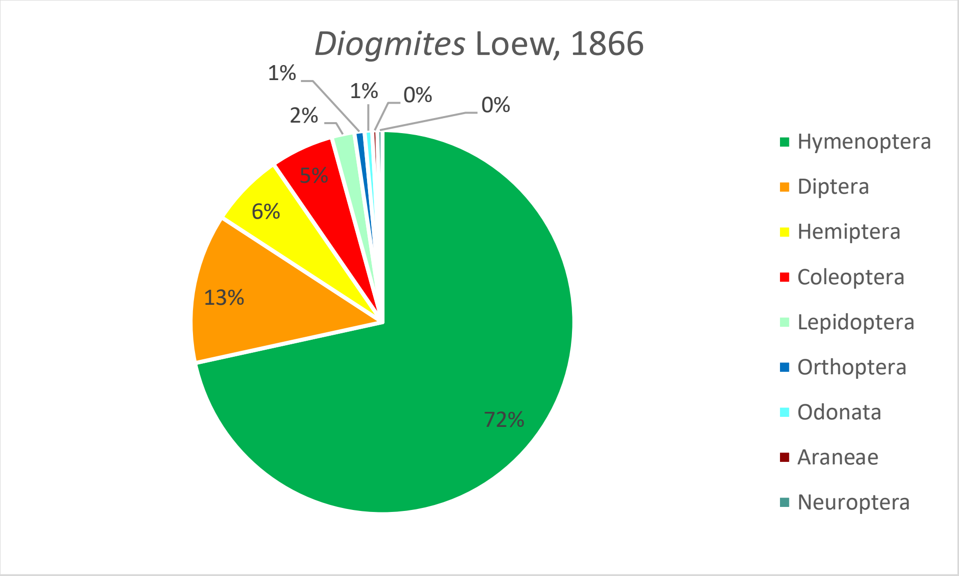


Figure 2.15.

Prey of *Diogmites* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 468)

Saropogon Loew, 1847 (48 records; Fig. 2.16): Hymenoptera (40), Coleoptera (4), Diptera (3), Neuroptera (1). *Saropogon* shows an oligophagous diet for Hymenoptera, 45% of which is from the family Apidae.

Bromley (1934) noted that H. B. Parks observed *Saropogon dispar* Coquillett, 1902 to be considerably destructive to apiaries. Though *S. dispar* feeds on various prey, its preference for honeybees makes it a species of serious economic importance. *S. combustus* Loew,1874, and *S. pritchardi* Bromley, 1934 are significant predators of harvester ant workers (*Pogonomyrmex*) in Eastern New Mexico and West Texas (Pollock 2020). The Lavigne (2016) database also confirms a preference for Hymenoptera, with 62% of their prey.

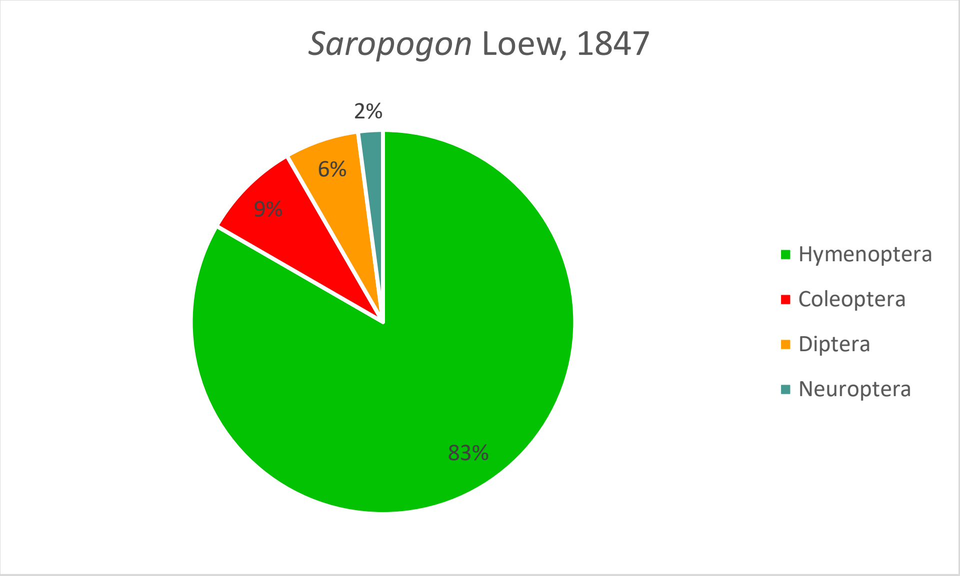


Figure 2.16.

Prey of *Saropogon* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 48)

Dioctriinae

With only 14 records representing three species from three genera, little can be concluded about this subfamily from this dataset alone. With the majority of the records, the genus *Dioctria* is analyzed below.

Dioctria Meigen, 1803 (11 records; Fig. 2.17): Diptera (4), Hymenoptera (4), Araneae (2), Hemiptera (1). Together, Diptera and Hymenoptera make up 73% of the prey records for *Dioctria*.

Though this dataset is small, it is similar to what the Lavigne (2016) database has for its 309 prey records for *Dioctria*, of which 52% are Hymenoptera and 35% are Diptera. Hobby (1932) also mentions that *Dioctria* is an important enemy of parasitic Hymenoptera and exercises preferential selection, especially for Ichneumonidae.

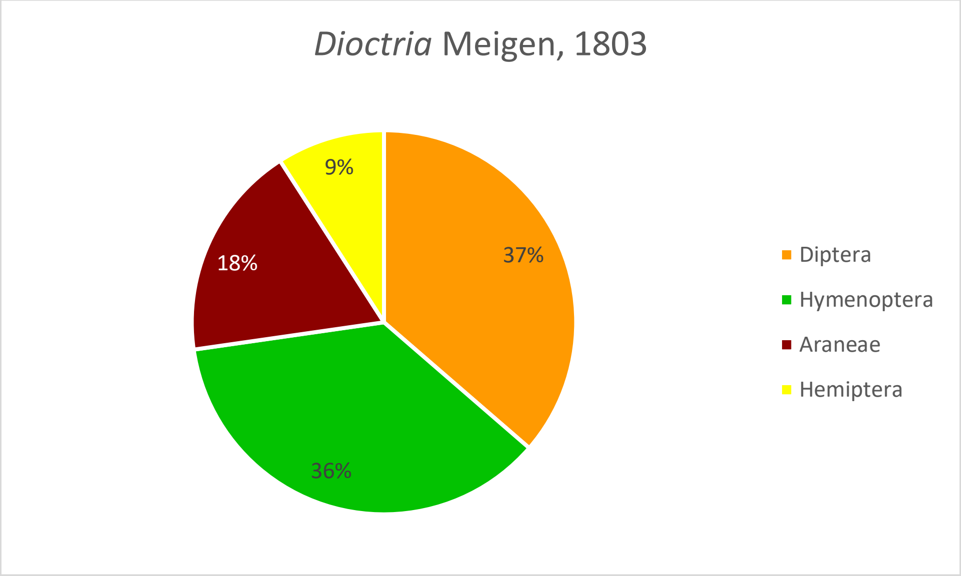


Figure 2.17.

Prey of *Dioctria* Meigen represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 11)

Laphriinae

The subfamily Laphriinae has 151 records, with 28 species representing ten genera in this dataset. Forty-three percent of the prey records are from the order Hymenoptera, and 32.5% of the prey records are Coleoptera. Further analysis of the best-represented genera (*Atomosia* and *Laphria*) is addressed below.

Atomosia Macquart, 1838 (25 records; Fig. 2.18): Diptera (10), Hymenoptera (9), Hemiptera (4), Lepidoptera (2). Though the dataset is small, *Atomosia* slightly prefers Diptera and Hymenoptera, which comprise 40% and 36% of their prey, respectively.

The literature also seems to support a slight preference for Diptera, around 37% for *Atomosia* (Scarbrough & Sraver 1979; Dennis & Lavigne 1975). Moreover, the Lavigne (2016) database has 263 prey records for *Atomosia*. The three most common prey orders are 48% Diptera, 23% Hemiptera (Heteroptera and Homoptera), and 16% Hymenoptera.

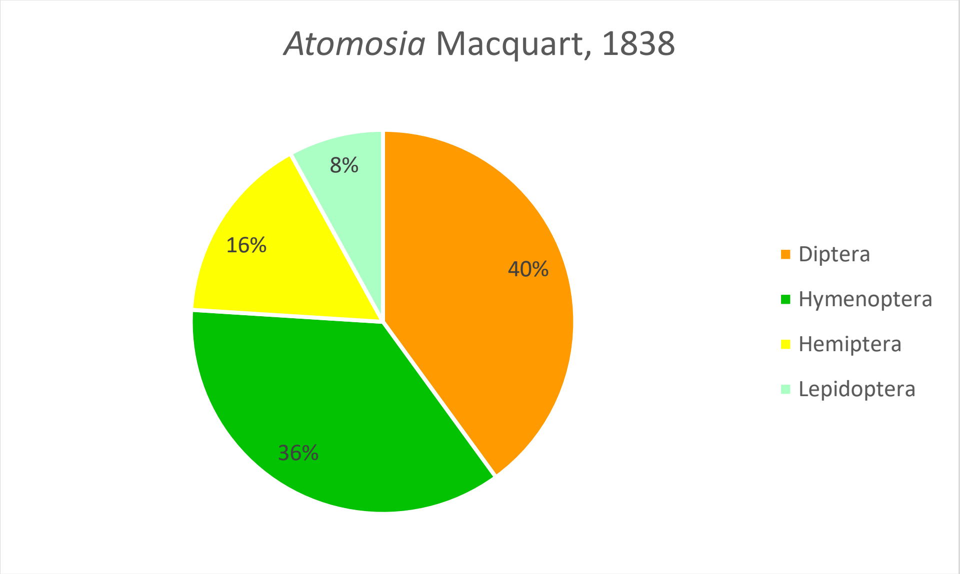


Figure 2.18.

Prey of *Atomosia* Macquart represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 25)

Laphria Meigen, 1803 (106 records; Fig. 2.19): Coleoptera (48), Hymenoptera (44), Diptera (9), Hemiptera (5). Coleoptera and Hymenoptera comprise 87% of the *Laphria* prey in this dataset. The dominant prey families in Coleoptera are Scarabaeidae (17), Lampyridae (8), Coccinellidae

(6), and Cerambycidae (4). Furthermore, Apidae makes up 79.5% of the Hymenoptera prey. Lampyridae seems to have an unusually high representation in this dataset. Very little literature refers to Lampyridae as prey of Asilidae, only one in the Lavigne (2016) database, which may be due to their distastefulness and brings to question why *Laphria affinis* Macquart, 1855 seems to prefer this family (57%) over other families of Coleoptera. Other species *L. flavicollis* Say, 1824, *L. thoracica* Fabricius, 1805*, L. vorax* (Bromley, 1929), and *Promachus bastardii,* are recorded eating Lampyridae.

Bromley (1945) talked about adult *Laphria (Bombomima) grossa* (Fabricius, 1775) as an enemy of significance for the Japanese Beetle in New England, and Fattig (1945) mentioned this species as a larva, also eating Japanese Beetle larvae. Bromley noted that *L. grossa* seems to prey upon other economically important insects, such as the clover-leaf weevil, the rose chafer, and the gypsy moth. There has also been an increase in sightings of this species four years after the introduction of the Japanese beetle to the U.S. in 1926. Bromley (1948a) discussed *L. (Bombomima) thoracica* and *L. (Bombomima) grossa* as significant enemies of honeybees.

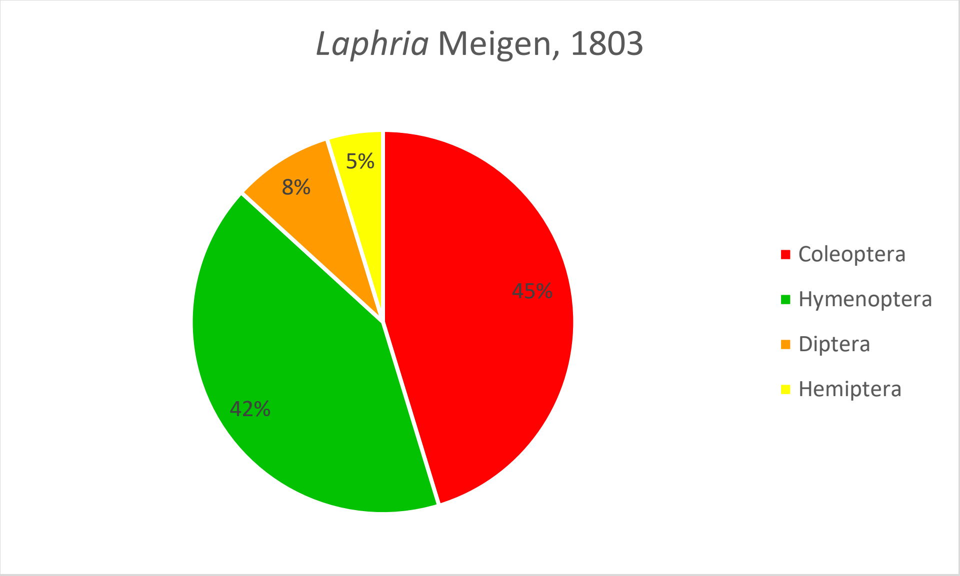


Figure 2.19.

Prey of *Laphria* Meigen represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 106)

Leptogastrinae

Leptogastrinae only has six records from four species in two genera in this dataset. Very little is known about *Beameromyia* predation, and no conclusion can be made currently from this dataset. Though there are only three records of *Leptogaster* in this dataset, there is a decent representation of this genus in other literature. They are often referenced for eating spider prey, and Dennis & Lavigne (2012) concluded that Leptogastrinae is often reported taking spiders as prey despite spiders only making up about 1% of asilid prey, which is most likely because genera like *Leptogaster* come across spiders more often because of their foraging strategies through long grass and the tendency to take static prey. The Lavigne (2016) database has 124 prey records for *Leptogaster*, 11% of which are spiders, and the dominant orders are 32% Hemiptera (Heteroptera and Homoptera) and 26% Diptera. This subfamily seems to be polyphagous despite a rumored higher-than-average preference for spiders. For complete information, see Supplemental Material 2.1.

Ommatiinae

This subfamily is only represented by eight records from two species within the genus *Ommatius* Wiedemann, 1821 (8 records; Fig. 2.20): 50% of its prey is Hemiptera, 25% Coleoptera, and only one record from Diptera and Hymenoptera each. This genus seems to have a very polyphagous diet, and this conclusion is in support of the Lavigne (2016) database, where the dominant orders are Diptera (31%) and Hymenoptera (21%), with the rest of the records split over another nine orders. Bullington and Lavigne (1984) also found that *Ommatius* did not strongly prefer any order of prey.

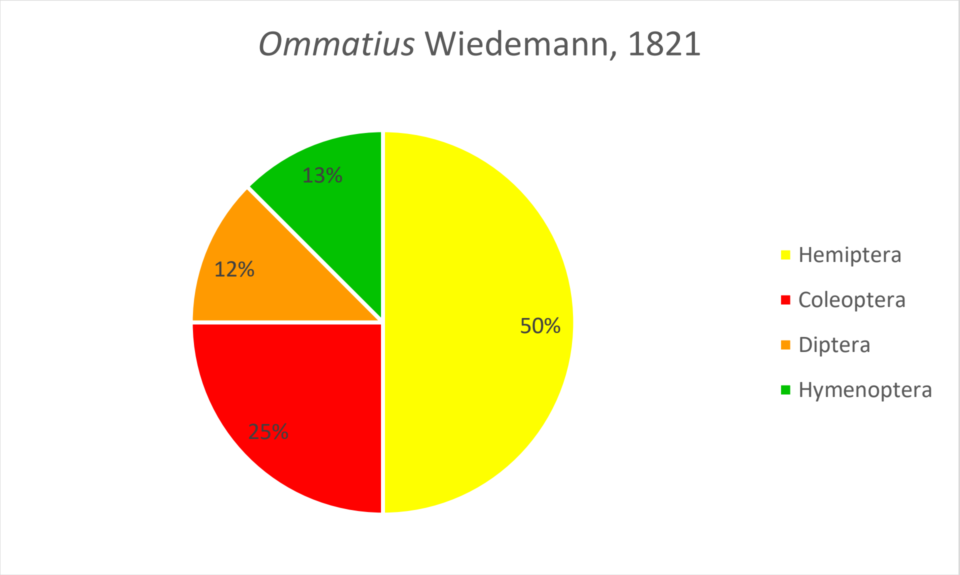


Figure 2.20.

Prey of *Ommatius* Wiedemann represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 8)

Stenopogoninae

The subfamily Stenopogoninae has 265 records, with 40 species representing 11 genera. Hymenoptera dominates the prey records with 46.5% of their prey. Further analysis of the five genera (*Callinicus*, *Microstylum*, *Ospriocerus*, *Scleropogon*, and *Stenopogon*) with over ten records in alphabetical order.

Callinicus Loew, 1872 (11 records; Fig. 2.21): Hymenoptera (10), Diptera (1). *Callinicus* shows a strong preference for Hymenoptera prey, representing a variety of families (Supplemental material 2.1). All nine records of prey in the Lavigne (2016) database are also Hymenoptera. Linsley (1944) found that *Callinicus* showed a preference for Megachilidae and Andrenidae (Hymenoptera). Overall, very little is known about the prey preference of *Callinicus*.

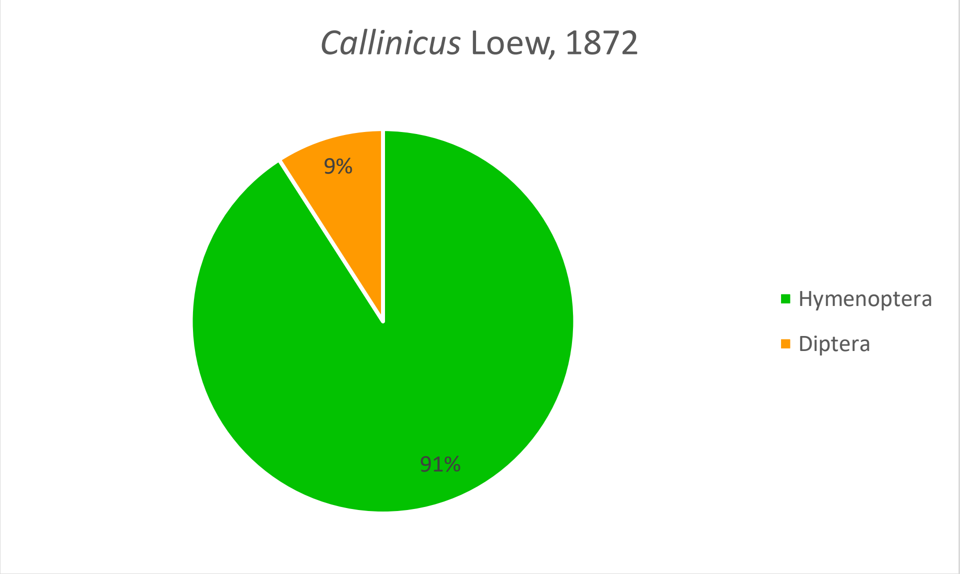


Figure 2.21.

Prey of *Callinicus* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 11)

Microstylum Macquart, 1838 (11 records; Fig. 2.22): Hemiptera (4), Orthoptera (4), Hymenoptera (2), Diptera (1). In this dataset, 73% of the prey of *Microstylum* is made up of Hemiptera and Orthoptera.

The Lavigne (2016) database has 167 prey records for *Microstylum*, of which the majority are Coleoptera (32%) and Orthoptera (21.5%). McKenzie (2019) presented more prey records for *M. galactodes* Loew, 1866 and *M. morosum* Loew, 1872 from eastern New Mexico and west Texas. She found that the dominant orders in their prey were 45% Hemiptera and 43% Orthoptera, which is proportional to the sampling in the present dataset.

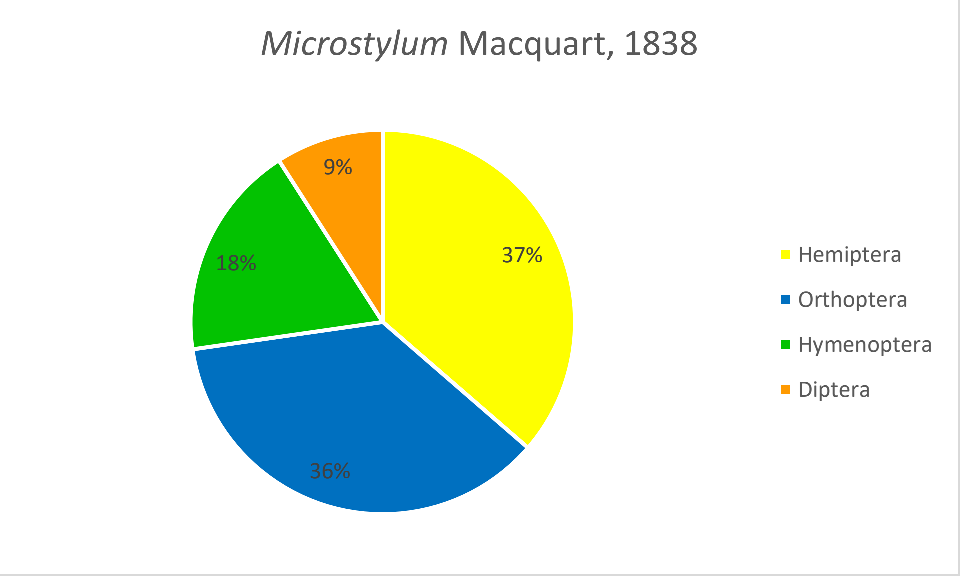


Figure 2.22.

Prey of *Microstylum* Macquart represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 11)

Ospriocerus Loew, 1866 (29 records; Fig. 2.23): Coleoptera (19), Hemiptera (4), Diptera (3), Hymenoptera (2), Orthoptera (1). *Ospriocerus* shows a preference for Coleoptera prey, with it constituting 65.5% of its prey. The Coleoptera prey records consist of Meloidae (16) and Cantharidae (3). Both families are highly toxic and bring to question why *Ospriocerus* prefers Meloidae over other less potent prey. *Ceraturgus*, *Dasypogon*, *Diogmites*, *Efferia*, *Gonioscelis*, *Laphria*, *Megaphorus*, *Prolepsis*, *Scleropogon*, and *Stenopogon* are also occasionally recorded eating Meloidae, but it is never a preference (Supplemental material 2.1, Lavigne 2016). There are many references to *Ospriocerus* preferring Meloidae and how unusual the choice seems (Dennis & Lavigne 1975, Lavigne & Dennis 1994).

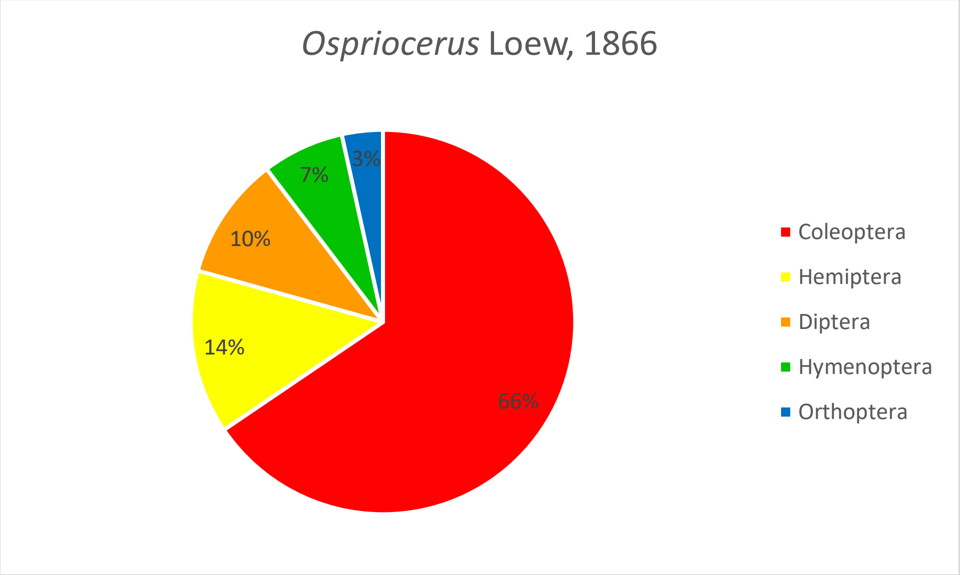


Figure 2.23.

Prey of *Ospriocerus* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 29)

Scleropogon Loew, 1866 (27 records; Fig. 2.24): Orthoptera (16), Hymenoptera (4), Diptera (2), Lepidoptera (2), Coleoptera (1), Hemiptera (1), Odonata (1). Over 59% of *Scleropogon* prey consists of Orthoptera, making it seem like the order is preferred. The Lavigne (2016) database includes 140 records for *Scleropogon*; 49% are Orthoptera which supports this order as preferential.

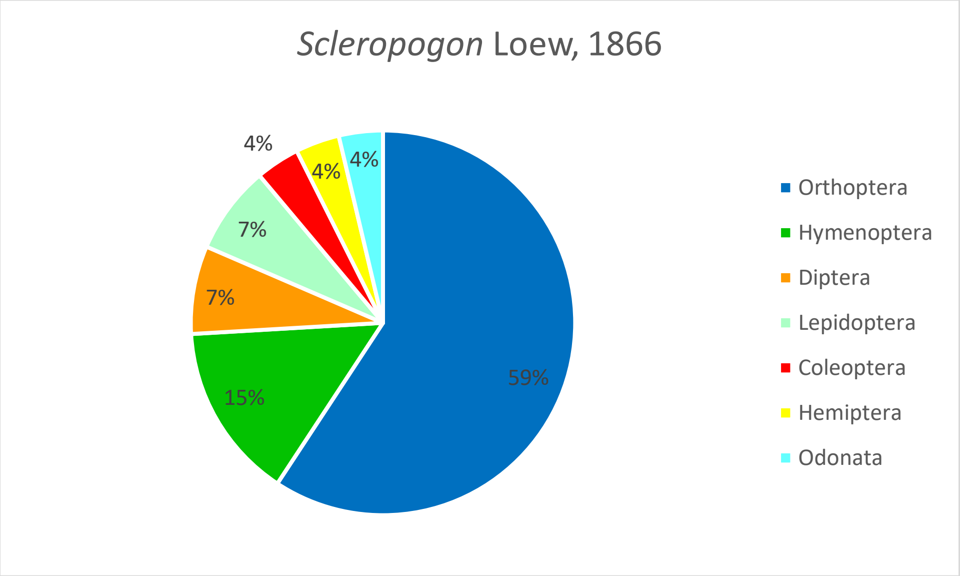


Figure 2.24.

Prey of *Scleropogon* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N =27)

Stenopogon Loew, 1847 (166 records; Fig. 2.25): Hymenoptera (99), Diptera (26), Coleoptera (15), Hemiptera (11), Lepidoptera (11), Odonata (2), Neuroptera (1), Orthoptera (1). *Stenopogon* prefers Hymenoptera prey, with it being 59.6% of its recorded prey. Diptera makes up 15.6% of *Stenopogon* prey.

Literature evidence supports *Stenopogon* being generally polyphagous with a slight preference for Hymenoptera prey (Cole 1958, Lavigne 2016). The Lavigne (2016) database has 641 prey records. Diptera (24%), Hymenoptera (21%), and Orthoptera (17%) are the three most common arthropod orders, with an additional eight orders making up the rest of the prey.

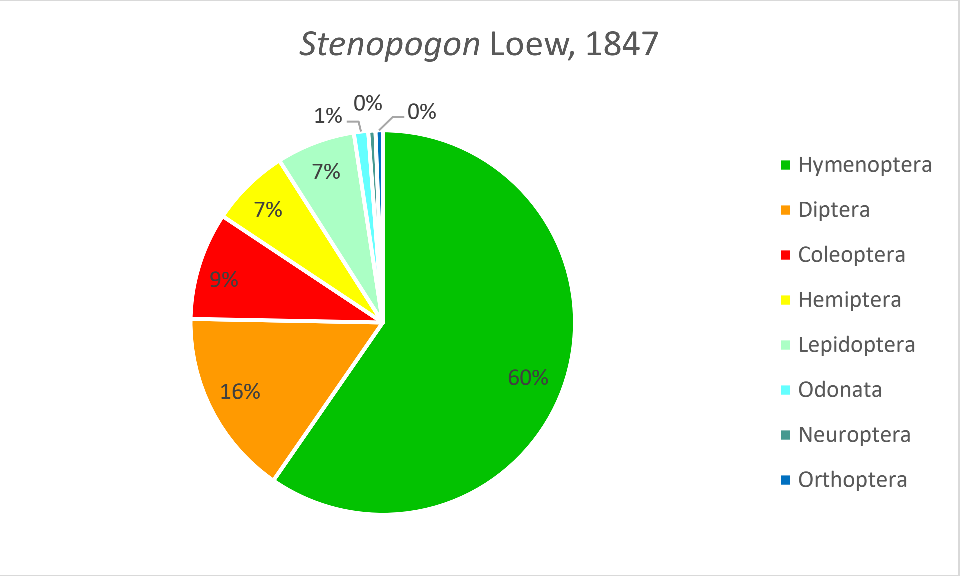


Figure 2.25.

Prey of *Stenopogon* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 166)

Stichopogoninae

The subfamily *Stichopogoninae* has 138 prey records for four species in two genera. The dominant order of prey is Diptera making up 65.2% of all Stichopogoninae prey. *Lasiopogon* and *Stichopogon* are briefly analyzed below.

Lasiopogon Loew, 1847 (4 records; Supplemental Material 2.1): Diptera (3), Trichoptera (1). Though there are only four records for *Lasiopogon*, the high representation of Diptera is supported by other literature. For example, Haab et al. (2019) noted that *Lasiopogon* seemed to prefer Diptera prey, with individuals representing Empididae, Simuliidae, and Anthomyiidae. A preference for Diptera is also supported by the Lavigne (2016) database, in which Diptera constitute 70.5%.

Stichopogon Loew, 1847 (134 records; Fig. 2.26): Diptera (87), Orthoptera (33), Araneae (7), Hymenoptera (4), Hemiptera (2), Coleoptera (1). Diptera dominates this dataset for *Stichopogon* with 65%. Also of note is the high relative percentage (5%) of spiders in this genus compared to other Asilidae.

Bromley (1934) mentions how *Stichopogon trifasciatus* (Say, 1823) feeds to a considerable extent on small spiders. Dennis and Lavigne (2012) also found that *Stichopogon* tends to prey on spiders more often than other Asilidae genera. However, this may be due more to a foraging strategy than a preference for spider prey. The Lavigne (2016) database shows Diptera making up 48% of *Stichopogon* prey and Araneae for 9% of the prey.

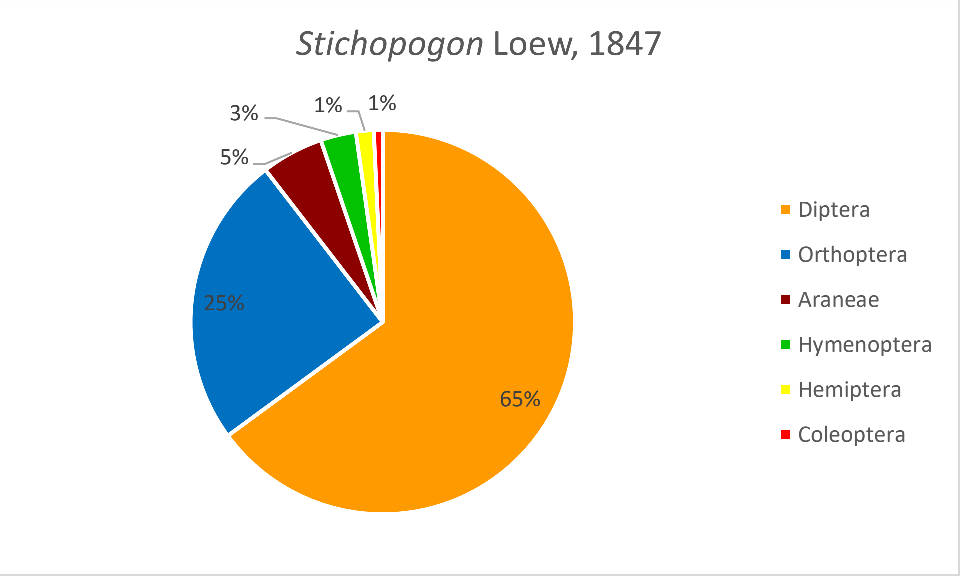


Figure 2.26.

Prey of *Stichopogon* Loew represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 134)

Trigonomiminae

The subfamily is represented with 267 prey records for four species in two genera for this dataset. With *Damalis* only making up one of the records, *Holcocephala* is analyzed below.

Holcocephala Jaennicke, 1867 (266 records; Fig. 2.27): Hymenoptera (105), Diptera (93), Coleoptera (24), Hemiptera (23), Blattodea (11), Lepidoptera (5), Araneae (3), Siphonaptera (1), Thysanoptera (1). Hymenoptera and Diptera dominate the prey for *Holcocephala,* with 74% of the prey records. Despite this preference, there is still a wide variety of representation from other orders.

Dennis (1979) also found that *Holcocephala fusca* Bromley, 1951 seems selective in its prey, preferring Hymenoptera and Diptera. Lavigne's (2016) database has 249 records for *Holcocephala,* with 36% Diptera and 23% Hymenoptera making up the majority of prey.

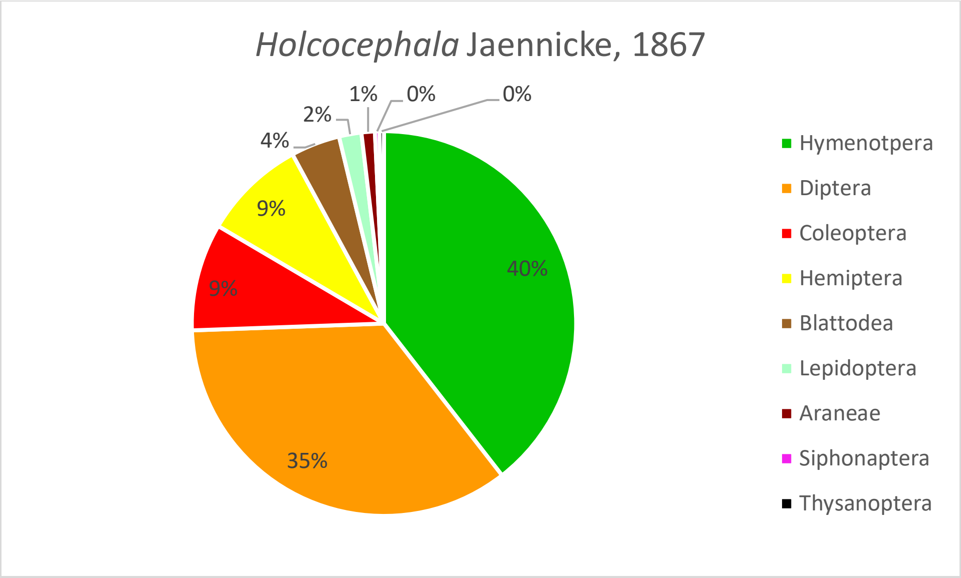


Figure 2.27.

Prey of *Holcocephala* Jaennicke represented with percentage of arthropod orders consumed. For full information, see Supplemental Material 2.1. (N = 266)

Willistonininae

With only one record, for *Ablautus mimus* Osten Sacken, 1877, there is not enough data to make any valuable conclusions using this dataset. However, the one record included is Diptera which is aligned with what the genus is thought to prefer. Lavigne (1972) recorded *Ablautus rufotibialis* Back, 1909 primarily consuming prey belonging to the dipterous families Anthomyiidae, Sepsidae, and Cecidomyiidae, and the Lavigne (2016) database show 60% of their prey dipterous. See Supplemental Material 2.1 for full detail.

Predator sex

Of the 3,421 predator-prey interactions recorded in this study, 1975 (58%) are female, 1,215 (35%) are male, and 231 (7%) sex unknown due to broken abdomen (Fig. 2.28; Supplemental

Material 2.1). Eight females were recorded cannibalizing another female asilid, and six mated pairs were caught while consuming prey.

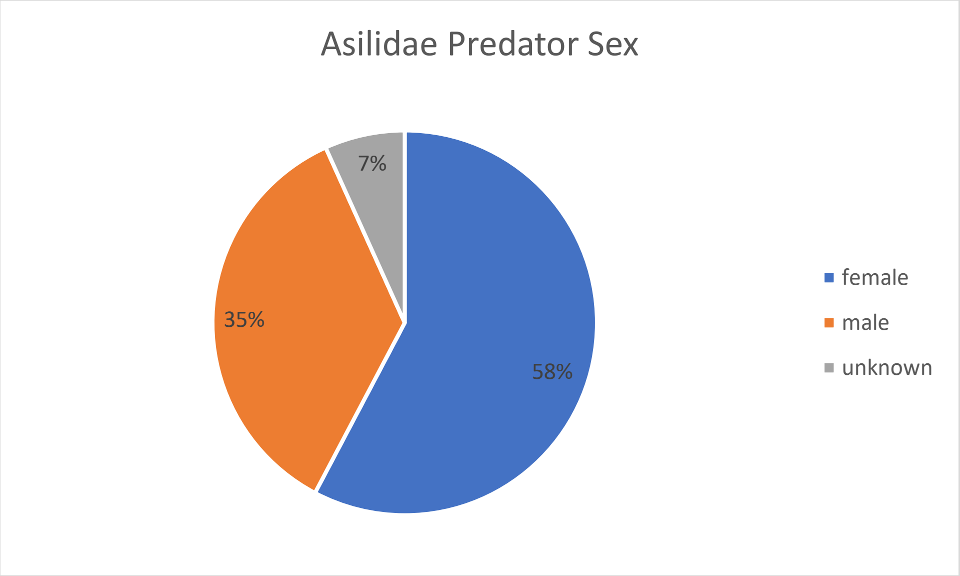


Figure 2.28.

Percent of assassin fly predator records: female (N = 1975), male (N = 1215), and unknown (N = 231). See Supplemental Material 2.1 for full information.

Discussion

Most Asilidae in this dataset seem to prefer a generalist or polyphagous diet. However, some species exhibit a tendency for a particular type of prey at the family, generic, or species level, which could be due to various reasons, some of which are discussed below. Several genera appear oligophagous – *Ceraturgus* on Coleoptera, *Diogmites* on Hymenoptera, *Laphria* on Lampyridae, *Mallophora* on Apidae, *Megaphorus* on Hymenoptera, *Nicocles* on Diptera, *Ospriocerus* on Meloidae, *Promachus* on Apidae, *Saropogon* on Hymenoptera, and *Stichopogon* on Diptera. This dataset also supports the hypothesis that females tend to catch more prey than males.

Findings of particular interest and future study

Both *Callinicus* and *Nicocles* have very few published prey records, and this dataset adds to their limited prey information. They are both interesting because they show signs of being oligophagous or even potentially monotropic. Collecting more prey records will potentially resolve whether they are genuinely oligophagous.

Though Lampyridae can be found in small numbers as prey for many genera of Asilidae, only *Laphria* strongly prefers this prey family. Reasons for this preference or specialization are unknown and indeed interesting due to the toxicity of Lampyridae.

Lastly, *Ospriocerus* is a known specialist predator of Meloidae beetles (Dennis & Lavigne 1975, Lavigne & Dennis 1994). Nearctic *Ospriocerus* are mostly distributed over the southwestern U.S. (Martin, 1968). Meloidae are found all over the U.S. but have the greatest diversity in arid/semiarid areas (Arnett et al. 2002). The common name "blister beetles" refers to the effect when the cantharidin toxin found in Meloidae touches your skin. The cantharidin can be secreted or involuntarily released through the hemolymph by pressing or squishing, and ingestion of Meloidae can be fatal to vertebrates. Meloidae are economically important because they can kill livestock and horses by being present in alfalfa feed and hay (Blodgett et al. 1991; Kinney et al. 2006). Many management strategies can help reduce the number of meloids. However, non will eliminate the problem. Future research may want to test if *Ospriocerus,* a natural and local predator of Meloidae, would be a viable biocontrol agent. Identifying and understanding potentially important predators is one of the many reasons that databasing biological information, such as prey preference from historical museum collections, is so important.

Factors influencing predator selectivity

Several reasons exist why some species of Asilidae may be more selective of some orders of prey. Many ethology studies attempt to examine this on a species level. Some of these studies include: Melin 1923, Dennis and Lavigne 1975, Scarbrough 1978, Scarbrough and Sraver 1979. Reasons provided include prey cuticle and predator proboscis hardness, predator and prey size ratio, prey availability in an environment, and flight characteristics, such as flight time or flight ability, of prey. These are all potentially significant factors influencing selectivity in some asilids.

Males vs. Females

In this data set of 3,421 prey records, 1,975 predators were female (8 were cannibalistic females feeding on other asilid females), and 1,215 were male predators. Another six records were mated pairs (1 female and 1 male) with prey, and 231 were of unknown or not recorded sex. Therefore, females make up 58% of the available sex records, which is very close to the commonly recorded Asilidae male-to-female ratio of 1:1.5 (Lavigne 2016). In addition, researchers have consistently found that more female Asilidae are recorded with prey than males (Dennis et al. 2010, Hobby 1931a, Lavigne 1971, Londt 2006).

Many possibilities to explain the bias towards females in collections have been presented, but experimental evidence has not yet supported a particular conclusion. The most referenced possibility is that the female's nutritional requirements are higher to complete the maturation of their ovaries, and they must consume more prey (Hobby 1931a, Londt 2006). Others include that males spend less time foraging and feeding because they spend more time searching for females (Dennis et al. 2010), there may be some populations that may have more females than males (Lavigne 1971), females may have shorter feeding or inter-feeding times and thus have more time to catch more prey (Dennis & Lavigne 1975). Lastly, females may feed throughout the day instead of at particular times (Dennis et al. 2010).

Sampling bias

It is important to note that this dataset is biased. Bias is unavoidable when utilizing entomological museum collections. Entomological collections are often a compilation of many different collecting and sampling methods. Some collections, like Dr. Steve Dennis's, were compiled to focus on Asilidae and their prey. Other collectors may have focused only on the Asilidae and not the prey, perhaps only keeping the largest and most charismatic prey items for display. Another bias at play in this dataset is a bias towards larger predators and prey. Larger predators and prey are easier to see in the field and capture. Even if an Asilidae is caught with prey, they sometimes drop it, which can then be lost, especially if the prey item is small. Though this data is biased, it is still important and potentially informative.

Prey preference following phylogeny

Even though Asilidae are top-level aerial predators in the insect world along with Odonata and have an essential role in natural environments, no phylogenetic studies, including prey preference for the family Asilidae published so far. Prey preference has been shown to follow phylogenies and show evolutionary dietary patterns in other animals (Goodheart *et al*. 2017). Though no conclusion can be drawn about the phylogenetic signaling of prey within Asilidae currently, the present dataset, combined with other resources such as the extensive Lavigne (2016) database, may provide enough data to map prey choice across the Asilidae phylogeny appropriately.

Broader picture

This dataset shows the importance of digitizing museum records for the potential taxonomic intended use and the biological information hidden within entomological collections. This dataset is based on only 15 collections, some of which have not been recorded fully. Many more entomological museum collections house similar information and should be included in future studies. Analyzing predator-prey interactions of Asilidae through museum collections provides the unique ability to keep vouchers of these interactions. Asilidae are top aerial predators that exist in almost every ecosystem across the globe. Datasets like this are essential to understanding how important their role is in natural environments.

Acknowledgements

I would like to thank my dissertation committee for providing valuable feedback that improved the manuscript. Many people have generously allowed me to visit their entomological collections or loaned specimens to me to add to this dataset. Their time, help, and loans are greatly appreciated, and the contributors are here listed in alphabetical order: C. Bills (UMNH), B. Brown (LACM ENT) S. Bundy (NMSU), S. Clark (BYU), S. Dennis (USNM), T. Dikow (USNM), C. Grinter (CASENT), G. Hall (UAIC), M. Hauser (CSCA), S. Hayden (BMEC), L. Kimsey (BMEC), G. Kung (LACM ENT), L. Leblanc (WFBM), C. Looney (JWSU), W. Moore (UAIC), R. Nelson (BYU), P. Oboski (EMEC), J. Oswald (TAMUIC), J. Schweikert (CASENT), S. Triapitsyn (UCR), H. Vessels (NMSU), S. Winterton (CSCA), K. Wright (TAMUIC), W. Xie (LACM ENT), and D. Yanega (UCR). I would also like to thank M. Alderman for helping me sort through the extensive Asilidae prey literature referenced in this manuscript. Lastly, I would like to thank my husband for accompanying me to many of these collections and supporting me throughout the writing of this manuscript.

This project was funded with the Lewis and Clark Fund for Exploration and Field Research (2017) and a 10-week graduate student research fellowship at the Smithsonian National Museum of Natural History (USNM), and the previous and continued support from Dr. Lynn Kimsey and Dr. Diane Ullman at the University of California, Davis.

References

Arnett RH, Thomas MC, Skelley PE, Frank JH (eds.) (2002) American Beetles, Volume II: Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press LLC, Boca Raton, FL. 880 pp. ISBN: 0849309549

Bakker F, Antonelli A, Clarke J, Cook J, Edwards S, Ericson PP, Faurby S, Ferrand N, Gelang M, Gillespie R, Irestedt M, Lundin K, Larsson E, Matos-Maraví P, Müller J, von Proschwitz T, Roderick G, Schliep A, Wahlberg N, Wiedenhoeft J, Källersjö M (2020) The Global Museum: natural history collections and the future of evolutionary science and public education. PeerJ. 8. https://doi.org/10.7717/peerj.8225

Barnes JK (2008) Review of the genus *Ceraturgus* Wiedemann (Diptera: Asilidae) in North America north of Mexico. Zootaxa. 1766: 1–45. ISSN 1175-5334. https://doi.org/10.11646/zootaxa.1766.1.1

Blodgett SL, Carrel JE, Higgins RA (1991) Cantharidin content of blister beetles (Coleoptera: Meloidae) collected from Kansas Alfalfa and implications for inducing cantharidiasis. Environmental Entomology. 20(2): 776–780. https://doi.org/10.1093/ee/20.3.776

Bromley SW (1934) The Robber Flies of Texas (Diptera, Asilidae). Annals Entomological Society of America. 27: 74 –113. https://doi.org/10.1093/aesa/27.1.74

Bromley SW (1945) Robber fly and Japanese Beetle. Bulletin of the Brooklyn Entomological Society. 40: 44–47. ISSN: 1051-8932

Bromley SW (1946) Bee-killing Asilidae of the southeastern states (Diptera). Proceedings of the Entomological Society of Washington. 48: 16–17.

Bromley SW (1948a) Honey-bee predators. New York Entomological Society. 56: 195–199. https://www.jstor.org/stable/25005271

Bromley SW (1948b) Insect Predators of Mosquitoes. Proceedings of the Entomological Society of Washington. 50(9): 235–238.

Bromley SW (1949) The Missouri bee-killer, *Proctacanthus milbertii* Macq. (Asilidae: Diptera). Bulletin of the Brooklyn Entomological Society. 44: 21–28. https://biostor.org/reference/239675

Bromley SW (1950) Florida Asilidae (Diptera) with Description of one new species. Annals Entomological Society of America. 43: 227–239. https://doi.org/10/1093/aesa/43.2.227

Bullington SW, Lavigne RJ (1984) Revies of the genus *Ommatius* Wiedemann (Diptera: Asilidae) in Eastern United Sates with descriptions of five new species. Annals of the Entomological Society of America. 77(4): 372–392. https://doi.org/10.1093/aesa/77.4.372

Bullington SW, Lavigne RJ (1992) Ethology of *Cyrtopogon montanus wilcoxi* James (Diptera: Asilidae) in Wyoming. Proceedings of the Entomological Society of Washington. 94(1): 123–131. ISSN 0013-8797 http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=5149078

Cannings RA (2014) The Robber Flies (Diptera: Asilidae) of Western Canadian Grasslands. *In*. Arthropods of Canadian Grasslands (Volume 4): Biodiversity and Systematics Part 2. (eds.) Giberson DJ, Cárcamo HA. Biological Survey of Canada. 269–297. http://dx.doi.org/10.3752/9780968932179.ch7

Cole FR (1958) Prey of robber flies of the genus *Stenopogon* (Diptera: Asilidae). The Pan-pacific Entomologist. 34(3): 176–178. https://digitalcommons.usu.edu/bee_lab_co/410

Cole FR (1969)

Dennis SD (1979) Ethology of *Holcocephala fusca* in Virginia (Diptera, Asilidae). Proceedings of the Entomological Society of Washington. 81: 366–378. http://biostor.org/reference/75985

Dennis SD (2014) Ethology of *Holopogon phaeonotus* Loew, 1874 (Diptera: Asilidae) in Northeastern Florida, U.S.A. Journal of the Entomological Research Society. 16(2): 141–158. https://www.entomol.org/journal/index.php/JERS/article/view/686

Dennis SD (2018) Ethology of *Holopogon snowi* Back, 1909 (Diptera: Asilidae) in Northeastern Florida, U.S.A. Journal of the Entomological Research Society. 20(1): 95–112. https://www.entomol.org/journal/index.php/JERS/article/view/1263

Dennis SD, Lavigne RJ (1975) Comparative behavior of Wyoming robber flies II (Diptera: Asilidae). University of Wyoming Agricultural Experimental Station Science Monograph. 30: 68 pp.

Dennis SD, Lavigne RJ (2012) Spiders (Araneae) as prey of robber flies (Diptera: Asilidae). Journal of the Entomological Research Society. 14(1): 65–76. https://www.entomol.org/journal/inex.php/JERS/article/view/357

Dennis SD, Lavigne RJ, Dennis JG (2010) Hemiptera (Heteroptera/Homoptera) as prey of robber flies (Diptera: Asilidae) with unpublished records. Journal of the Entomological Research Society. 12(1): 27–47. https://www.entomol.org/journal/index.php/JERS/article/view/190

Dikow T (2009) A phylogenetic hypothesis for Asilidae based on a total evidence analysis of morphological and DNA sequence data (Insects: Diptera: Brachycera: Asiloidea). Organisms, Diversity & Evolution. 9: 165–188. https://doi.org/10.1016/j.ode.2009.02.004

Farr TH (1962) A new species of Schildia from Jamaica (Diptera: Asilidae). The Florida Entomologist. 45(4): 191–194. https://doi.org/10.2307/3492401.

Fattig PW (1945) The Asilidae or robber flies of Georgia. Emory University Museum Bulletin. 3: 1–33. https://doi.org/10.1093/aesa/38.3.440.

GBIF.org (2022): GBIF Registry of Scientific Collections. Available from: https://www.gbif.org/grscicoll

Google Earth Pro (2021) Version 7.3.4.8248 Available through: https://www.google.com/earth/version/ [Accessed August 20, 2022].

Haab KA, McKnight TA, McKnight KB (2019) Phenology and ethology of adult *Lasiopogon slossonae* Cole and Wilcox Robber Flies (Diptera: Asilidae) in a New York riparian habitat. Proceedings of the Entomological Society of Washington. 121(4): 594–615. https://doi.org/10.4289/0013-8797.121.4.594

Hobby BM (1930) The British species of Asilidae (Diptera) and their prey. Transactions of the Entomological Society of London. 6:1–42.

Hobby BM (1931a) The relationship between courtship and predacious habits in *Dioctria rufipes* De G., and *D. atricapilla* Mg. (Diptera, Asilidae). Proceedings of the Royal Entomological Society of London. 6.

Hobby BM (1931b) Local abundance as a factor governing prey selection by predacious insects. Proceedings of the Royal Entomological Society of London. 6.

Hobby BM (1932) A study of the prey of *Dioctria rufipes* de G. (Diptera, Asilidae) in an Oxford Community. Journal of Animal Ecology. 1(1): 77–82. https://doi.org/10.2307/997

Kinney KK, Peairs FB, Swinker AM, Ishmael W, Rich G (2006) Blister beetles in forage crops. Colorado State University, Service in action no. 5.524.

Kirk-Spring AH, Sinclair BJ (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. Suricata 5. South African National Biodiversity Institute, Pretoria. 1097–1182.

Lavigne RJ (1970) Courtship and predation behavior of *Heteropogon maculinervis* (Diptera: Asilidae). Journal of the Kansas Entomological Society. 43(3): 270–273. https://www.jstor.org/stable/25082329

Lavigne RJ (1971) *Backomyia seminoensis* sp. n. from Wyoming with ethological notes on *B. limpidipennis*. Journal of the Kansas Entomological Society. 44(3): 337–342. https://www.jstor.org/stable/25082428

Lavigne RJ (1972) Ethology of *Ablautus rufotigbialis* on the Pawnee grasslands IBP site. Journal of the Kansas Entomological Society. 45(3): 271–274. https://www.jstor.org/stable/25082499

Lavigne RJ (1979) Notes of the Ethology of *Efferia argyrogaster* (Diptera: Asilidae) in Mexico. Proceedings of the Entomological Society of Washington. 81(4): 544–551. http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCALZOOLINEINRA8050602399

Lavigne RJ (2016) Predator-prey database. http://www.gellergrimm.de/catalog/lavigne.htm [Accessed 14 July 2022]

Lavigne RJ, Bullington SW (1999) Ethology of *Heteropogon paurosomus* Pritchard (Diptera: Asilidae) in Mexico. Journal of the Entomological Research Society. 1(3): 9–19. ISSN:1302-0250.

Lavigne RJ, Bullington SW, Stephens G (1993) Ethology of *Holopogon seniculus* (Diptera: Asilidae) Annals of the Entomological Society of America. 86(1): 91–95. https://doi.org/10.1093/aesa/86.1.91

Lavigne RJ, Dennis DS (1994) New records of Coleoptera as prey for Asilidae (Diptera) in Wyoming and Colorado. The Coleopterists Bulletin. 48: 131–139. https://www.jstor.org/stable/4009123

Linsley EG (1944) Prey of the robber fly *Callinicus calcaneus* Loew (Diptera: Asilidae). Pan-Pacific Entomologist. 20(2): 67–68.

Londt JGH (1993) Afrotropical robber fly (Diptera: Asilidae) predation of honey bees, *Apis mellifera* Linnaeus (Hymenoptera: Apidae). African Entomology. 1(2): 167–173. https://hdl.handle.net/10520/AJA10213589_57

Londt JGH (2006) Predation by Afrotropical Asilidae (Diptera): an analysis of 2000 prey records. African Entomology. 14(2): 317–328. https://hdl.handle.net/10520/EJC32691

Martin CH (1968) A revision of *Ospriocerus* (Diptera: Asilidae). Proceedings of the California Academy of Sciences fourth series. 35(18): 401–424.

McKenie CB (2019) Presentation: Distribution and prey choice of *Microstylum galactodes* Loew and *M. morosum* Loew (Diptera: Asilidae) in eastern New Mexico and West Texas. Student Ten-Minute Paper Competition (SysEB 2). Entomology 2019.

Melin D (1923) Contributions to the knowledge of the biology, metamorphosis and distribution of the Swedish Asilids in relation to the whole family of Asilids. Zoologiska bidrag från Uppsala. 8: 317 pp.

O'Neill KM, Seibert C (1996) Foraging Behavior of the Robber Fly *Megaphorus willistoni* (Cole) (Diptera: Asilidae). Journal of the Kansas Entomological Society. 69(4): 317–325. https://www.jstor.org/stable/25085691

Pape T, Blagoderov V, Mostovski MB (2011) Order Diptera Linnaeus, 1758. *In*: Z.-Q. (Ed.) Animal Biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa. 3148(1): 224 pp. https://doi,org/10.11646/zootaxa.3148.1.42

Pollock DA (2020) Robber Flies (Diptera: Asilidae) as predators of harvester ant workers (Hymenoptera: Formicidae: *Pogonomyrmex*) in Eastern New Mexico and West Texas. The Southwestern Naturalist. 65(1): 19–27. https://doi.org/10.1894/0038-490965.1.3

Scarbrough AG, Sraver BE (1979) Predatory behavior and prey of *Atomosia puella* (Diptera: Asilidae). Proceedings of the Entomological Society of Washington. 81(4): 630–639. ISSN: 0013-8797

Shorthouse DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. Available from https://www.simplemappr.net [Accessed August 31, 2022]

Wagner JD, Grames EM, Forister ML (2021) Insect decline in the Anthropocene: Death by a thousand cuts. Biological Sciences. 118(2): e2023989118. https://doi.org/10.1073/pnas.2023989118

Wieczorek J, Bloom D, Guralnick R, Blum S, Döring M, Giovanni R, Robertson T, Vieglais D (2012) Darwin Core: An evolving community-developed biodiversity data standard. PLOS One. 7(1). https://doi.org/10.1371/journal.pone.0029715

Winston J (2007) Archives of a small planet: The significance of museum collections and museum-based research in invertebrate taxonomy. Zootaxa. 1668(1): 47–54. https://doi.org/10.11646/zootaxa.1668.1.6

A molecular phylogeny of Assassin Flies (Diptera: Asilidae) with ancestral state reconstruction of arthropod prey preference

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1. Abstract

Assassin flies (Diptera: Asilidae) are a diverse family that plays an essential ecological role as top aerial and venomous predators. Little is known about the evolution of their predatory habits. This study provides a novel phylogenetic hypothesis of Asilidae along with prey preference and ancestral state reconstruction in a maximum likelihood framework. This study is based on 176 assassin fly species, 35 Asiloidea outgroup species, prey preference data accumulated from literature and museum collections, and approximately 7,913 bp of nuclear DNA from five genes (*18S* and *28S* rDNA, *AATS*, *CAD*, and *EF-1*α protein-encoding DNA) and mitochondrial DNA from one gene (*COI*). Of the 12 asilid subfamilies included in the analysis the monophyly of six was supported. We used ancestral state reconstruction and stochastic character mapping to test whether a polyphagous arthropod predator is the ancestral state for Asilidae. Assassin flies are

polyphagous arthropod predators, with specialized arthropod prey preferences evolving 20 times independently across the Asilidae phylogeny.

Keywords

Asilidae, phylogeny, diet, sanger-sequencing, predator, prey

2. Introduction

Asilidae (‘assassin flies’ or ‘robber flies’) are the third most speciose family of Diptera, with more than 550 genera and 7,500 described species (Pape et al. 2011), they are found in all zoogeographical regions except Antarctica. They are essential and unique predators that feed on various arthropod prey (Fig. 3.1., Alberts Chap II; Londt 1994). Assassin flies are the only family within Diptera composed entirely of arthropod predators, both as larvae and adults. Some Dolichopodidae are also arthropod predators as adults and larvae, but not all (Cicero et al. 2017). Their predatory lifestyle is reflected in their distinctive adult appearance. Assassin flies have large eyes with sunken vertex and often enlarged frontal facets for stereoscopic vision-based hunting (Melin 1923). Proportionally long legs are usually covered with bristles and long hairs to help grasp prey when captured in flight. Their faces often have a distinctive mystax or beard of bristles and hairs to protect their eyes from struggling prey (Oldroyd 1964). Lastly, they have a hypodermic needle-like hypopharynx that injects their prey with paralytic neurotoxins and digestive enzymes that quickly incapacitate their prey (Drukewitz et al. 2018). These character states related to proboscis morphology are the only autapomorphies of Asilidae (Dikow 2009) and make them highly effective and ecologically important arthropod predators (Bromley 1945, 1950; Londt 1993; Resh and Cardé 2009).

Fig. 3.1. Photographs of select representatives of Asilidae with prey. **A**. *Laphria thoracica* (with Apidae prey) by Paul Reeves Photography, **B**. *Asilus sericeus* (with Lepidoptera prey) by David Mozzoni, **C**. *Hoplistomerus nobilis* (with Coleoptera prey) by Tamara Szentivanyi, **D**.

Saropogon pyrodes (with Hymenoptera prey) by Jeff Gruber, **E**. *Promachus rufus* (with *Apis mellifera* prey) by Rose Payne, and **F**. *Ospriocerus aeacus* (with Meloidae prey) by Jeff Gruber.

There is a consensus in the Asilidae scientific community that assassin flies are opportunistic predators with little preference for what prey they hunt and consume (Cannings 2014; Lavigne 2016; Londt and Dikow 2017; Alberts Chap II). However, there is significant evidence of variable prey specificity within Asilidae. Some species prefer a generalized diet of arthropod prey while other Asilidae prefer a particular family of prey (Londt 1994; Pollock 2019, 2021; Alberts Chap. II). Preferring or strictly eating a particular prey type can significantly impact the environment. For example, there have been many reports of certain species of Asilidae decimating apiaries (Bromley 1945, 1950; Londt 1993) or taking advantage of an emergence event such as alate ants and potentially impacting the population (Londt 1991). Though these are of great economic and ecological concern, especially regarding honey bees because society depends heavily on them for agriculture, there are just as many potentially beneficial predator-prey interactions, such as mosquitoes (Culicidae: Harmston 1948; Newkirk 1963), black flies (Simuliidae: Werner and Pont 2003), invasive Japanese beetles (*Popillia japonica:* Bromley 1945a), house flies (*Musca domestica*: Bromley 1945b), invasive Hymenoptera (*Bombus terrestris*: Barahona-Segovia and Pañinao-Monsálvez 2020), and blister beetles (Meloidae: Lavigne and Dennis 1994).

The higher classification problems across the family are still being resolved, and further phylogenetic studies are needed to clarify our understanding of the relationships between taxa (Papavero 1973, Bybee et al. 2004, Dikow 2009a, 2009b; Cohen et al. 2021). Herein we propose a phylogeny based on 176 Asilidae species (211 total taxa) using 7,913 bp of five nuclear genes (18S, 28S, CAD, *EF-1α*, AATS) and one mitochondrial gene (COI), as well as providing the first attempt at understanding arthropod prey specialization through ancestral state reconstruction and stochastic character mapping. Predator-prey data is accumulated from the Lavigne (2016) predator-prey literature reference database and a museum predator-prey specimen database (Alberts Chap. II). This study attempts to test four hypotheses:

1) The majority of Asilidae are polyphagous arthropod predators.
2) The most recent common ancestor was a polyphagous arthropod predator.
3) Oligophagous and specialist arthropod predators have evolved multiple times within Asilidae.
4) Further test subfamily relationships and monophyly within Asilidae.

3. Materials and methods

3.1. Taxon sampling and DNA acquisition

Both previously published (Dikow 2009b) and unpublished genomic DNA sequences are included here. Despite the addition of 123 specimens, the subfamily sampling remains the same as in Dikow (2009b), with 12 of the 14 subfamily taxa proposed in Dikow (2009a) being represented. The missing two subfamilies are Bathypogoninae and Phellinae, two species-poor southern Hemisphere taxa.

The outgroup taxa are sampled extensively, with 35 species represented within six families (Apioceridae, Apsilocephalidae, Bombyliidae, Mydidae, Nemestrinidae, Scenopinidae, and Therevidae). We chose to include these specimens for future comparison between this sanger-based study and an in-progress Asiloidea ultra-conserved elements (UCE) phylogenetic study (Alberts et al. in prep). Many of the relationships within Asiloidea remain unresolved (Dikow 2009a, 2009b; Trautwein et al. 2010, Winterton and Ware 2015, Winterton and Hardy 2016, Shin et al. 2018), and these two studies aim to resolve some of these issues (see Table 3.1 for a list of all included taxa and supplemental material 3.1 for more information). In 29 cases where the species identification is not certain, 'sp.' is given along with the collecting locality as a reference for future studies. "These species are either undescribed or belong to speciose genera which need to be revised before species identification can be undertaken" (Dikow 2009b).

Table 3.1. Specimens included (Diptera: Asiloidea) with family, subfamily, and locality. Specimens are in alphabetical order by species name. Full locality information can be found in supplemental material 3.1.

Name	**Family: Subfamily**	**Locality**
***Ablautus coquilletti* Wilcox, 1935**	Asilidae: Willistonininae	NEA - USA, Arizona
Ablautus sp.	Asilidae: Willistonininae	NEA - USA, Oregon
***Acasilus tigrimontis* Londt, 2005**	Asilidae: Asilinae	AFR - South Africa, Northern Cape
***Afroestricus chiastoneurus* (Speiser, 1910)**	Asilidae: Ommatiinae	AFR - South Africa, KwaZulu-Natal
***Afroholopogon mauros* Londt, 2005**	Asilidae: Brachyrhopalinae	AFR - South Africa, Northern Cape
Afroleptomydas sp.	Mydidae: Syllegomydinae	AFR - South Africa, Western Cape
Afroleptomydas sp.	Mydidae: Syllegomydinae	AFR - South Africa
Alcimus sp.	Asilidae: Asilinae	AFR - South Africa, Northern Cape
***Ammophilomima indiae* Martin, 1973**	Asilidae: Leptogastrinae	ORI - India, Karnataka
Ammophilomima sp.	Asilidae: Leptogastrinae	ORI - Singapore
***Ancylorhynchus cruciger* (Loew, 1858)**	Asilidae: Stenopogoninae	AFR - South Africa, Limpopo

***Anypodetus arachnoides* Oldroyd, 1974**	Asilidae: Laphriinae	AFR - South Africa, Northern Cape
***Anypodetus fasciatus* Hermann, 1907**	Asilidae: Laphriinae	AFR - South Africa, Northern Cape
***Apachekolos crinita* Martin, 1957**	Asilidae: Leptogastrinae	NEA - USA, Arizona
***Apachekolos scapularis* (Bigot, 1878)**	Asilidae: Leptogastrinae	NEA - USA, California
***Apachekolos tenuipes* (Loew, 1862)**	Asilidae: Leptogastrinae	NEA - USA, Tennessee
Aphoebantus sp.	Bombyliidae: Lomatiinae	NEA - USA, Arizona
***Apiocera (Pyrocera) haruspex* Osten Sacken, 1877**	Apioceridae: N/A	AUS - Australia, Queensland
***Apiocera (Pyrocera) painteri* Cazier, 1963**	Apioceridae: N/A	NEA - Mexico, Baja California Norte
Apiocera sp.	Apioceridae: N/A	NEA - USA, Arizona
***Apsilocephala longistyla* (Kröber, 1914)**	Apsilocephalidae: N/A	NEA - USA, Utah
***Asilus crabroniformis* Linnaeus, 1758**	Asilidae: Asilinae	PAL - United Kingdom, Wales
***Asilus sericeus* Say, 1823**	Asilidae: Asilinae	NEA - USA, Connecticut
***Astochia armata* (Becker, 1909)**	Asilidae: Asilinae	AFR - South Africa, KwaZulu-Natal
***Atomosia mucida* Osten Sacken, 1887**	Asilidae: Laphriinae	NEA - USA, Arizona
***Atomosia puella* (Wiedemann, 1828)**	Asilidae: Laphriinae	NEA - USA, New York
***Atractia marginata* (Osten Sacken, 1887)**	Asilidae: Laphriinae	NEO - Costa Rica, Alajuela
***Beameromyia bifida* (Hardy, 1942)**	Asilidae: Leptogastrinae	NEA - USA, Arizona
***Beameromyia disfascia* (Martin, 1957)**	Asilidae: Leptogastrinae	NEA - USA, Rhode Island
***Beameromyia lacinia* Martin, 1957**	Asilidae: Leptogastrinae	NEA - USA, Arizona
***Bombylius major* Linnaeus, 1758**	Bombyliidae: Bombyliinae	NEA - USA, North Carolina
***Cephalocera imitata* Hesse, 1969**	Mydidae: Syllegomydinae	AFR - South Africa, Western Cape
Cephalocera sp.	Mydidae: Syllegomydinae	AFR - South Africa, Western Cape
***Ceraturgus fasciatus* Walker, 1849**	Asilidae: Brachyrhopalinae	NEA - USA, Rhode Island
***Cerotainia albipilosa* Curran, 1930**	Asilidae: Laphriinae	NEA - USA, Illinois
***Cerotainia macrocera* (Say, 1823)**	Asilidae: Laphriinae	NEA - USA, Illinois
***Choerades bella* (Loew, 1858)**	Asilidae: Laphriinae	AFR - South Africa, KwaZulu-Natal
***Choerades marginata* (Linnaeus, 1758)**	Asilidae: Laphriinae	PAL - Germany, Thüringen
Clephydroneura sp.	Asilidae: Asilinae	ORI - Malaysia, Selangor
***Connomyia leonina* (Engel, 1932)**	Asilidae: Stenopogoninae	AFR - South Africa, KwaZulu-Natal
***Connomyia varipennis* (Ricardo, 1925)**	Asilidae: Stenopogoninae	AFR - South Africa, KwaZulu-Natal
***Cophinopoda pulchripes* (Bigot, 1859)**	Asilidae: Ommatiinae	AFR - Madagascar, Mahajanga
***Cyrtopogon rattus* Osten Sacken, 1877**	Asilidae: Brachyrhopalinae	NEA - USA, Oregon
***Cyrtopogon vandykei* Wilcox and Martin, 1936**	Asilidae: Brachyrhopalinae	NEA - USA, California
***Damalis annulata* Loew, 1858**	Asilidae: Trigonomiminae	AFR - South Africa, Western Cape
***Damalis brevis* Scarborough, 2005**	Asilidae: Trigonomiminae	ORI - Malaysia, Selangor

Damalis monochaetes **Londt, 1989**	Asilidae: Trigonomiminae	AFR - South Africa, KwaZulu-Natal
Damalis sp.	Asilidae: Trigonomiminae	ORI - India, Kerala
Damalis sp.	Asilidae: Trigonomiminae	ORI - Singapore
Dasophrys crenulatus **Londt, 1981**	Asilidae: Asilinae	AFR - South Africa, KwaZulu-Natal
Dasypogon diadema **(Fabricius, 1781)**	Asilidae: Dasypogoninae	PAL - Germany, Hessen
Dasypogon sp.	Asilidae: Dasypogoninae	PAL - Spain, Islas Baleares
Dioctria atricapilla **Meigen, 1804**	Asilidae: Dioctriinae	PAL - Germany, Mecklenburg-Vorpommern
Dioctria hyalipennis **(Fabricius, 1794)**	Asilidae: Dioctriinae	NEA - USA, New York
Dioctria hyalipennis **(Fabricius, 1794)**	Asilidae: Dioctriinae	PAL - Germany, Hessen
Dioctria rufipes **(De Geer, 1776)**	Asilidae: Dioctriinae	PAL - Germany, Mecklenburg-Vorpommern
Dioctria vera **(Back, 1909)**	Asilidae: Dioctriinae	NEA - USA, New Mexico
Diogmites angustipennis **Loew, 1866**	Asilidae: Dasypogoninae	NEA - USA, Oregon
Dipalta serpentina **Osten Sacken, 1877**	Bombyliidae: Anthracinae	NEA - USA, New Mexico
Dysmachus trigonus **(Meigen, 1804)**	Asilidae: Asilinae	PAL - Germany, Hessen
Efferia aestuans **(Linnaeus, 1763)**	Asilidae: Asilinae	NEA - USA, Rhode Island
Efferia albibarbis **(Macquart, 1838)**	Asilidae: Asilinae	NEA - USA, Connecticut
Efferia pogonias **(Wiedemann, 1821)**	Asilidae: Asilinae	NEA - USA, New York
Efferia producta **(Hine, 1919)**	Asilidae: Asilinae	NEA - USA, California
Efferia sp.	Asilidae: Asilinae	NEA - USA, Arizona
Emphysomera conopsoides **(Wiedemann, 1828)**	Asilidae: Ommatiinae	ORI - Malaysia, Sabah
Emphysomera pallidapex **(Bigot, 1891)**	Asilidae: Ommatiinae	AFR - South Africa, Limpopo
Eudioctria albius **(Walker, 1849)**	Asilidae: Dioctriinae	NEA - USA, Tennessee
Eudioctria brevis **(Banks, 1941)**	Asilidae: Dioctriinae	NEA - USA, Rhode Island
Eudioctria denuda **(Wilcox and Martin, 1941)**	Asilidae: Dioctriinae	NEA - USA, California
Euscelidia brunnea **(Loew, 1858)**	Asilidae: Leptogastrinae	AFR - South Africa, KwaZulu-Natal
Euscelidia pulchra **Dikow, 2003**	Asilidae: Leptogastrinae	AFR - South Africa, KwaZulu-Natal
Euscelidia zumpti **Janssens, 1957**	Asilidae: Leptogastrinae	AFR - South Africa, KwaZulu-Natal
Gonioscelis ventralis **Schiner, 1867**	Asilidae: Stenopogoninae	AFR - South Africa, Northern Cape
Gonioscelis zulu **Londt, 2004**	Asilidae: Stenopogoninae	AFR - South Africa, KwaZulu-Natal
Heligmonevra sp.	Asilidae: Asilinae	AFR - South Africa, KwaZulu-Natal
Hemigephyra atra **Lyneborg, 1972**	Therevidae: Xestomyzinae	AFR - South Africa, Western Cape
Hemipenthes jaennickeana **(Osten Sacken, 1886)**	Bombyliidae: Anthracinae	NEA - USA, New Mexico
Heteropogon cirrhatus **(Osten Sacken, 1877)**	Asilidae: Brachyrhopalinae	NEA - USA, California

Heteropogon spatulatus Pritchard, 1935	Asilidae: Brachyrhopalinae	NEA - USA, New Mexico
Holcocephala abdominalis Say, 1823	Asilidae: Trigonomiminae	NEA - USA, New York
Holcocephala calva (Loew, 1872)	Asilidae: Trigonomiminae	NEA - USA, New York
Holopogon phaeonotus Loew, 1874	Asilidae: Brachyrhopalinae	NEA - USA, Rhode Island
Hoplistomerus nobilis Loew, 1858	Asilidae: Laphriinae	AFR - South Africa, KwaZulu-Natal
Ischiolobos mesotopos (Londt, 2005)	Asilidae: Brachyrhopalinae	AFR - South Africa, KwaZulu-Natal
Lamyra gulo (Loew, 1851)	Asilidae: Laphriinae	AFR - South Africa, KwaZulu-Natal
Laphria aktis McAtee, 1919	Asilidae: Laphriinae	NEA - USA, New York
Laphria felis (Osten Sacken, 1877)	Asilidae: Laphriinae	NEA - USA, New Mexico
Laphria grossa (Fabricius, 1775)	Asilidae: Laphriinae	NEA - USA, Rhode Island
Laphria sicula (McAtee, 1919)	Asilidae: Laphriinae	NEA - USA, Illinois
Laphria sp.	Asilidae: Laphriinae	PAL - Italy, Piemonte
Laphria thoracica Fabricius, 1805	Asilidae: Laphriinae	NEA - USA, New York
Laphystia cf. canadensis (Curran, 1927)	Asilidae: Laphriinae	NEA - USA, Utah
Laphystia tolandi Wilcox, 1960	Asilidae: Laphriinae	NEA - USA, Oregon
Laphystotes ariel Londt, 2004	Asilidae: Laphriinae	AFR - South Africa, Northern Cape
Lasiocnemus lugens Loew, 1858	Asilidae: Leptogastrinae	AFR - South Africa, KwaZulu-Natal
Lasiopogon aldrichii Melander, 1923	Asilidae: Stichopogoninae	NEA - USA, Oregon
Lasiopogon cinctus (Fabricius, 1781)	Asilidae: Stichopogoninae	PAL - Germany, Mecklenburg-Vorpommern
Lasiopogon sp.	Asilidae: Stichopogoninae	NEA - USA, California
Laxenecera albicincta (Loew, 1852)	Asilidae: Laphriinae	AFR - South Africa, KwaZulu-Natal
Laxenecera engeli (Oldroyd, 1974)	Asilidae: Laphriinae	AFR - South Africa, Northern Cape
Leptarthrus brevirostris (Meigen, 1804)	Asilidae: Brachyrhopalinae	PAL - Germany, Bayern
Leptogaster aganniphe Janssens, 1957	Asilidae: Leptogastrinae	AFR - South Africa, Northern Cape
Leptogaster arborcola Martin, 1957	Asilidae: Leptogastrinae	NEA - USA, Utah
Leptogaster arida Cole, 1919	Asilidae: Leptogastrinae	NEA - USA, Utah
Leptogaster carotenoides Tomasovic, 1999	Asilidae: Leptogastrinae	AFR - South Africa, KwaZulu-Natal
Leptogaster cf. eudicrana Loew, 1874	Asilidae: Leptogastrinae	NEA - USA, Arizona
Leptogaster cylindrica (De Geer, 1776)	Asilidae: Leptogastrinae	PAL - Germany, Mecklenburg-Vorpommern
Leptogaster flavipes Loew, 1862	Asilidae: Leptogastrinae	NEA - USA, Rhode Island
Leptogaster lanata Martin, 1957	Asilidae: Leptogastrinae	NEA - USA, Arizona
Leptogaster pubicornis Loew, 1847	Asilidae: Leptogastrinae	PAL - Italy, Lombardia
Lestomyia fraudiger Williston, 1883	Asilidae: Dasypogoninae	NEA - USA, California
Lestomyia sp.	Asilidae: Dasypogoninae	NEA - USA, California
Lobus sp.	Asilidae: Leptogastrinae	AFR - South Africa, Western Cape

***Lycostommyia albifacies* (Hermann, 1907)**	Asilidae: Tillobromatinae	AFR - South Africa, Northern Cape
***Machimus autumnalis* (Banks, 1914)**	Asilidae: Asilinae	NEA - USA, New York
***Machimus callidus* (Williston, 1893)**	Asilidae: Asilinae	NEA - USA, Oregon
***Machimus occidentalis* (Hine, 1909)**	Asilidae: Asilinae	NEA - USA, Oregon
***Mahafalymydas wiegmanni* Kondratieff, Carr, and Irwin, 2005**	Mydidae: Syllegomydinae	AFR - Madagascar, Toliara
***Mallophora nigrifemorata* Macquart, 1838**	Asilidae: Asilinae	NEO - Costa Rica, Heredia
***Megaphorus pulcher* (Pritchard, 1935)**	Asilidae: Asilinae	NEA - USA, New Mexico
Mesoleptogaster sp.	Asilidae: Leptogastrinae	ORI - Malaysia, Pahang/Selangor
***Messiasia californica* (Cole, 1969)**	Mydidae: Mydinae	NEA - USA, Arizona
***Metatrichia bulbosa* (Osten Sacken, 1877)**	Scenopinidae: Scenopininae	NEA - USA, Arizona
***Michotamia compedita* (Wiedemann, 1828)**	Asilidae: Ommatiinae	ORI - India, Kerala
Microstylum sp.	Asilidae: Stenopogoninae	AFR - South Africa, KwaZulu-Natal
***Miltinus cardinalis* Gerstaecker, 1868**	Mydidae: Apiophorinae	AUS - Australia, New South Wales
***Mitrodetus dentitarsis* (Macquart, 1850)**	Mydidae: Diochlistinae	NEO - Chile, Santiago
***Molobratia teutonus* (Linnaeus, 1767)**	Asilidae: Dasypogoninae	PAL - France, Gard
***Mydas arizonensis* Wilcox, Papavero, and Pimentel, 1989**	Mydidae: Mydinae	NEA - USA, Arizona
***Mydas clavatus* (Drury, 1773)**	Mydidae: Mydinae	NEA - USA, North Carolina
***Nannolaphria nigra* Londt, 1977**	Asilidae: Laphriinae	AFR - South Africa, KwaZulu-Natal
***Nemomydas brachyrhynchus* (Osten Sacken, 1886)**	Mydidae: Leptomydinae	NEA - USA, Arizona
Nemomydas sp.	Mydidae: Leptomydinae	NEA - USA, Mexico
***Nemomydas venosus* (Loew, 1866)**	Mydidae: Leptomydinae	NEA - USA, New Mexico
***Neoitamus cyanurus* (Loew, 1849)**	Asilidae: Asilinae	PAL - Germany, Mecklenburg-Vorpommern
***Neoitamus flavofemoratus* (Hine, 1909)**	Asilidae: Asilinae	NEA - USA, New York
***Neolophonotus bimaculatus* Londt, 1986**	Asilidae: Asilinae	AFR - South Africa, Northern Cape
***Neolophonotus kalahari* Londt, 1985**	Asilidae: Asilinae	AFR - South Africa, Northern Cape
***Neolophonotus pellitus* (Wiedemann, 1819)**	Asilidae: Asilinae	AFR - South Africa, Northern Cape
***Nicocles politus* (Say, 1823)**	Asilidae: Brachyrhopalinae	NEA - USA, Connecticut
***Nusa infumata* (Loew, 1851)**	Asilidae: Laphriinae	AFR - South Africa, KwaZulu-Natal
***Ommatius flavipes* Macquart, 1834**	Asilidae: Ommatiinae	AFR - South Africa, KwaZulu-Natal
***Ommatius parvulus* Schaeffer, 1916**	Asilidae: Ommatiinae	NEA - USA, Arizona
***Ommatius terminalis* (Bromley, 1936)**	Asilidae: Ommatiinae	AFR - South Africa, KwaZulu-Natal
***Ommatius tibialis* (Say, 1823)**	Asilidae: Ommatiinae	NEA - USA, Rhode Island
***Ophionomima solocifemur* (Enderlein, 1914)**	Asilidae: Leptogastrinae	ORI - Singapore

***Opomydas townsendi* (Williston, 1898)**	Mydidae: Ectyphinae	NEA - USA, Arizona
***Ospriocerus aeacus* (Wiedemann, 1828)**	Asilidae: Stenopogoninae	NEA - USA, New Mexico
***Pamponerus germanicus* (Linnaeus, 1758)**	Asilidae: Asilinae	PAL - Germany, Mecklenburg-Vorpommern
***Paracosmus rubicundus* Melander, 1950**	Bombyliidae: Tomomyzinae	NEA - USA, Arizona
***Pegesimallus aulicus* (Wiedemann, 1828)**	Asilidae: Dasypogoninae	AFR - South Africa, KwaZulu-Natal
***Pegesimallus laticornis* (Loew, 1858)**	Asilidae: Dasypogoninae	AFR - South Africa, Northern Cape
***Perasis transvaalensis* Ricardo, 1925**	Asilidae: Laphriinae	AFR - South Africa, Limpopo
Pherocera sp.	Therevidae: Phycinae	NEA - USA, Arizona
***Philodicus fraterculus* (Walker, 1855)**	Asilidae: Asilinae	AFR - South Africa, Limpopo
Philodicus sp.	Asilidae: Asilinae	ORI - Malaysia, Selangor
***Philodicus tenuipes* Loew, 1858**	Asilidae: Asilinae	AFR - South Africa, KwaZulu-Natal
***Philonicus albiceps* (Meigen, 1820)**	Asilidae: Asilinae	PAL - Germany, Mecklenburg-Vorpommern
***Philonicus arizonensis* (Williston, 1893)**	Asilidae: Asilinae	NEA - USA, Arizona
***Philonicus fuscatus* (Hine, 1909)**	Asilidae: Asilinae	NEA - USA, Massachusetts
***Philonicus plebeius* (Osten Sacken, 1887)**	Asilidae: Asilinae	NEA - USA, New Mexico
***Phycus frommeri* Webb and Irwin, 1988**	Therevidae: Phycinae	NEA - USA, California
***Pilica erythrogaster* (Wiedemann, 1828)**	Asilidae: Laphriinae	NEO - Costa Rica, Heredia
***Pilica formidolosa* (Walker, 1860)**	Asilidae: Laphriinae	NEO - Costa Rica, Heredia
Plesiomma sp.	Asilidae: Stenopogoninae	NEO - Nicaragua, Granada
***Proctacanthella cacopiloga* (Hine, 1909)**	Asilidae: Asilinae	NEA - USA, Utah
***Proctacanthus nearno* (Martin, 1962)**	Asilidae: Asilinae	NEA - USA, New Mexico
***Proctacanthus philadelphicus* Macquart, 1838**	Asilidae: Asilinae	NEA - USA, New York
***Proctacanthus rufus* Williston, 1885**	Asilidae: Asilinae	NEA - USA, Rhode Island
***Prolatiforceps fulviventris* (Schaeffer, 1916)**	Asilidae: Asilinae	NEA - USA, Arizona
***Prolepsis tristis* (Walker, 1851)**	Asilidae: Stenopogoninae	NEA - USA, AR - Arkansas
***Promachus albifacies* Williston, 1885**	Asilidae: Asilinae	NEA - USA, Utah
***Promachus amastrus* (Walker, 1849)**	Asilidae: Asilinae	AFR - South Africa, KwaZulu-Natal
***Promachus rufipes* (Fabricius, 1775)**	Asilidae: Asilinae	NEA - USA, North Carolina
Promachus sp.	Asilidae: Asilinae	AFR - South Africa, Northern Cape
Prorates sp.	Scenopinidae: Proratinae	NEA - USA, Utah
***Psilonyx annulatus* (Say, 1823)**	Asilidae: Leptogastrinae	NEA - USA, Tennessee
***Pycnopogon fasciculatus* (Loew, 1847)**	Asilidae: Brachyrhopalinae	PAL - Italy, Sicilia
***Rhabdogaster pedion* Londt, 2006**	Asilidae: Brachyrhopalinae	AFR - South Africa, KwaZulu-Natal
***Rhaphiomidas hasbroucki* Cazier, 1985**	Mydidae: Rhaphiomidinae	NEA - USA, Arizona
***Rhaphiomidas parkeri* Cazier, 1941**	Mydidae: Rhaphiomidinae	NEA - USA, California
***Rhaphiomidas xanthos* Townsend, 1895**	Mydidae: Rhaphiomidinae	NEA - Mexico, Baja California Sur

***Rhipidocephala* sp.**	Asilidae: Trigonomiminae	AFR - South Africa, KwaZulu-Natal
***Saropogon luteus* Coquillett, 1904**	Asilidae: Dasypogoninae	NEA - USA, California
***Scenopinus fenestralis* (Linnaeus, 1758)**	Scenopinidae: Scenopininae	NEA - USA, New Jersey
***Scylaticus costalis* (Wiedemann, 1819)**	Asilidae: Stenopogoninae	AFR - South Africa, KwaZulu-Natal
***Sporadothrix gracilis* Hermann, 1908**	Asilidae: Willistonininae	AFR - South Africa, Northern Cape
***Stenopogon albibasis* Bigot, 1878**	Asilidae: Stenopogoninae	NEA - USA, California
***Stenopogon rufibarbis* Bromley, 1931**	Asilidae: Stenopogoninae	NEA - USA, California
***Stichopogon catulus* Osten Sacken, 1887**	Asilidae: Stichopogoninae	NEA - USA, Arizona
***Stichopogon elegantulus* (Meigen, 1820)**	Asilidae: Stichopogoninae	PAL - Israel, Negev
***Stichopogon hermanni* Bezzi, 1910**	Asilidae: Stichopogoninae	AFR - South Africa, Northern Cape
***Stichopogon punctus* Loew, 1851**	Asilidae: Stichopogoninae	AFR - South Africa, KwaZulu-Natal
***Stichopogon trifasciatus* (Say, 1823)**	Asilidae: Stichopogoninae	NEA - USA, Connecticut
***Stiphrolamyra angularis* (Loew, 1858)**	Asilidae: Laphriinae	AFR - South Africa, Northern Cape
***Stiphrolamyra schoemani* (Londt, 1983)**	Asilidae: Laphriinae	AFR - South Africa, Northern Cape
***Syllegomydas palestinensis* Bequaert, 1961**	Mydidae: Syllegomydinae	PAL - Israel, South
***Synolcus dubius* (Macquart, 1846)**	Asilidae: Asilinae	AFR - South Africa, KwaZulu-Natal
***Tillobroma punctipennis* (Philippi, 1865)**	Asilidae: Tillobromatinae	NEO - Chile, Araucanía
***Tipulogaster glabrata* (Wiedemann, 1828)**	Asilidae: Leptogastrinae	NEA - USA, Tennessee
***Tolmerus atricapillus* (Fallen, 1814)**	Asilidae: Asilinae	PAL - Germany, Mecklenburg-Vorpommern
***Toxophora maxima* Coquillett, 1886**	Bombyliidae: Toxophorinae	NEA - USA, Arizona
***Trichardis effrena* Londt, 2008**	Asilidae: Laphriinae	AFR - South Africa, Northern Cape
***Trichophthalma* sp.**	Nemestrinidae: Nemestrininae	AUS - Australia, Queensland
***Trichoura pardeos* Londt and Dikow, 2016**	Asilidae: Willistonininae	AFR - South Africa, Northern Cape
***Trigonomima* sp.**	Asilidae: Trigonomiminae	ORI - Malaysia, Selangor
***Triorla interrupta* (Macquart, 1834)**	Asilidae: Asilinae	NEA - USA, Arizona
***Wilcoxius acutulus* Martin, 1975**	Asilidae: Asilinae	NEO - Nicaragua, Rivas
***Willistonina bilineata* (Williston, 1883)**	Asilidae: Willistonininae	NEA - USA, California
***Wyliea mydas* (Brauer, 1885)**	Asilidae: Asilinae	NEA - USA, New Mexico

For this study, we included six genes, for a total of 7,913 base pairs (bp) of DNA, Fig 3.2; 2,000 bp of the nuclear ribosomal gene *18S*, 2,200 bp of the nuclear ribosomal gene (*28S*; Bertone et al. 2008), 658 bp of the mitochondrial gene Cytochrome Oxidase I (*COI*; Simon et al. 1994), three protein-encoding genes: 1,100 bp of the Elongation Factor-1 alpha (*EF-1*α*;* Friedlander et al.

1992), 1,405 bp of carbamoyl-phosphate synthase (CPS) domain of carbamoyl-phosphate synthetase 2, aspartate transcarbamylase and dihydroorotase (*CAD*; Moulton and Wiegmann 2004), and 550 bp of the protein-coding nuclear gene alanyl-tRNA-synthetase (AATS-ala; Wiegmann et al. 2009).

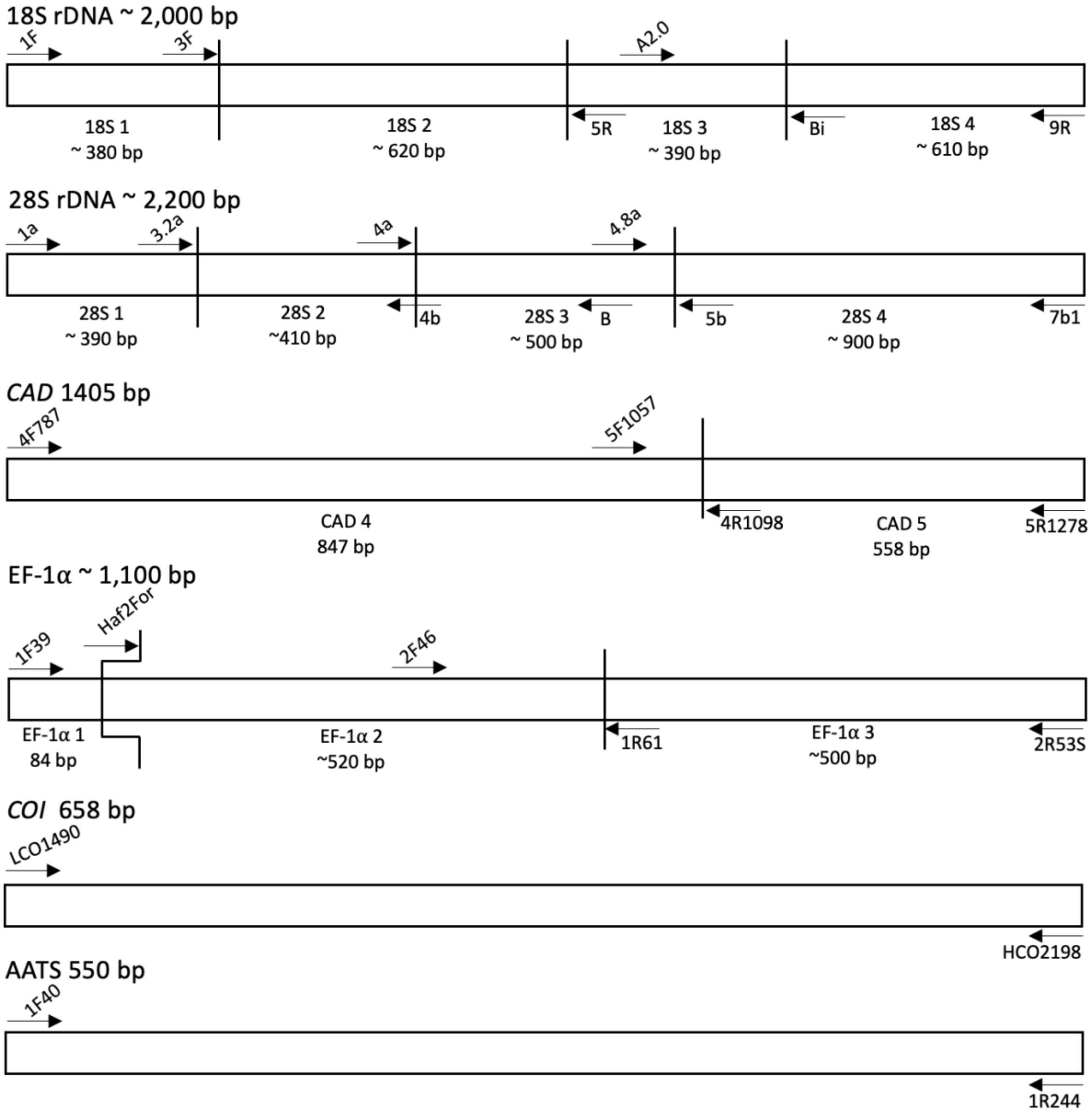

Fig. 3.2. Schematic maps of genes with amplification primers and cutting points for fragments of ML analysis are indicated. Based on Figure 1 published initially in Dikow (2009b) with the addition of *COI* and *AATS*.

Dikow (2009b) states that each of the four genes previously published at the time (1*8S*, *28S*, *EF-1α.*, and *CAD*) were chosen because they have been widely used in Diptera studies (e.g., Wiegmann et al. 2000; Yang et al. 2000; Collins and Wiegmann 2002; Whiting 2002; Moulton 2003; Bybee et al. 2004; Moulton and Wiegmann 2004 2007; Holston et al. 2007; Winterton et al. 2007) and are suitable genetic markers for radiations within Asiloidea. When Dikow (2009b) was published, *AATS* was a novel gene locus for phylogenetic studies introduced by Wiegmann et al. (2009). In addition, *COI* has been used in various Diptera studies (e.g., Bernasconi et al. 2000; Mengual et al. 2008; Zhang et al. 2010; Morita et al. 2016). Through funding by the Smithsonian Institution Barcode Initiative, *COI* was sequenced for all specimens available to the second author in 2013 to provide *COI* barcode sequences for authoritatively identified Asiloidea flies.

3.2. DNA extraction, amplification, and sequencing

All nuclear genes were extracted, amplified, and sequenced following the methods stated in Dikow (2009b). The primer sequences used to amplify the genes are listed in Table 3.2. The amplification and DNA sequencing took place between 2004 – 2007 (4 genes, Dikow 2009b), 2008 – 2012 (5 genes, additional taxa), and 2013 (*COI*, all taxa). The samples were extracted for *COI* using the silica-based protocol outlined in Ivanova, deWaard, and Hebert (2006). DNA samples are PCR amplified and sequenced following protocols detailed in Hebert et al. (2013) and Prosser et al. (2015) that target overlapping fragments of the cytochrome c oxidase I (COI) gene.

Table 3.2. Primer sequences for genes amplified. Modified from Table 1 in Dikow (2009b). "p.c." stands for personal communication with Dikow.

Gene Fragment	Primer	Sequence	Source and remarks
18S 1	1F	TACCTGGTTGATCCTGCCAGTAG	Giribet at al. (1996)
	5R	CTTGGCAAATGCTTTCGC	Giribet at al. (1996)
18S 2	3F	GTTCGATTCCGGAGAGGGA	Giribet at al. (1996)
	Bi	GAGTCTCGTTCGTTATCGGA	Giribet at al. (1996)
18S 3	A2.0	ATGGTTGCAAAGCTGAAAC	Giribet at al. (1996)
	9R	GATCCTTCCGCAGGTTCACCTAC	Giribet at al. (1996)
28S 1	1a	CCCSCGTAAYTTAGGCATAT	Whiting (2002)
	4b	CCTTGGTCCGTGTTTCAAGAC	Whiting (2002)
28S 2	3.2a	TCGGAAGGAACCAGCTACTA	Whiting (2002)
	B	TCGGAAGGAACCAGCTACTA	Whiting (2002)
28S 3	4a	GGAGTCTAGCATGTGYGCAAGTC	Whiting (2002)
	5b	CCACAGCGCCAGTTCTGCTTACC	Whiting (2002)
28S 4	4.8a	ACCTATTCTCAAACTTTAAATGG	Whiting (2002)
	7b1	GACTTCCCTTACCTACAT	Whiting (2002)
AATS	1F40	GNATGAAYCARTTYAARCCNAT	Kim & Wiegmann p.c.
	1R244	CATNCCRCARTCNATRTGYTT	Kim & Wiegmann p.c.
CAD 4	4F787	GGDGTNACNACNGCNTGYTTYGARCC	Moulton & Wiegmann (2004)
	4R1098	TTNGGNAGYTGNCCNCCCAT	Moulton & Wiegmann (2004)
CAD 5	5F1057	ACNGAYTAYGAYATGTGYGA	Moulton & Wiegmann (2004)

	5R1278	TCRTTNTTYTTWGCRATYAAYTGCAT	Moulton & Wiegmann (2004)
EF-1α 1	1F72	GGGCAAGGAAAAGATTCACATTAAC	Scheffer & Wiegmann p.c. (=EF46F)
	1F39	CACCACTGGACATTTGATTTA	Dikow (2009b)
	1R61	GATGGTTCCAACATGTTGTC	Scheffer & Wiegmann p.c. (=AGEF61R)
EF-1α 2	2F46	TGAGGAAATCAAGAAGGAAG	Scheffer & Wiegmann p.c. (= EF46F)
	HaF2For	GGGYAAAGGWTCCTTCAARTATGC	Danforth et al. (1999)
	2R53S	GCGAACTTGCAAGCAATGTGAGC	Scheffer & Wiegmann p.c. (= EF53R)
	2R71L	CTTGCCCTTGGTGGCCTTCTCGG	Scheffer & Wiegmann p.c. (= EF71R)
COI 1	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	

3.3 Preparation and storage of sequence data

Primer sites were used to cut the sequences at the homologous sites, as illustrated (Figure 3.2, see also Dikow 2009b). All sequences were split into fragments, except *AATS* and *COI*, based on primer sites according to Figure 3.2. Each fragment was aligned separately with MUSCLE (Edgar 2004) as implemented in AliView (Larsson 2014). Each non-ribosomal (*AATS*, C*AD*, *Ef-1α*, *COI*) alignment was then examined by eye and edited to ensure that the corresponded to the amino acid triplets. Finally, all taxa without sequence data for a particular fragment were added to the aligned fragments and concatenated using Alignment manipulation and summary statistics AMAS (Borowiec 2016). The edited gene fragments used for this study (<*gene_name_frag#_final_alltaxa.fas*>), and the concatenated final dataset (*concatenated.nex*) are available in the supplemental material and will be available at FigShare/Zenodo.

GenBank accession numbers and voucher specimen numbers are provided in supplemental material 3.1. New data from this study will be submitted to GenBank and made public as soon as possible. USNM voucher information is stored in GenBank to ensure the correct linkage with the USNM collections database and voucher specimens. The species' systematic position, the specimens' geographic origin, and the completeness of the included gene fragments are summarized in supplemental material 3.1. The most recent classification of Asilidae (Dikow 2009a) was used for the systematic position of each species.

3.4. Phylogenetic analyses

Three separate phylogenetic analyses were completed for this study in IQ-TREE (version 2.2.0; Minh et al. 2020) with the *concatenated.nex* data matrix (supplemental material 3.2): (i) an analysis partitioned by gene fragment using *partitions_frag.nex* (Command: iqtree2 -s concatenated.nex -p partitions_frag.nex -T 12 -B 2000) (supplemental material 3.3), (ii) an analysis partitioned by gene fragment and codon position using *partitions_frag_codon.nex* (Command: iqtree2 -s concatenated.nex -p partitions_frag_codon.nex -T 12 -B 2000) (supplemental material 3.4), (iii) an analysis with IQ-TREE selecting the best basepair partitioning (Chernomor et al. 2016) and best model for each partitioning scheme using ModelFinder (Kalyaanamoorthy et al. 2007) using *partitions_frag.nex* (Command: iqtree2 -s concatenated.nex -p partitions_frag.nex -mMFP+MERGE -T -B2000). Each run had two analyses running in parallel to diagnose convergence in the trace files easier. For all analyses, 2000 bootstrap replicates were generated using ultrafast bootstrap (UFBoot2; Hoang et al. 2018). The partitioning scheme and model selection were all assessed for best fit using Akaike

Information Criterion (AIC), Akaike Information Criterion with correction (AICc), and Bayesian Information Criterion (BIC). The phylogenetic tree with the best BIC score was then rooted on *Trichophthalma sp.* (Nemestrinidae) in R using the ape package (Paradis and Schliep 2019).

3.5. Ancestral state reconstruction

Predator-prey data was compiled from two principal resources (i) CHEA Asilidae Predator-Prey Database (Alberts Chap II) and (ii) a web-based predator-prey database for Asilidae created by Lavigne (2016). A raw file of the Lavigne (2016) predator-prey database can be found in supplemental material 3.5, and a file of the Lavigne (2016) predator-prey database with the names used in this publication can be found in supplemental material 3.6. The version used for this study contains 14,387 records. However, these records do not necessarily provide exact numbers since many authors used language such as “many,” “multiple,” “often takes,” and “several,” or gave a percentage of prey taken without reference numbers. Therefore, these instances were conservatively estimated as two prey for this study.

The CHEA Predator-Prey Database is compiled from pinned prey with Asilidae predators from 15 entomological collections in the USA and contains 3,421 prey records utilized in this study. The database was created in FileMaker Pro (Alberts Chap II, supplemental material 2.1) and is exported in Excel for ease of use. The combined data summary using the CHEA Predator-Prey Database and Lavigne (2016) database can be found in supplemental material 3.7.

All taxa, including outgroups, were coded from four states in *asilidae_pp_2022.nex* (supplemental material 3.8). All scores were based on the predatory diet of adult individuals:

- (0) non-predators (e.g., nectar, honeydew, or pollen feeders)
- (1) polyphagous arthropod predators (consume a wide variety of prey)
- (2) oligophagous arthropod predator (feeding is mainly restricted to a few related taxa, >60% of prey is dominated by one order of arthropods)
- (3) specialized arthropod predator (feeding is restricted mainly (>50% of prey) to one family of arthropod prey).
- (123) Asilidae genera that had inadequate data (> 10 prey records) to preclude meaningful conclusions about their prey preference. Because they are known arthropod predators, but their preference is unknown. Scoring prey preference in this manner precludes the non-predator state and only allows character states 1, 2, or 3 to be optimized for Asilidae on this phylogeny. It is important to note that the scoring of (123) does not mean that all three states were observed for the species in question. To properly do the ASR analysis using RevBayes missing data (absence of our knowledge of prey preference) need to be encoded this way and not by a simple '?' as in other phylogenetic analysis packages.

Although these types of categories may be generally informative about the predators' prey breadth and prey preference, we recognize that these character states or delimitations are subjective and have no predictive value for prey specificity of individual species. Some of the biases and factors that may influence these scores are discussed later in this study.

Using the assigned predator character states, we compared the fit of four discrete trait models on the final Maximum Likelihood tree (*mltree_rooted_Neme.tree;* supplemental material 3.9) using Bayes Factors from log marginal likelihoods calculated using a stepping stone analysis in RevBayes (Höhna et al. 2016; Table 3.3). Model (i) equal rates, where all rates are identical and can transition between any states (*equal_rates;* supplemental material 3.10). Model (ii) symmetric unordered Markov model, where prey preference may transition directly from state 0 to state 3 without going through states 1 and 2 and all transition rates are equal (*unordered_12-rate;* supplemental material 3.11). Model (iii) asymmetric ordered Markov model, where there is no immediate evolutionary path between states 0 and 3, states 1 and 2 must be used to reach 3 from 0 (*ordered_2-rate;* supplemental material 3.12). Model (iv) order restricted Markov model, where prey preference can only transition from 0 to 1, 1 to 2, 2 to 3 or in reverse. (*ordered_6-rate;* supplemental material 3.13). Trees were visualized in IcyTree (Vaughan 2017) and FigTree v1.4.4 (Rambaut 2018).

Table 3.3. The number of records (N) of arthropod prey used for each Asiloidea (Diptera) species used in this study. “G” = prey data only for genus, “S” = prey data for species, and “-“ = for prey unknown. Character state “0” = non-predators (non-Asilidae species), “1” = polyphagous arthropod predators, “2” = oligophagous arthropod predator, “3” = specialized arthropod predator, and “(123)” = is unknown prey preference (<10 prey records available). Arthropod prey records are compiled from Alberts (Chap II in prep) and Lavigne (2016).

Species	Character State	# prey records	prey data available
Machimus autumnalis	1	5818	G
Dasypogon sp.	3	4883	G
Dasypogon diadema	3	4749	S
Stenopogon albibasis	1	4694	G

Promachus amastrus	1	4389	G
Promachus sp.	1	4389	G
Molobratia teutonus	3	3685	S
Psilonyx annulatus	1	2277	S
Atomosia mucida	1	1831	G
Atomosia puella	1	1113	S
Mallophora nigrifemorata	3	973	G
Efferia producta	1	877	G
Efferia sp.	1	877	G
Philonicus arizonensis	1	776	G
Philonicus fuscatus	1	776	G
Philonicus plebeius	1	776	G
Philonicus albiceps	2	765	S
Cerotainia macrocera	1	733	G
Cerotainia albipilosa	1	729	S
Laphria aktis	1	643	G
Laphria felis	1	643	G
Laphria sicula	1	643	G
Laphria sp.	1	643	G
Holcocephala abdominalis	1	632	S
Cyrtopogon rattus	1	550	G
Cyrtopogon vandykei	1	550	G
Holcocephala calva	1	535	S
Neolophonotus kalahari	1	446	G
Neolophonotus pellitus	1	446	G
Neoitamus flavofemoratus	1	439	G
Dioctria vera	1	402	G
Heteropogon cirrhatus	1	391	G
Heteropogon spatulatus	1	391	G
Alcimus sp.	1	390	G
Choerades bella	1	386	G
Eudioctria albius	1	373	G
Eudioctria brevis	1	373	G
Eudioctria denuda	1	373	G
Proctacanthus philadelphicus	2	351	S
Stichopogon catulus	2	343	G
Stichopogon elegantulus	2	343	G
Stichopogon hermanni	2	343	G
Stichopogon punctus	2	343	G
Philodicus sp.	1	277	G

Triorla interrupta	1	259	S
Leptogaster aganniphe	1	257	G
Leptogaster arborcola	1	257	G
Leptogaster arida	1	257	G
Leptogaster carotenoides	1	257	G
Leptogaster cf. eudicrana	1	257	G
Leptogaster lanata	1	257	G
Leptogaster pubicornis	1	257	G
Tolmerus atricapillus	2	245	S
Diogmites angustipennis	2	244	S
Proctacanthella cacopiloga	1	237	S
Asilus crabroniformis	1	208	S
Lasiopogon aldrichii	2	201	G
Lasiopogon sp.	2	201	G
Megaphorus pulcher	2	196	S
Machimus callidus	1	183	S
Microstylum sp.	1	183	G
Ommatius flavipes	1	181	G
Ommatius parvulus	1	181	G
Ommatius terminalis	1	181	G
Damalis annulata	3	180	G
Damalis brevis	3	180	G
Damalis sp. 1	3	180	G
Damalis sp. 2	3	180	G
Machimus occidentalis	1	172	S
Efferia albibarbis	1	160	S
Saropogon luteus	2	160	G
Pegesimallus aulicus	1	157	G
Efferia aestuans	1	152	S
Dioctria rufipes	1	143	S
Laphystia cf. canadensis	1	138	G
Laphystia tolandi	1	138	G
Stichopogon trifasciatus	1	131	S
Laphria thoracica	3	124	S
Holopogon phaeonotus	1	120	S
Proctacanthus rufus	2	111	S
Neolophonotus bimaculatus	1	86	S
Neoitamus cyanurus	2	76	S
Prolatiforceps fulviventris	2	70	S
Philodicus fraterculus	1	68	S

Promachus rufipes	3	68	S
Dioctria hyalipennis	1	66	S
Dioctria hyalipennis	1	66	S
Dasophrys crenulatus	1	60	G
Dysmachus trigonus	2	60	S
Laphria grossa	1	57	S
Gonioscelis ventralis	2	55	G
Gonioscelis zulu	2	55	G
Ospriocerus aeacus	3	51	S
Stenopogon rufibarbis	2	50	S
Laxenecera engeli	1	48	G
Proctacanthus nearno	2	45	S
Dioctria atricapilla	1	42	S
Laxenecera albicincta	1	40	S
Efferia pogonias	1	39	S
Nicocles politus	2	38	S
Ceraturgus fasciatus	2	37	G
Stiphrolamyra angularis	1	37	G
Stiphrolamyra schoemani	1	37	G
Asilus sericeus	2	34	S
Lasiopogon cinctus	2	32	S
Leptogaster cylindrica	1	32	S
Astochia armata	1	28	G
Lamyra gulo	2	27	S
Hoplistomerus nobilis	3	22	S
Leptogaster flavipes	1	19	S
Choerades marginata	1	18	S
Damalis monochaetes	1	18	S
Pamponerus germanicus	1	17	S
Promachus albifacies	2	16	S
Ablautus coquilletti	2	15	G
Ablautus sp.	2	15	G
Cophinopoda pulchripes	1	14	G
Pilica erythrogaster	2	14	G
Pilica formidolosa	2	14	S
Ommatius tibialis	1	13	S
Euscelidia brunnea	1	12	G
Euscelidia pulchra	1	12	G
Euscelidia zumpti	1	12	G
Rhabdogaster pedion	2	12	G

Scylaticus costalis	1	12	G
Trichardis effrena	1	12	G
Nusa infumata	1	11	G
Pegesimallus laticornis	1	11	S
Philodicus tenuipes	1	11	S
Leptarthrus brevirostris	2	10	S
Afroholopogon mauros	(123)	9	G
Nannolaphria nigra	(123)	8	S
Prolepsis tristis	(123)	8	G
Pycnopogon fasciculatus	(123)	7	G
Rhipidocephala sp.	(123)	6	G
Atractia marginata	(123)	5	G
Clephydroneura sp.	(123)	5	G
Anypodetus arachnoides	(123)	4	G
Anypodetus fasciatus	(123)	4	G
Lasiocnemus lugens	(123)	4	S
Lestomyia fraudiger	(123)	4	G
Lestomyia sp.	(123)	4	G
Beameromyia disfascia	(123)	3	G
Beameromyia lacinia	(123)	3	G
Laphystotes ariel	(123)	3	G
Plesiomma sp.	(123)	3	G
Beameromyia bifida	(123)	2	S
Heligmonevra sp.	(123)	2	G
Synolcus dubius	(123)	2	G
Tipulogaster glabrata	(123)	2	S
Wyliea mydas	(123)	2	-
Acasilus tigrimontis	(123)	1	-
Apachekolos crinita	(123)	1	G
Apachekolos scapularis	(123)	1	G
Apachekolos tenuipes	(123)	1	S
Perasis transvaalensis	(123)	1	G
Tillobroma punctipennis	(123)	1	-
Afroestricus chiastoneurus	(123)	0	-
Afroleptomydas sp. 1	0	0	-
Afroleptomydas sp. 2	0	0	-
Ammophilomima indiae	(123)	0	-
Ammophilomima sp.	(123)	0	-
Ancylorhynchus cruciger	(123)	0	-
Aphoebantus sp.	0	0	-

Apiocera haruspex	0	0	-
Apiocera painteri	0	0	-
Apiocera sp.	0	0	-
Apsilocephala longistyla	0	0	-
Bombylius major	0	0	-
Cephalocera imitata	0	0	-
Cephalocera sp.	0	0	-
Connomyia leonina	(123)	0	-
Connomyia varipennis	(123)	0	-
Dipalta serpentina	0	0	-
Emphysomera conopsoides	(123)	0	-
Emphysomera pallidapex	(123)	0	-
Hemigephyra atra	0	0	-
Hemipenthes jaennickeana	0	0	-
Ischiolobos mesotopos	(123)	0	-
Lobus sp.	(123)	0	-
Lycostommyia albifacies	(123)	0	-
Mahafalymydas wiegmanni	0	0	-
Mesoleptogaster sp.	(123)	0	-
Messiasia californica	0	0	-
Metatrichia bulbosa	0	0	-
Michotamia compedita	(123)	0	-
Miltinus cardinalis	0	0	-
Mitrodetus dentitarsis	0	0	-
Mydas arizonensis	0	0	-
Mydas clavatus	0	0	-
Nemomydas brachyrhynchus	0	0	-
Nemomydas sp.	0	0	-
Nemomydas venosus	0	0	-
Ophionomima solocifemur	(123)	0	-
Opomydas townsendi	0	0	-
Paracosmus rubicundus	0	0	-
Pherocera sp.	0	0	-
Phycus frommeri	0	0	-
Prorates sp.	0	0	-
Rhaphiomidas hasbroucki	0	0	-
Rhaphiomidas parkeri	0	0	-
Rhaphiomidas xanthos	0	0	-
Scenopinus fenestralis	0	0	-
Sporadothrix gracilis	(123)	0	-

Syllegomydas palestinensis	0	0	-
Toxophora maxima	0	0	-
Trichophthalma sp.	0	0	-
Trichoura pardeos	(123)	0	-
Trigonomima sp.	(123)	0	-
Wilcoxius acutulus	(123)	0	-
Willistonina bilineata	(123)	0	-

3.6. Stochastic character mapping

Trees with a stochastic character map were also generated during each of the above ancestral state reconstruction analyses in RevBayes. Trees were visualized using an R script (*plot_simmap.R*; supplemental material 3.14) with RColorBrewer (Neuwirth 2022) and phytools (Revell 2012).

4. Results

4.1. Model selection and phylogenetic analysis

The phylogenetic tree is based on the *concatenated.nex* data matrix inferred with Maximum Likelihood in IQ-TREE, is shown in Fig. 3.3. The raw matrix, alignment of each gene fragment, and concatenated matrix can be found as supplemental material 3.2. Of the tested models, the analysis with IQ-TREE selecting the partitions and best model for each partition, fit the data best with the highest BIC, AICc, and AIC scores (Table 3.4).

Table 3.4. Akaike Information Criterion (AIC), Akaike Information Criterion with correction (AICc), and Bayesian Information Criterion (BIC) generated in RevBayes.

	BIC	**AICc**	**AIC**	
Partitioned by fragment	439457.9107	434849.571	434952.6149	Good
Partitioned by fragment & codon	439457.9959	434842.5664	434945.9400	Better
Partitioned with best fit	439590.2240	435676.6801	435750.1384	Best

The models of best fit for each partition are listed in Table 3.5 below. The overall length of the alignment is 7,913 bp with *18S* and *28S* separated into four partitions, *EF-1*α with three partitions, *CAD* with two partitions, and *AATS* and *COI* with one partition each (Table 3.5).

Table 3.5. Best-fit model for *concatenated.nex* according to BIC score calculated using ModelFinder as implemented in IQTREE.

Partition #	**Partition name**	**Best-fit model according to BIC**
1	p1_18s_frag1_final_alltaxa	GTR+F+I+I+R4
2	p2_18s_frag2_final_alltaxa	GTR+F+I+I+R4
3	p3_18s_frag3_final_alltaxa	GTR+F+I+G4
4	p4_18s_frag4_final_alltaxa	TVM+F+I+I+R5
5	p5_28s_frag1_final_alltaxa	TVM+F+I+I+R5
6	p6_28s_frag2_final_alltaxa	GTR+F+I+G4
7	p7_28s_frag3_final_alltaxa	GTR+F+I+G4
8	p8_28s_frag4_final_alltaxa	GTR+F+I+G4
9	p9_aats_frag1_final_alltaxa	TIM2+F+I+I+R5
10	p10_cad_frag4_final_alltaxa	GTR+F+R6
11	p11_cad_frag5_final_alltaxa	GTR+F+R6
12	p12_coi_frag1_final_alltaxa	GTR+F+I+G4
13	p13_ef1a_frag1_final_alltaxa	GTR+F+I+G4
14	p14_ef1a_frag2_final_alltaxa	TIM2+F+I+I+R5
15	p15_ef1a_frag3_final_alltaxa	GTR+F+I+G4

4.2. Phylogeny

Bombyliidae is the sister group to the rest of the Asiloidea. Within Asiloidea, there are two monophyletic clades: the therevoid clade (Apsilocephalidae, Scenopinidae, and Therevidae in this study), and the asiloid clade (Mydidae plus Apioceridae sister to Asilidae).

Asilidae is supported as monophyletic with sister taxon composed of Apioceridae plus Mydidae (Fig. 3.3). Six of the included 12 subfamily taxa of Asilidae are recovered as monophyletic: Asilinae, Dioctriinae, Laphriinae, Leptogastrinae, Ommatiinae, and Stichopogoninae (sensu Dikow 2009a). The remaining five subfamilies: Brachyrhopalinae, Dasypogoninae, Stenopogoninae, Tillobromatinae, Trigonomiminae, and Willistonininae (sensu Dikow 2009a) were recovered as paraphyletic and polyphyletic. Laphriinae was recovered as sister to the rest of Asilidae.


Trichophthalma sp. (Daintree)
Nemestrinidae
Toxophora maxima
Paracosmus rubicundus
Dipalta serpentina
Hemipenthes jaennickeana
Bombylius major
Aphoebantus sp. (Portal)
Bombyliidae
Prorates sp. (Escalante)
Scenopinus fenestralis
Metatrichia bulbosa
Scenopinidae
Hemigephyra atra
Phycus frommeri
Pherocera sp. (Hurdi)
Therevidae
Apsilocephala longistyla
Apsilocephalidae
Apiocera sp. (Barakula)
Apiocera haruspex
Apiocera painter
Apioceridae
Rhaphiomidas hasbroucki
Rhaphiomidas xanthos
Rhaphiomidas parkeri
Mitrodetus dentitarsis
Opomydas townsendi
Miltinus cardinalis
Messiasia californica
Mydas clavatus
Mydas arizonensis
Cephalocera imitata
Cephalocera sp. (Montegu)
Nemomydas venosus
Nemomydas brachyrhynchus
Nemomydas sp. (Rosario)
Mahafalymydas wiedmanni
Syllegomydas palestinensis
Afroleptomydas sp. (Clanwilliam)
Afroleptomydas sp. (RSA)
Mydidae
Laphystotes ariel
Trichardis effrena
Perasis transvaalensis
Laphystia cf. canadensis
Laphystia tolandi
Nusa infumata
Anypodetus arachnoides
Anypodetus fasciatus
Hoplistomerus nobilis
Laxenecera albicincta
Laxenecera engeli
Nannolaphria nigra
Cerotainia albipilosa
Cerotainia macrocera
Atractia marginata
Atomosia mucida
Atomosia puella
Pilica erythrogaster
Pilica formidolosa
Lamyra gulo
Stiphrolamyra schoemani
Stiphrolamyra angularis
Choerades bella
Laphria felis
Laphria sp. (Cortemillia)
Laphria sicula
Choerades marginata
Laphria aktis
Laphria grossa
Laphria throacica
Laphriinae
Sporadothrix gracilis
Willistonininae*
Afroholopogon mauros
Rhabdogaster pedion
Brachyrhopalinae*
Damalis annulata
Damalis monochaetes
Damalis brevis
Damalis sp. (Singapore)
Damalis sp. (Kerala)
Trigonomiminae*
Pegesimallus laticornis
Pegesimallus aulicus
Dasypogoninae*
Diogmites angustipennis
Dasypogoninae*
Plesiomma sp. (Guanacaste)
Stenopogoninae*
Lestomyia fraudiger
Lestomyia sp. (Largo Vista)
Saropogon luteus
Dasypogon diadema
Dasypogon sp. (Ibiza)
Dasypogoninae*
Molobratia teutonus
Dasypogoninae*
Ischiolobos mesotopos
Brachyrhopalinae*
Rhipidocephala sp. (Harold Johnson)
Trigonomima sp. (Kepong)
Holcocephala abdominalis
Holcocephala calva
Trigonomiminae*
Holopogon phaeonotus
Pycnopogon fasciculatus
Heteropogon cirrhatus
Heteropogon spatulatus
Brachyrhopalinae*
Ceraturgus fasciatus
Cyrtopogon rattus
Cyrtopogon vandykei
Brachyrhopalinae*
Leptarthrus brevirostris
Brachyrhopalinae*
Nicocles politus
Ablautus coquilletti
Ablautus sp. (Fish)
Willistonininae*
Microstylum sp. (Karkloof)
Stenopogoninae*
Prolepsis tristis
Stenopogoninae*
Tillobroma punctipennis
Tillobromatinae*
Lycostommyia albifacies
Tillobromatinae*
Ancylorhynchus cruciger
Scylaticus costalis
Connomyia leonine
Connomyia varipennis
Stenopogoninae*
Eudioctria denuda
Eudioctria albius
Eudioctria brevis
Dioctria vera
Dioctria atricapilla
Dioctria rufipes
Dioctria hyalipennis (USA)
Dioctria hyalipennis (Germany)
Dioctriinae
Trichoura pardeos
Willistonininae*
Gonioscelis ventralis
Gonioscelis zulu
Ospriocerus aeacus
Stenopogon rufibarbis
Stenopogon albibasis
Stenopogoninae*
Willistonina bilineata
Willistonininae*
Lasiopogon sp. (Descanso)
Lasiopogon aldrichii
Lasiopogon cinctus
Stichopogon trifasciatus
Stichopogon catulus
Stichopogon punctus
Stichopogon elegantulus
Stichopogon hermanni
Stichopogoninae
Lobus sp. (Clanwilliam)
Psilonyx annulatus
Beameromyia disfascia
Beameromyia bifida
Beameromyia lacinia
Leptogaster arida
Leptogaster cf. eudicrana
Leptogaster pubicornis
Leptogaster cylindrica
Leptogaster flavipes
Apachekolos tenuipes
Apachekolos crinite
Apachekolos scapularis
Leptogaster carotenoides
Tipulogaster glabrata
Mesoleptogaster sp. (Bukit Fraser)
Ophionomima solocifemur
Lasiocnemus lugens
Ammophilomima indiae
Ammophilomima sp. (Singapore)
Leptogaster arborcola
Leptogaster lanata
Leptogaster aganniphe
Euscelidia pulchra
Euscelidia brunnea
Euscelidia zumpti
Leptogastrinae
Michotamia compedita
Emphysomera conopsoides
Emphysomera pallidapex
Afroestricus chiastoneurus
Cophinopoda pulchripes
Ommatius flavipes
Ommatius terminalis
Ommatius parvulus
Ommatius tibialis
Ommatiinae
Proctacanthus rufus
Proctacanthella cacopiloga
Proctacanthus nearno
Proctacanthus philadelphicus
Wilcoxius acutulus
Triorla interrupta
Efferia aestuans
Efferia pogonias
Efferia sp. (Portal)
Efferia albibarbis
Efferia producta
Philodicus tenuipes
Alcimus sp. (Witsand)
Philodicus fraterculus
Philodicus sp. (Kepong)
Promachus amastrus
Promachus sp. (Witsand)
Mallophora nigrifemorata
Megaphorus pulcher
Promachus albifacies
Promachus rufipes
Acasilus tigrimontis
Dasophrys crenulatus
Synoclus dubius
Neolophonotus pellitus
Neolophonotus bimaculatus
Neolophonotus kalahari
Astochia armata
Neoitamus cyanurus
Neoitamus flavofemoratus
Clephydroneura sp. (Kepong)
Heligmonevra sp. (Mhlopeni)
Wyliea mydas
Dysmachus trigonus
Pamponerus germanicus
Philonicus albiceps
Philonicus arizonensis
Philonicus fuscatus
Philonicus plebeius
Prolatiforceps fulviventris
Machimus autumnalis
Machimus callidus
Machimus occidentalis
Tolmerus atricapillus
Asilus crabroniformis
Asilus sericeus
Asilinae
89
88
97
94
89
79
81
93
99
92
99
96
97
98
99
84
99
98
99
94
94
93
94
99
92
92
96
62
72
68
81
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73
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98
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78
89
80
86
63
99
99
97
88
99
99
99
99
99
98
99
87
93
66
85
80
49
89
97
66
95
93
74
95
99
88
64
96
0.08

Fig 3.3. Maximum Likelihood tree of Asilidae inferred using IQ-Tree. Ultrafast Bootstrap (UFB) shown for the internal nodes. Nodes without a UFB value are 100. The Asilidae subfamily classification follows Dikow (2009a). The family or subfamily of each taxon is shown on the right, with those in a non-monophyletic position denoted with an asterisk (*). Colored circles before the species name are the codes for known predator habits: The red circle represents state 0 (non-arthropod predator). The purple circle represents state 1 (polyphagous arthropod predator). The blue circle represents state 2 (oligophagous arthropod predator). The green circle represents state 3 (specialist arthropod predator). Specimens without a circle are unknown. A full-sized version of this tree can be found in supplemental material 3.15.

4.3. Asilidae predator and prey data

For the 176 Asilidae specimens a total of 65,357 prey records were available for this study (Table 3.6; supplemental material 3.16). Hymenoptera was the most common prey item with 41%, followed by Diptera 24%, and Coleoptera 12%. Dasypogoninae shows a particularly strong preference for Hymenoptera with 90% of its diet being dominated by this order. Leptogastrinae has a relatively high percentage (8%) of spiders (Araneae) in its diet, when compared to the other Asilidae subfamilies. Stichopogoninae and Willistonininae have high percentages of Diptera in their diets, 60% and 67% respectively, when compared to the other subfamilies.

Table 3.6. Summary table of Asilidae subfamilies and their prey preference. Abbreviations stand for: Asi – Asilinae, Bra – Brachyrhopalinae, Das – Dasypogoninae, Dio – Dioctriinae, Lap –

Laphriinae, Lep – Leptogastrinae, Omm – Ommatiinae, Ste – Stenopogoninae, Sti – Stichopogoninae, Til – Tillobromatinae, Tri – Trigonomiminae, Wil – Willistonininae. Percentages in bold are statistics of note.

Prey Order	**Total #**	**Asilidae Subfamilies**											
	%	Asi	Bra	Das	Dio	Lap	Lep	Omm	Ste	Sti	Til	Tri	Wil
Araneae	556	46	3	3	9	54	315	0	12	88	0	26	0
	1%	0%	0%	0%	1%	1%	**8%**	0%	0%	4%	0%	1%	0%
Blattodea	628	62	25	3	12	299	49	30	11	8	0	129	0
	1%	0%	1%	0%	1%	4%	1%	5%	0%	0%	0%	6%	0%
Coleoptera	7832	3835	337	136	181	1757	32	96	1172	21	0	265	0
	12%	15%	16%	1%	10%	21%	1%	17%	23%	1%	0%	13%	0%
Diptera	15847	7038	686	928	504	2717	1574	157	510	1178	1	534	20
	24%	28%	33%	7%	28%	32%	38%	28%	10%	**60%**	100%	25%	**67%**
Hemiptera	6707	1609	431	284	546	1438	1452	107	441	165	0	226	8
	10%	6%	21%	2%	31%	17%	35%	19%	9%	8%	0%	11%	27%
Hymenoptera	26978	9011	518	12508	493	1906	350	137	1099	74	0	880	2
	41%	36%	25%	**90%**	28%	23%	8%	24%	22%	4%	0%	42%	7%
Lepidoptera	2496	1687	20	22	16	92	365	30	252	6	0	6	0
	4%	7%	1%	0%	1%	1%	9%	5%	5%	0%	0%	0%	0%
Neuroptera	104	76	3	3	0	1	0	0	21	0	0	0	0
	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
Odonata	406	376	0	2	0	4	0	0	17	7	0	0	0
	1%	1%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
Orthoptera	3336	1389	3	6	7	13	39	6	1566	305	0	2	0
	5%	6%	0%	0%	0%	0%	1%	1%	31%	15%	0%	0%	0%
Thysanoptera	72	0	3	0	3	48	1	0	0	0	0	17	0
	0%	0%	0%	0%	0%	1%	0%	0%	0%	0%	0%	1%	0%
Trichoptera	94	59	0	1	0	0	0	7	0	16	0	11	0
	0%	0%	0%	0%	0%	0%	0%	1%	0%	1%	0%	1%	0%
Other	301	26	56	1	1	100	0	0	10	106	0	1	0
	0%	0%	3%	0%	0%	1%	0%	0%	0%	5%	0%	0%	0%
Total #	65357	25214	2085	13897	1772	8429	4177	570	5111	1974	1	2097	30

4.4. Ancestral state reconstruction (ASR)

Of the four tested models, the *ordered_6-rate* model strongly fits the data best (Table 3.7). The script including the rate matrix used for this model can be found in supplemental material 3.13. The ancestral state reconstruction (ASR) results support the hypothesis that the most recent common ancestor (MRCA) of Asilidae was a polyphagous arthropod predator (Fig. 3.4). All of the clades within Asilidae also have MRCAs as polyphagous arthropod predators.

Table 3.7. Log Marginal Likelihoods (logML) of the four models tested, listed in order of best fit. Bayes Factors (BF) are shown comparing the logML for each consecutive model. Interpretation of Bayes Factors from Jeffreys, 1961.

Model	logML	BF	Interpretation
ordered_6-rate	-113.9315	3.5702 (1 > 2)	“Strong”
unordered_12-rate	-117.5017	8.2396 (2 > 3)	“Decisive”
ordered_2-rate	-125.7413	8.7737 (3 > 4)	“Decisive”
equal_rates	-134.515	-	-

The posterior probabilities for each state at each internal and terminal node with missing data were calculated and the state with the highest probability can be seen in Figure 3.4. For the 45 species with unknown prey preference, the posterior probabilities for each possible ancestral character state: polyphagous arthropod predator (anc_state_1_pp; Table 3.8), oligophagous arthropod predator (anc_state_2_pp; Table 3.8), and specialized arthropod predator (anc_state_3_pp; Table 3.8) were calculated, and the state with the highest probability was selected. Most species are estimated to be state_1 (polyphagous arthropod predator), except for *Lestomyia* Williston, 1884 and *Plesiomma* Macquart, 1838, which are probably state_2 (oligophagous arthropod predator). No species of unknown prey preference were predicted to be state_3 (specialized arthropod predator).

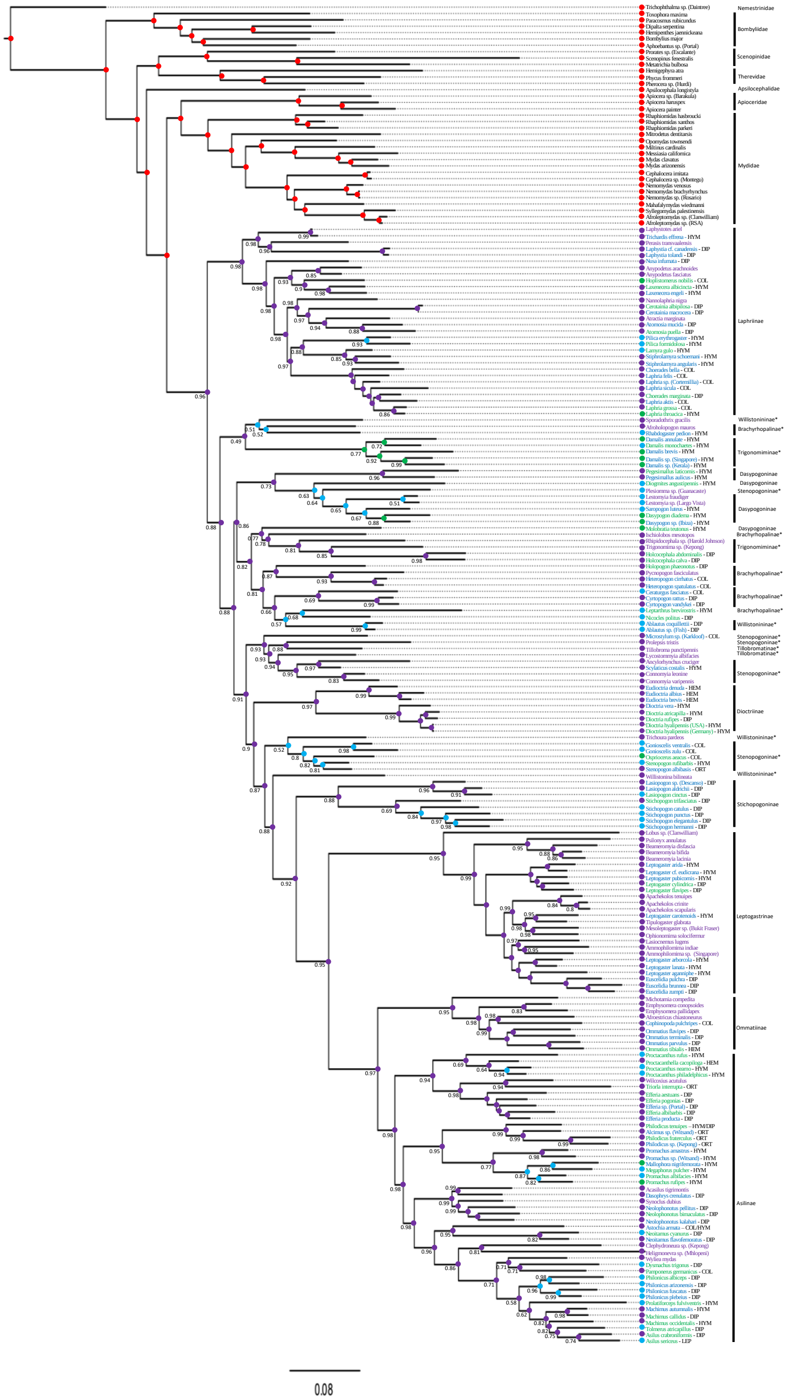

Fig. 3.4 Ancestral state reconstruction of Asilidae prey preference as inferred in RevBayes using the ordered_6-rate model. Red circle = state 0 (non-arthropod predator), purple circle = state 1 (polyphagous arthropod predator), blue circle = state 2 (oligophagous arthropod predator), green circle = state 3 (specialist arthropod predator), purple name = taxa whose states were optimized on this tree, blue name = taxa character-coded at generic level, green name = taxa character-coded at species level, abbreviations (DIP = Diptera, COL = Coleoptera, HEM = Hemiptera, HYM = Hymenoptera, LEP = Lepidoptera, and ORT = Orthoptera) are for the taxa's dominant prey order. Numbers at internal nodes = posterior predictions for the prey preference character state. A full-sized version of this tree can be found in supplemental material 3.17.

Table 3.8. Posterior probabilities for predicted ancestral state prey preference in Asilidae with unknown prey preference. polyphagous arthropod predator (anc_state_1_pp), oligophagous arthropod predator (anc_state_2_pp), and specialized arthropod predator (anc_state_3_pp).

Species	Voucher ID	anc_state_1_pp	anc_state_2_pp	anc_state_3_pp
Acasilus trigrimontis	Asil _0068	**0.842**	0.142	0.016
Clephydroneura sp. (Kepong)	Asil_0289	**0.629**	0.283	0.088
Heligmonevra sp. (Mhlopeni)	Asil_ 0073	**0.566**	0.313	0.121
Synolcus dubius	Asil _0042	**0.874**	0.093	0.032
Wilcoxius acutulus	Asil _0275	**0.834**	0.132	0.035
Wyliea mydas	Asil _0365	**0.648**	0.304	0.049
Afroholopogon mauros	Asil _0065	**0.440**	0.426	0.134
Ischiolobos mesotopos	Asil _0111	**0.701**	0.227	0.072
Pycnopogon fasciculatus	Asil _0292	**0.789**	0.166	0.045
Lestomyia fraudiger	Asil _0125	0.222	**0.522**	0.256
Lestomyia sp. (Largo Vista)	Asil_ 0293	0.224	**0.522**	0.254
Anypodetus arachnoides	Asil _0109	**0.800**	0.154	0.045
Anypodetus fasciatus	Asil _0108	**0.844**	0.120	0.036
Atractia marginata	Asil _0301	**0.801**	0.159	0.040
Laphystotes ariel	Asil _0054	**0.991**	0.007	0.002
Perasis transvaalensis	Asil _0024	**0.778**	0.172	0.050
Ammophilomima indiae	Asil _0212	**0.789**	0.156	0.054

Ammophilomima sp. (Singapore)	Asil_0347	**0.832**	0.129	0.039
Apachekolos crinita	Asil _0222	**0.799**	0.155	0.046
Apachekolos scapularis	Asil _0271	**0.795**	0.156	0.049
Apachekolos tenuipes	Asil _0100	**0.815**	0.142	0.043
Beameromyia bifida	Asil _0097	**0.831**	0.134	0.036
Beameromyia disfascia	Asil _0319	**0.797**	0.155	0.048
Beameromyia lacinia	Asil _0223	**0.819**	0.138	0.043
Lasiocnemus lugens	Asil _0040	**0.817**	0.140	0.042
Lobus sp. (Clanwilliam)	Asil_ 0209	**0.623**	0.270	0.107
Mesoleptogaster sp. (Bukit Fraser)	Asil_ 0352	**0.848**	0.116	0.035
Ophionomima solocifemur	Asil _0342	**0.860**	0.113	0.028
Tipulogaster glabrata	Asil _0098	**0.896**	0.084	0.020
Afroestricus chiastoneurus	Asil _0077	**0.793**	0.157	0.050
Emphysomera conopsoides	Asil _0182	**0.801**	0.151	0.048
Emphysomera pallidapex	Asil _0202	**0.770**	0.174	0.056
Michotamia compedita	Asil _0179	**0.718**	0.218	0.064
Ancylorhynchus cruciger	Asil _0218	**0.757**	0.185	0.057
Connomyia leonina	Asil_0102	**0.799**	0.157	0.044
Connomyia varipennis	Asil _0103	**0.776**	0.172	0.052
Plesiomma sp. (Guanacaste)	Asil_0302	0.320	**0.488**	0.191
Prolepsis tristis	Asil _0255	**0.673**	0.250	0.077
Lycostommyia albifacies	Asil_ 0066	**0.782**	0.166	0.052
Tillobroma punctipennis	Asil_ 0167	**0.743**	0.202	0.056
Rhipidocephala sp. (Harold Johnson)	Asil_ 0072	**0.690**	0.227	0.083
Trigonomima sp. (Kepong)	Asil_ 0343	**0.707**	0.226	0.067
Sporadothrix gracilis	Asil_ 0057	**0.460**	0.406	0.134
Trichoura pardeos	Asil_ 0067	**0.583**	0.335	0.082
Willistonina bilineata	Asil_ 0334	**0.694**	0.238	0.068

4.5. Stochastic character mapping (SCM)

The Stochastic character map reveals a transition from state 0 (non-predator) to state 1 (polyphagous arthropod predator) happens once at the most common ancestor of Asilidae; a transition from state 1 to state 2 (oligophagous arthropod predator) is inferred 21 times (arrows in Fig 3.5); and a transition from state 2 to state 3 (specialized arthropod predator) inferred eight times. There are also five instances of a reversal from a more specialized prey preference to a more generalist preference (bold species names in Fig 3.5). There are two transitions from state 1 through state 2 to state 3 across the lineage comprising (*Hoplistomerus nobilis* and *Molobratia teutonus*; Fig 3.5).

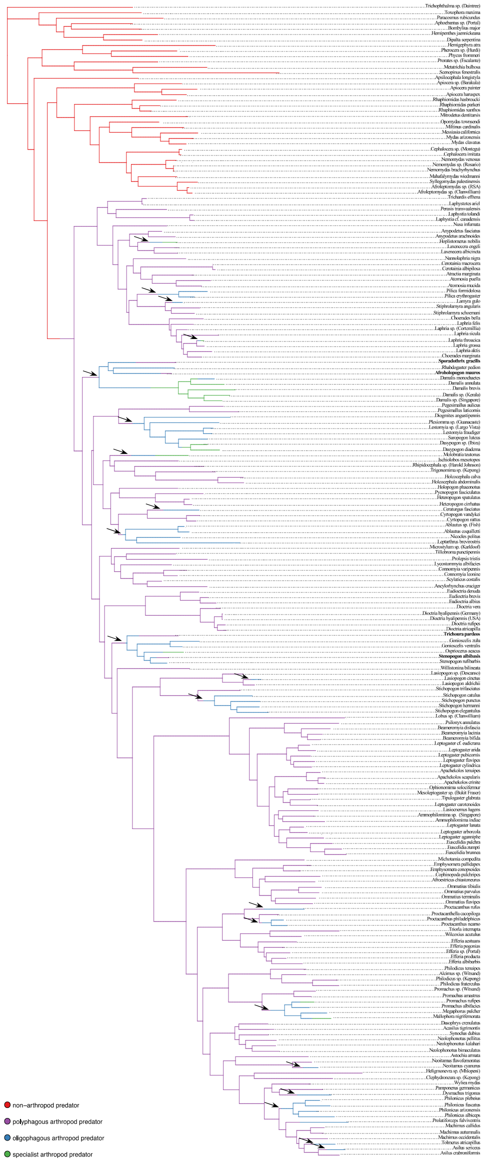

Fig. 3.5. Stochastic character mapping of Asilidae prey preference as inferred in RevBayes. Red branches = state 0 (non-arthropod predator), purple branches = state 1 (polyphagous arthropod

predator), blue branches = state 2 (oligophagous arthropod predator), green branches = represent state 3 (specialist arthropod predators). Arrows = evolution of a more specialized diet evolved. Bold species names = a reversal to a more generalized diet. A full-sized version of this tree can be found in supplemental material 3.18.

5. Discussion

First, we discuss the deep and species-level relationships with a particular focus on subfamily-level groupings and how these compare to other phylogenetic hypotheses for Asilidae. Second, the general findings from the ancestral state reconstruction analysis are discussed and how they may relate to the known biology of these groups. Lastly, we discuss the important trends revealed by the ancestral state reconstruction and stochastic character map optimizations and their real-life implications.

5.1. Phylogeny (Monophyly of and relationships among higher-level taxa)

Many deep relationships recovered in this topology are congruent with those found in previous studies. Bombyliidae is sister to the rest of the Asiloidea. Within Asiloidea, there are two monophyletic clades: the therevoid clade (Apsilocephalidae, Scenopinidae, and Therevidae in this study) and the asiloid clade (Mydidae plus Apioceridae sister to Asilidae) as also hypothesized in Trautwein et al. (2010), and Wiegmann et al. (2011). Shin et al. (2018) found Mydidae as paraphyletic with the early diverging mydid *Tongamya* Stuckenberg, 1966 being separate from the rest of Mydidae. No specimens from *Tongamya* or close relatives were included in this analysis (Fig. 3.3).

Within Asilidae: The subfamilies Asilinae, Laphriinae, Leptogastrinae, Ommatiinae, and Stichopogoninae are recovered as monophyletic, as previously hypothesized by Dikow (2009a, 2009b) and Cohen et al. (2021). Dioctriinae was also recovered as monophyletic, as previously hypothesized by Dikow (2009a, 2009b) but not by Cohen et al. (2021). Brachyrhopalinae, Dasypogoninae, Stenopogoninae, Tillobromatinae, Trigonomiminae, and Willistonininae are non-monophyletic. Laphriinae as sister to the rest of Asilidae was recovered by Dikow (2009a), and the relationship of Stichopogoninae (Leptogastrinae, [Ommatiinae, Asilinae]) was proposed by Dikow (2009b), and by Cohen et al. (2021)

We recovered a clade consisting of Willistonininae (e.g., *Sporadothrix*), Brachyrhopalinae (e.g., *Afroholopogon*), and Trigonomiminae (e.g., *Damalis*). All species of *Damalis* form a clade so that the tribe Xenomyzini is monophyletic. *Damalis* and *Holcocephala* + *Rhipidocephala* are routinely recovered in unrelated clades (Dikow 2009b, Cohen et al. 2021) despite having distinct ‘goggle-eyes’ and pronounced tentorial pits. This study suggests that these unusual traits have evolved at least twice in Asilidae, and a proper test of the evolution of this character state is advised.

Dasypogoninae is monophyletic except for the insertion of *Plesiomma* which is currently is placed in Stenopogoninae (Dikow 2009a) and *Molobratia* and recovered near the Trigonomimini (e.g., Holcocephala). *Plesiomma* resembles other Dasypogoninae and has been observed hanging while consuming prey, which is characteristic of other Dasypogoninae. Therefore, *Plesiomma* may belong within Dasypogoninae instead of Stenopogoninae. On the other hand, *Molobratia* is somewhat unusual in that it has a large fore-tibial spur, characteristic of Dasypogoninae, but does not possess spines on its acanthophorite plates. Therefore, *Molobratia* may not belong within Dasypogoninae, but without further analyses, these relationships remain unresolved.

We recovered a clade consisting of Dasypogoninae (*Molobratia*), Trigonomiminae (*Holcocephala*), Brachyrhopalinae (*Holopogon*), and Willistonininae (*Ablautus*) similar to the molecular only analysis by Dikow (2009b) and Cohen et al. (2021). *Holcocephala, Trigonomima*, and *Rhipidocephala* form a clade in support of the monophyly of Trigonomimini.

We recovered genera of Stenopogoninae (*Microstylum*) and Tillobromatinae (*Tillobroma*) together in a clade. Dikow (2009b) also recovered this clade. *Microstylum*, *Prolepsis* Walker, 1851, and *Connomyia* Londt, 1992 (=Enigmomorphini), whereas, *Ancylorhynchus* Berthold in Latreille, 1827 and *Scylaticus* were included in Dikow (2009a, 2009b), but were unplaced. *Tillobroma* and *Lycostommyia* (=Tillobromatini) were found to be paraphyletic (Fig. 3.3).

The Dioctriinae represented by the genera *Eudioctria*, and *Dioctria* (=Dioctriini) are recovered monophyletic in this analysis. In other similar analyses, morphology supports the placement of the Australian taxa (Dikow 2009a) but molecular data from Australian specimens in Cohen et. al (2021) does not support the monophyly of Dioctriinae.

We recovered a clade of Willistonininae (e.g., *Trichoura)* and Stenopogoninae (e.g., *Stenopogon*). Stenopogoninae is polyphyletic, however, not the genera *Gonioscelis*, *Ospriocerus*, and *Stenopogon*. They all belong to the clade Stenopogonini. *Willistonina* as sister to the clade of Stichopogoninae, Leptogastrinae, Ommatiinae, and Asilinae (Fig. 3.3).

Leptogastrinae is monophyletic. However, *Leptogaster* is non-monophyletic. *Beameromyia*, *Apachekolos,* and *Euscelidia* are monophyletic. Leptogastrinae is sister to Ommatiinae plus Asilinae. Ommatiinae is also recovered as monophyletic. *Michotamia* is sister to the rest of Ommatiinae. *Emphysomera* is sister to *Afroestricus* plus *Cophinopoda* and the Ommatiini (e.g., *Ommatius*) (Fig. 3.3).

Asilinae is recovered as monophyletic. A clade of unplaced genera, *Proctacanthus, Proctacanthella, Wilcoxius*, *Triorla*, and *Efferia* was recovered as sister to the rest of Asilinae. Cohen et al. (2021) also recovered this clade and believe that they likely represent an unnamed tribe. We recovered a clade of *Philodicus*, *Promachus*, and *Megaphorus* (=Apocleini) with the addition of two unplaced genera *Alcimus* and *Mallophora* that were not studied by Dikow (2009a, 2009b). *Promachus albifacies* and *Promachus rufipes* are recovered closer to *Megaphorus pulcher* and *Mallophora nigrifemorata,* all species found in the Americas, whereas *Promachus amastrus* and *Promachus sp.* are both from South Africa (supplemental material 3.1).

A clade of unplaced Asilinae genera (Dikow 2009a, 2009b), *Acasilus*, *Dasophrys*, *Synoclus*, and *Neolophonotus* was recovered sister to the remaining Asilinae. A clade comprising of *Astochia* Becker in Becker and Stein, 1913, which was not studied by Dikow (2009a, 2009b), and

Neoitamus, which was studied (Dikow 2009a) both of which were unplaced. *Clephydroneura* is sister to *Heligmonevra*, which was included in Dikow (2009a, 2009b) but unplaced. *Wyliea*, *Dysmachus*, and *Pamponerus* form are a clade of unplaced genera. *Philonicus*, represented by four species from the Nearctic and Palearctic regions, is recovered as monophyletic (=Philonicini). *Prolatiforceps* is sister to *Machimus*, *Tolmerus*, plus *Asilus* (Fig. 3.3).

5.2. Ancestral state reconstruction (ASR) and prey preference

Of the 176 species of Asilidae included in this phylogeny, 46 species did not have enough prey records available (known only from <10 records) to assign prey preference character states to them (Table 3.3). Using ancestral state reconstruction, we calculated the probability of each predatory state for each species with insufficient data for prey preference character state inclusion. The most recent common ancestor of Asilidae was optimized as a polyphagous arthropod predator. Oligophagous and specialist predators evolved 21 times across the phylogenetic tree. Ancestral state reconstruction analysis results are discussed alphabetically by subfamily and generally in the order that they are recovered in the phylogenetic tree. An overview of prey preference patterns within the higher-level taxa influenced by potential behavioral and morphological correlations are discussed at the end of each subfamily section.

Asilinae

Of the 46 species in this analysis, 30 are considered polyphagous arthropod predators, 14 are oligophagous arthropod predators, and two are specialist arthropod predators. Diptera and

Hymenoptera comprise 67% of the Asilinae prey (Alberts Chap II; Fig 3.4; supplemental material 3.7). Six species were missing prey data, and their predatory preference was predicted to be polyphagous arthropod predator.

Proctacanthus is represented by three species (*P. nearno*, *P. philadelphicus*, and *P. rufus*). Over 60% of the prey these species consume are Hymenoptera with the dominant family being Apidae. Ninety-eight percent of *P. rufus* were recorded with Hymenoptera prey (supplemental material 3.7). Though the diet of *P. rufus* is dominated by Apidae, particularly honeybees, they do not constitute over 50% of their diet, making them oligophagous and not true specialists as defined here (supplemental material 3.7).

There are around 30 described species of *Proctacanthus* all found in the Americas. This large genus is known to perch primarily on the ground or low plant matter and will sometimes perch vertically on small branches when the substrate becomes too hot (Dennis 2012). They typically inhabit open environments such as wood clearing or dry sandy plains. Prey is primarily captured in flight, however, some Hymenoptera are captured on flowers (Dennis and Lavigne 1975).

Proctacanthella is represented by one species (*P. cacopiloga*) nested within *Proctacanthus* in this study. Despite being closely related according to this tree, they have a vastly different diet from *Proctacanthus. Proctacanthella* strongly prefers Hemiptera (e.g., Cicadellidae; supplemental material 3.7). Found primarily in short grass plains and dry sandy areas and fed primarily in the mornings, whereas *Proctacanthus* fed mainly in the afternoons (Dennis and Lavigne 1975). Like *Proctacanthus* they forage primarily from the ground, and sometimes on low vegetation, catching prey in flight. *Proctacanthella* species are polyphagous arthropod predators because they feed on various prey, unlike *Proctacanthus* which prefer Hymenoptera (Fig 3.4; supplemental material 3.7; Dennis and Lavigne 1975). Their smaller size (12–15 mm) makes them only able to capture soft-bodied prey (Shelly and Pearson 1980).

A clade (*Wilcoxius*, *Triorla*, and *Efferia*) was recovered with all polyphagous internal and terminal taxa. This clade includes *Wilcoxius*, which is represented by one species (*W. acutulus*) did not have any associated prey. The ASR optimization predicts that *W. acutulus* has a polyphagous arthropod diet with an 83% probability (Fig 3.4; Table 3.8). There are 11 Neotropical species without much recorded for their ethology.

Also in this clade is *Triorla* represented by one species (*T. interrupta* which is polyphagous, with a slight preference (36%) for Orthoptera (Fig 3.4; supplemental material 3.7). Currently, 14 species of *Triorla* are found in the Nearctic and Neotropical regions. They are primarily found on sandy meadow edges.

Finally, *Efferia* is also included in this clade of unplaced Asilinae genera. There are five species represented (*E. aestuans*, *E. albibarbis*, *E. pogonias*, *E. producta*, and one unidentified species from Arizona, USA). All of them are polyphagous with a slight preference (46-59%) for Diptera prey (Fig 3.4; supplemental material 3.7). Most *Efferia* species prefer grasslands or shrubby vegetation and do most of their foraging from the bare ground and low vegetation (Lavigne and Holland 1969, Dennis et al. 1986). Dennis et al. 1986 found that when comparing the ethology of multiple species of *Efferia*, they all shared similar behavior patterns with respect to prey preference and only differed in their behavior during copulation and chosen oviposition site.

The tribe Apocleini forms a monophyletic clade of *Philodicus*, *Promachus*, and *Megaphorus* with the addition of two previously unplaced genera *Alcimus* and *Mallophora*. There are two clades within the Apocleini, the first being *Philodicus* represented by three species (*P. tenuipes* and *P. fraterculus* from South Africa, and an unidentified species from Selangor, Malaysia) and an *Alcimus sp.* from Northern Cape, South Africa. All these species are observed to prefer polyphagous arthropod prey with a slight preference (31% - 41%) for Orthoptera prey, except *P. tenuipes*, which with limited data (N = 11) seem to prefer Hymenoptera and Diptera (Fig 3.4; supplemental material 3.7).

The second clade of Apocleini consists of *Promachus* (*P. amastrus*, *P. albifacies, P. rufipes,* and a *Promachus sp.* from Northern Cape, South Africa) *Mallophora nigrifemorata*, and *Megaphorus pulcher*. *Promachus sp.* and *P. amastrus* are from South Africa and polyphagous arthropod predators. *P. albifacies* and *P. rufipes* are from North America and prefer Hymenoptera (69% and 75%, respectively; supplemental material 3.7). However, it is important to note that there are over 230 species of *Promachus,* and even though these four seem to have different predatory habits, many more species would need to be studied to conclude if there is an actual pattern of prey preference. "*Promachus dimidiatus* forages from the soil in the early morning and late afternoon when the soil temperatures are not extreme but resorts to vertical stalks of shrubs, two to four feet above the ground during midday" (Lavigne and Holland 1969).

Mallophora and Megaphorus also prefer Hymenoptera (99% and 75%, respectively; supplemental material 3.7). *Mallophora* is known to prey on honeybees, so much so that they are considered harmful to Florida and Texas apiaries (Bromley 1950). *Mallophora* also mimic bumblebees and carpenter bees in their size and coloration (Stange 1992) and sound when flying (Linsley 1960). *Megaphorus* does not show as strong of a preference for Apidae as *Mallophora*, however, they almost always choose Hymenoptera in their environment (Cole, 1964).

The next clade of Asilinae consists of four unplaced genera (*Acasilus, Dasophrys*, *Synolcus*, and *Neolophonotus*). They are all genera found exclusively in the Afrotropical region and are polyphagous. Though there is only one known record (Hemiptera) of *Acasilus tigrimontis* feeding, there is an 84% probability (Table 3.8) of this monotypic genus having a polyphagous diet (Fig 3.4). Londt (2005) found *Acasilus* resting on woody shrubs in rocky areas, which is a very different foraging niche compared to sister taxa *Dasophrys crenulatus*. *Dasophrys* is found in grasslands (Londt 1981), mostly (38%) feeding on Diptera, but has been recorded also to feed on Hymenoptera, Hemiptera, Orthoptera, Blattodea, and Coleoptera (supplemental material 3.7).

Synolcus dubius is one of 13 species in the genus. They are known to forage and be collected in savannah (Londt 1980). Only two prey records (one termite and one Orthoptera) are included in this dataset (supplemental material 3.3). According to the ASR analysis, there is an 87% probability (Table 3.8) that this species is a polyphagous arthropod specialist (Fig 3.4). *Neolophonotus* is a much more specious genus with 257 known species. The genus is known to forage among grass, low vegetation, shrubs, and tall trees. This diverse genus is polyphagous, with prey records from 12 orders and a slight preference for Diptera (29% – 34%; supplemental material 3.7).

There are 46 species of *Astochia* found in the Afrotropical, Australasian, Oriental, and Palearctic regions. The genus is represented by *A. armata* in this study. *A. armata* are found on forest margins, open woodland, and savannah environments (Londt 2019). They are polyphagous arthropod predators, preferring Coleoptera and Hymenoptera equally with Diptera, Lepidoptera, and Odonata also represented (Fig 3.4; supplemental material 3.7).

Sister to *Astochia* is *Neoitamus*. There are 60 species of *Neoitamus* currently described from the Nearctic, Palearctic, Oriental, and Australasian regions. The two species represented in this study are *N. cyanurus* from Germany and *N. flavofemoratus* from the United States. This genus likes to forage from the leaves of plants on the edge of pasture or meadow clearings (Lavigne, 1982). Over 60% of *N. cyanurus*'s diet consists of Diptera, and hence an oligophagous arthropod predator (Fig 3.4; supplemental material 3.7). Because there were not enough species-level prey records for *N. flavofemoratus,* we used generic-level records, which may or may not reflect what the species prefers.

Neither *Clephydroneura,* nor *Heligmonevra*, have sufficient records about their biology to code their prey preference (<10 prey records; supplemental material 3.7). However, *Clephydroneura* has been recorded consuming prey from four orders (Hemiptera, Diptera, Lepidoptera, and Odonata) and *Heligmonevra* from two (Hemiptera and Lepidoptera). The ASR analysis predicts that *Clephydroneura* has a 61% and *Heligmonevra* has a 56.6% (Fig 3.4; Table 3.8) probability of being a polyphagous arthropod predator. *Clephydroneura* is known to forage from twigs or leaves and eat a variety of small soft-bodied insects especially damselflies, bugs, and small butterflies (Joseph and Parui 1976). Whereas *Heligmonevra* perches within shrubs and bushes (Londt 1994).

The next clade of unplaced genera (*Wyliea*, *Dysmachus*, and *Pamponerus*) are sister to the Philonicini + Machimini + Asilini. *Wyliea* has only two described species and *W. mydas* is represented in this analysis and has only two prey records, both of which are Lepidoptera. With the limited data available, there is a 64.8% probability of *Wyliea* being a polyphagous arthropod predator (Fig 3.4; Table 3.8). *Dysmachus* are known for having a broad habitat preference, though most are caught in meadows (Çaliskan 2019). There are 60 species found in the Palearctic region. *Dysmachus trigonus* is the representative in this study, with 67% of their diet dipterous (supplemental material 3.7), making them an oligophagous arthropod predator (Fig 3.4). Lastly, *Pamponerus germanicus* from Germany is considered a polyphagous arthropod predator with prey records from three orders (Coleoptera, Hymenoptera, and Diptera). Its preference for Coleoptera is slightly higher than the rest, with 53% of its diet (supplemental material 3.7). *P. germanicus* is known to inhabit the edges of dry deciduous woodland (Bronte et al. 2002). Its relatively high percentage of Coleoptera in its diet may be due to the availability of the order with proximity to wooded areas.

Philonicini is represented by four species of *Philonicus* Loew, 1849 (*P. albiceps*, *P. arizonensis*, *P. fuscatus*, and *P. plebeius*). Most prey records belong to *P. albiceps* (765/776; supplemental material 3.7) and due to a lack of prey records for the other three species, they were all coded at the generic level. 69% of the *P. albiceps* diet is dominated by Diptera, with 30% from the family Muscidae (supplemental material 3.7) making it an oligophagous arthropod predator (Fig 3.4). Interestingly, Ricardo (1920) observed this species entering houses and hunting house flies around windows.

Prolatiforceps is sister to the Machimini and Asilini. There are ten described species in this genus found in the Americas. The species represented in this study is *Prolatiforceps fulviventris* from the United States. *P. fulviventris* shows a strong preference (87%; supplemental material 3.7) for Hymenoptera, with 27% of the Hymenopteran prey taken belonging to the family Apidae. The only other order this species has been observed eating is Diptera, making this species an oligophagous arthropod predator (Fig 3.4). Not much is known about the ethology of this genus.

The last major clade in Asilinae belongs to *Machimus*, *Tolmerus*, and *Asilus*. All the included *Machimus* (*M. autumnalis*, *M. callidus*, and *M. occidentalis*) are polyphagous arthropod predators (Fig 3.4). *M. occidentalis* has the most polyphagous diet of the three, with prey records representing seven orders and a slight preference (52%; supplemental material 3.7) for Diptera. *Tolmerus atricapillus* showed a significant preference for Diptera (69%), 16% of which were from the family Muscidae (supplemental material 3.7). *T. atricapillus* perches on branches and leaves of trees and vegetation on deciduous forest edges (Broek et al. 2018).

Asilus has 26 species found in the Nearctic, Palearctic, and oriental regions. There are two species, *A. crabroniformis* from the United Kingdom, and *A.* sericeus from the United States in this phylogeny. *A. crabroniformis* is a polyphagous arthropod predator, whereas Lepidoptera make up 76% of *A. sericeus* diet making it oligophagous (Fig 3.4; supplemental material 3.7). *Asilus sericeus* is the only species in this study that prefers Lepidoptera. An interesting note is that *Machimus* have been known to perch in and around the entrances of gopher tortoise burrows (Bullinton and Beck 1991), and *Asilus* is sometimes also collected within and around animal burrows (Lavigne 1968). This behavior is highly unusual, and it is interesting to see it repeated with relatively closely related taxa.

Brachyrhopalinae

Brachyrhopalinae is non-monophyletic with five clades and is represented by 12 species (Fig. 3.3.) Most species (N = 8) are polyphagous arthropod predators, with the remaining four species being oligophagous arthropod predators (Fig. 3.4.). No prey preference data are available for *Afroholopogon mauros*, *Ischiolobos mesotopos*, and *Pycnopogon fasciculatus*. These species are all estimated to be polyphagous arthropod predators. Diptera is the dominant prey order within Brachyrhopalinae (Table 3.6; supplemental material 3.17.). Very little is known about the biology and ethology of *Ischiolobos*. However, *Pycnopogon* is known to perch various of twigs, leaves, and ground cover in open habitats. *Afroholopogon* resides in grass-dominated biomes and is often collected while sweep netting (Londt 2005).

Rhabdogaster is within a clade with *Sporadothrix* (Willisoninninae) and *Afroholopogon*, three relatively small-sized genera. *Rhabdogaster* is known to perch on grass tips (Londt 1994) and is oligophagous on Hymenoptera (Fig 3.4; supplemental material 3.7). There are 40 described species found in the Afrotropical and Oriental regions.

Holopogon are very small asilids that perch on the tips of twigs and leaves. Like other small asilids, this genus may prefer small, soft-bodied prey like Diptera or booklice (Alberts Chap II). There are 63 species of *Holopogon* found in the Nearctic, Palearctic, and Neotropical regions.

Ceraturgus is relatively large and often looks like Hymenoptera. They perch on leaves, grass, and sometimes flowers, and are oligophagous on Coleoptera (Alberts Chap II), specifically, Scarabaeidae. There are 13 species of this genus in the Nearctic and Palearctic regions.

There are 56 species of *Heteropogon* found in the Palearctic, Nearctic, Afrotropical, and Neotropical regions. This analysis includes two species. *H. cirrhatus* and *H. spatulatus* are both species in the United States. *Heteropogon* is unique from other Asilidae because it perches on the tips of dead twigs and is often found facing head-downward (Lavigne and Bullington, 1999). This genus has a polyphagous diet with a slight preference for Coleoptera (Fig 3.4; supplemental material 3.7). Perching on dead twigs and facing toward the ground may give the genus a better chance of spotting beetle prey.

Cyrtopogon has 121 described species in the Nearctic, Palearctic, and Oriental regions. They are found in a wide variety of habitats and hunt from various of perches (Lavigne and Holland 1969). *Cyrtopogon* is polyphagous with a slight preference for Diptera (Fig 3.4; supplemental material 3.7).

Four species of *Leptarthrus* are in the Palearctic and Oriental regions. This analysis includes one species *Leptarthrus brevirostris* from Germany. Like *Cyrtopogon,* they hunt from a variety of perches but primarily are found on grass or leaf tips. They are oligophagous arthropod predators that prefer Hymenoptera (Fig 3.4; supplemental material 3.7).

Nicocles has 16 species that can be found in the Nearctic and Neotropical regions. They pretty much solely hunt and perch on the twig and leaf tips. They are oligophagous specialists on Diptera (Fig 3.4; supplemental material 3.7). There is little literature discussing this genus's biology or predator ethology.

Dasypogoninae

Dasypogoninae is almost monophyletic. There is a main clade with the addition of *Plesiomma*, and *Molobratia* is non-monophyletic (Fig. 3.3.). There are nine Dasypogoninae under the current classification. However, *Plesiomma* is most likely a Dasypogoninae, and *Molobratia* is most likely not. Dasypogoninae has a spectrum of prey specialization within the subfamily. Two of the species are polyphagous arthropod predators, four are oligophagous arthropod predators, and three are specialist arthropod predators (Fig. 3.4.). The specialization of *Lestomyia* was unknown due to missing data, however, the ancestral state reconstruction analysis predicts them to be oligophagous arthropod specialists. The dominant prey order is Hymenoptera (Table 3.6; supplemental material 3.7).

There are 52 species of *Pegesimallus*, found in the Afrotropical and Oriental regions. They are found within grass, shrubs, and bushes (Londt 1994). Both species that are included in this analysis (*P. laticornis* and *P. aulicus*) are from South Africa and are polyphagous arthropod specialists (Fig 3.4; supplemental material 3.7). They do slightly prefer Hymenoptera (supplemental material 3.7), which is common in the Dasypogoninae (Table 3.6).

Diogmites has 73 species described from the Nearctic and Neotropical regions. This analysis only includes one species (*D. angustipennis*) from the United States. Their perch preference depends on the ambient temperature. They are found both on the ground and on vegetation, with the temperature too high to perch on the ground (Lavigne and Holland 1969). Over 68% of their prey are Hymenoptera, making them an oligophagous arthropod predators (Fig 3.4; supplemental material 3.7).

Two species of *Lestomyia* included in this study (*L. fraudiger* and *Lestomyia sp.* from Largo Vista, California). *Lestomyia* perches mainly on the ground or rocks. There are only four prey records in this dataset for the genus, so we used ancestral state reconstruction to find the probability of each state. There is a 52% probability that they are both oligophagous arthropod specialists (Table 3.8). This state seems plausible as genera in the Dasypogoninae are mostly specialized to some extent. Also, it is important to note that all four prey records for *Lestomyia* are Hymenoptera (Fig 3.4; supplemental material 3.7).

Saropogon is one of the few genera found in almost all zoogeographical regions. There are 134 current species, and this analysis included one (*Saropogon luteus*) from the United States.

Saropogon are oligophagous arthropod predators on Hymenoptera (Fig 3.4; supplemental material 3.7). *Saropogon* perch on various surfaces including twigs, grass, leaves, and stones. They have perched near anthills and preyed upon the workers (Pollock 2021).

There are 22 species of *Dasypogon*, found in the Palearctic and Afrotropical regions. Two specimens were included in this study (*D. diadema* and *Dasypogon sp.* (Ibiza) from Spain). They are both specialist arthropod predators of Hymenoptera from the family Apidae (Fig 3.4; supplemental material 3.7). Over 60% of their prey are from this family.

The placement of *Molobratia* within Dasypogoninae is debatable. While they have the characteristic fore-tibial spur or other Dasypogoninae, they lack acanthophorite spines. There are currently 15 species found in the Palearctic and Oriental regions. They like to perch and hunt on leaves and flowers and hang from a foreleg while consuming prey. They are Hymenoptera specialist predators that vastly prefer the family Apidae (Fig 3.4; supplemental material 3.7).

Dioctriinae

Dioctriinae is monophyletic in this phylogeny (Fig. 3.3.). Seven species from two genera are represented from the United States and Germany. All species are polyphagous arthropod specialists (Fig. 3.4.). The dominant prey order is Hemiptera, with Diptera and Hymenoptera as a close second (Table 3.6; supplemental material 3.7).

There are 14 species of *Eudioctria*, in the Nearctic region. This study included three species (*E. denuda*, *E. albius*, and *E. brevis*). While all three species are coded as polyphagous, it is important to note that these were calculated at a generic level due to a lack of data about these species (Fig 3.4). *Eudioctria* does have a slight preference (47%) for Hemiptera and Aphididae. *Eudioctria* perch on leaves and twigs and eat mainly small, soft-bodied insects (Scarbrough 1981).

Dioctria can be found in the Palearctic, Nearctic, and Australasian regions. There are currently 99 recognized species, and this study included four (*D. vera*, *D. atricapilla*, *D. rufipes*, and *D. hylapennis*) none of which are Australasian species. Despite all these species being coded as polyphagous arthropod predators (Fig 3.4), it is important to note that they do prefer Hymenoptera with a surprisingly high representation of Ichneumonidae, which is not often seen as prey for Asilidae (supplemental material 3.7). Hobby (1931) mentions their preference for Ichneumonidae and goes as far as to say that some of the species mimic their Ichneumonid prey. They also perch on grass or low leaves, mostly within meadows (Hobby 1931).

Laphriinae

Laphriinae is monophyletic with representation from 29 species (Fig. 3.3). Most species (N = 24) are polyphagous arthropod predators, four are oligophagous arthropod predators, and one is a specialist arthropod predator (Fig. 3.4). The predatory habits of *Laphystotes*, *Perasis*, *Anypodetus*, and *Atractia* were unknown due to insufficient data. All these genera are predicted to be polyphagous arthropod predators, using ASR. The dominant prey for Laphriinae species is

Diptera. However, Hymenoptera and Coleoptera are close behind (Table 3.6; supplemental material 3.7)

The first clade within Laphriinae consists entirely of polyphagous arthropod predators. Two species of *Laphystotes*, are found in the Afrotropical region. *Laphystotes ariel* from South Africa and are mostly found perching on the ground (Londt, 1994). Unfortunately, there was not enough prey information for this species, so ancestral state reconstruction estimated it to be a polyphagous arthropod predator with a high probability of 99% (Fig 3.4; Table 3.8). *Trichardis* has 29 species in the Afrotropical region. They prefer perching on the ground and stones (Londt 1994). This study included *Trichardis effrena* for the phylogeny, and the predator-prey data was gathered at the generic level. *Trichardis* has a slight (50%) preference for Hymenoptera prey (supplemental material 3.7). *Perasis* consists of ten species in the Neotropical, Palearctic, and Afrotropical regions. One species (*P. transvaalensis*) was included in this study from South Africa. There was insufficient prey data to assign about prey preference character states, so using ASR, we found there is a 78% probability that the species is polyphagous (Fig 3.4; Table 3.8). There are 50 species of *Laphystia*, found in the Palearctic, Nearctic, and Oriental regions. This study includes two species from the United States (*Laphystia cf. canadensis* and *L. tolandi*). Both species were coded at the generic level due to insufficient data. *Laphystia* is a polyphagous arthropod predator with a slight preference for Diptera (58%; supplemental material 3.7).

Nusa is sister to *Anypodetus*, *Hoplistomerus,* and *Laxencera,*and consists of 29 species in the Oriental, Afrotropical, and Palearctic regions. They are mainly found perching on the ground or stones (Londt 1994). This study includes *Nusa infumata* from South Africa. *Nusa* is a polyphagous arthropod predator with a slight preference for Diptera (45%; supplemental material 3.7).

The next clade consists of *Anypodetus* spp., *Hoplistomerus* spp., and *Laxenecera* spp. and mostly consists of polyphagous arthropod predators. *Anypodetus* is an Afrotropical genus currently with ten species. This phylogeny includes two species, *A. arachnoides* and *A. fasciatus*. Both of which perch on the ground (Londt 1994). Neither of these species had sufficient prey data to assign prey preference character states. However, ASR analysis postulates an 80% and 84% probability that both species are polyphagous arthropod predators (Fig 3.4; Table 3.8). *Hoplistomerus* spp. is also an Afrotropical genus with twelve species, one of which (*H. nobilis*) is included in this study. *Hoplistomerus* is well known to specialize on Scarab beetles, making up 82% of its prey (supplemental material 3.7). There are 33 species of *Laxenecera*, found in the Afrotropical and Oriental regions. This genus is represented by two species *L. albicincta* and *L. engeli*. This genus is known to perch on the tips of grass. Both species are polyphagous arthropod predators with a slight preference for Hymenoptera (Fig 3.4; supplemental material 3.7).

The next clade comprises of all polyphagous arthropod predators. There is only one species of *Nannolaphria*, *N. nigra*. *Nannolaphria* perches on the tips of shrubs and bushes (Londt1994). However, there are few prey records for this species, and the ASR analysis revealed that this species is a polyphagous arthropod predator (Fig 3.4). *Cerotainia* contains 37 species, all found in the Americas (Nearctic and Neotropical regions with two species from the United States (*C. albipilosa* and *C. macrocera*) were included in this phylogeny. *Cerotainia* is a polyphagous arthropod predator with a slight preference for Diptera (Fig 3.4; supplemental material 3.7).

There are only two species of *Atractia*, both are found in the Neotropical region, are known and *A. marginata* from Costa Rica is included here. Insufficient prey records for this species are available but the ASR analysis finds that it has an 80% probability of being a polyphagous arthropod predator (Fig 3.4; Table 3.8). *Atomosia* consists of 54 species, all from the Nearctic and Neotropical regions. This study includes two species from the United States (*A. mucida* and *A. puella*). Both species are polyphagous arthropod predators who slightly prefer Diptera (Fig 3.4; supplemental material 3.7).

The genus *Pilica*, is sister to *Lamyra* and *Stiphrolamyra*, and is strictly Neotropical. We have included two species *P. erythrogaster* and *P. formidolosa*, from Costa Rica. Both species are oligophagous predators of Hymenoptera, with 86% of their prey of that order (Fig 3.4; supplemental material 3.7). *Lamyra* is an Afrotropical genus with four described species. They like to perch on the tips of trees, shrubs, and bushes (Londt 1994). Only one species was included in this study, *L. gulo* from South Africa. *L. gulo* is an oligophagous pedators on Hymenoptera (Fig 3.4; supplemental material 3.7). *Stiphrolamyra* is found in the Afrotropical and Palearctic regions. This analysis includes two (*S. schoemani* and S. angularis) of the 15 known species. They like to perch on shrubs and bush tips (Londt 1994). They are polyphagous arthropod predators with a slight (57%) preference for Hymenoptera (Fig 3.4; supplemental material 3.7).

There are 59 species of *Choerades*, two of which are included in this study (*C. bella* and *C. marginata*). Like other genera in this subfamily, they also perch on the tips of trees, shrubs, and bushes (Londt 1994). Both species are coded as polyphagous arthropod predators (Fig 3.4).

However, there was insufficient data for *C. bella*, so it was coded at the generic level. Interestingly, *C. bella* at the generic level shows a slight preference (41%) for Coleoptera, whereas *C. marginata* at the species level has a slight preference (33%) for Diptera (Fig 3.4; supplemental material 3.7). These species are a good example of how species-level prey data can change what we believe predatory preference is for a particular species.

Lastly, there are 218 species of *Laphria* found in almost every zoogeographical region except for the Afrotropics. This study includes five species from the United States (*L. felis*, *L. sicula*, *L. aktis*, *L. grossa*, and *L. thoracica*, and one *Laprhia sp.* from Italy). *Laphria* is known to forage from sunny spots on horizontal logs (Lavigne and Bullington 1984). All species included in this study are considered polyphagous arthropod specialists with a slight preference for Coleoptera (47-58%), except for *L. thoracica,* a specialist arthropod predator for Hymenoptera and Apidae (Fig 3.4; supplemental material 3.7).

Leptogastrinae

Leptogastrinae is monophyletic with representation from 26 species (Fig. 3.3). All species were coded as polyphagous arthropod predators, mainly at the generic level (Fig 3.4). Very little predator-prey data is included in this study despite the numbers found in Table 3.6 (e.g., all nine *Leptogaster* species were recorded as just *Leptogaster* and are therefore duplicate records). The prey preference character states could not be established for 13 species due to insufficient data. The ASR analysis predicts them all to be polyphagous arthropod predators by interpolating from the observed prey preferences on the tree and phylogenetic relationships (Fig. 3.4). This subfamily is known to hunt spiders more than any other clade, and the data in this study support the hypothesis (Table 3.6; supplemental material 3.7). Many of the Leptogastrinae species are caught hunting within grasslands and on grass tips (Londt 1994), and some (e.g., *Lasiocnemus*) have been observed hovering in front of spider webs and capturing the spiders (Londt 1994). This clade is morphologically unique, with elongated bodies and legs. Despite the findings in this study, Leptogastrinae may be more specialized than we know. Many species are collected while sweep netting, and any associated prey is lost, hence the amount of unavailable data for this subfamily.

Ommatiinae

Ommatiinae is a monophyletic clade that is sister to the Asilinae. Nine species are represented in this study, all of which are polyphagous arthropod predators (Fig. 3.4). They are generally "shade-seeking" species (Shelly 1984), meaning that they like to perch on vegetation and often not in direct sunlight like many other species (Londt, 1994). Four species (*Michotamia compedita*, *Emphysomera conopsoides*, *E. pallidapex*, and *Afroestricus chiastoneurus*) are predicted, with ancestral state reconstruction, to have a polyphagous arthropod diet like the rest of the Ommatiinae. Like Leptogastrinae, there are limited prey capture data available for the Ommatiinae. *Ommatius tibialis* was the only species to be coded at the species level, with over ten prey records available (supplemental material 3.7).

Stenopogoninae

Stenopogoninae is non-monophyletic in this study (Fig. 3.3) and all other recent molecular phylogenies that include this subfamily (Dikow 2009a; Cohen et al. 2021). Twelve species in this study represent the subfamily. There are two main clades, minus *Plesiomma*, which is most likely a Dasypogoninae, as stated above. The first clade consists of *Microstylum*, *Prolepsis tristis*, *Ancylorhynchus cruciger*, *Scylaticus costalis*, two *Connomyia* species, all of which are polyphagous arthropod predators (Fig 3.4). *Microstylum* and *S. costalis* were coded for this using supplemental material 3.7, and *P. tristis* was estimated to have a 67% probability of being a polyphagous arthropod predator (Table 3.8). Many of these species are known to hunt for prey from various perches (Londt 1994), reflecting their non-selectivity to prey.

The second Stenopogoninae clade (Stenopogonini) consists of two species of *Gonioscelis*, *Ospriocerus aeacus*, and two species of *Stenopogon*. Again, these species have a variety of different perching locations, such as the ground, grass, bush, and shrub tips, and rocks (Londt 1994), and they sometimes change perch location according to the temperature on the ground (Lavigne and Holland 1969). Despite this similarity to the other Stenopogoninae, this clade is much more specialized (Fig 3.4).

Ospriocerus shows a strong preference for the order Coleoptera, and in particular, Meloidae and Cantharidae. Both prey families contain high levels of cantharidin, making them distasteful and most likely harmful to other species of Asilidae. However, this diet specialization suggests behavioral, mechanical, or biological adaptations that allow this genus to feed upon such toxic prey (Dennis and Lavigne 1975, Lavigne and Dennis 1994).

Stichopogoninae

Stichopogoninae is a monophyletic group represented by two genera and eight species in this study (Fig. 3.3). All these species prefer Dipteran prey making up 60% of their diet (Table 3.6). They also have a relatively high percentage (4%) of spiders in their diet (Table 3.6). Three species (*Lasiopogon sp., L. aldrichii*, and *Stichopogon trifasciatus*) are polyphagous arthropod predators, while the remaining five species (*L. cinctus, S. catulus, S. punctus, S. elegantulus*, and *S. hermanni*) are oligophagous arthropod predators (Fig 3.4).

Lasiopogon is known to hunt mainly from rocks along riverbanks (Lavigne 1969) and are thought to have potentially weak mouthparts and are therefore restricted to soft-bodied prey, such as Diptera (Lavigne and Holland 1969), which is supported by this analysis. *Stichopogon* also forages close to the ground, whether it is from sand, rocks, or other debris (Lavigne and Holland 1969). Feeding on Hemiptera, Orthoptera, Arachnida, and Diptera (supplemental material 3.7) is generally observed.

Tillobromatinae

Only two species were included in this study and recovered as paraphyletic. Neither of which had enough data to code for their species. However, the ancestral state reconstruction predicts that they are both polyphagous arthropod predators (Fig 3.4), with a 78% probability for *Lycostommyia albifacies* and a 74% probability for *Tillobroma punctipennis* (Table 3.6). In addition, *Lycostommyia* is known to hunt from rocks (Londt 1994).

Trigonomiminae

Trigonomiminae is non-monophyletic and splits into two main clades the Trigonomimini (*Holcocephala abdominalis*, *H. calva*, *Rhipidocephala sp.,* and *Trigonomima sp.*) and the Xenomyzini, which is made up of five *Damalis* species (Fig. 3.3). The Trigonomimini are all polyphagous arthropod predators including *Rhipidocephala sp.* and *Trigonomima sp.* with the probability of 69% and 70% respectively (Fig 3.4; Table 3.8). About 60% of the diet of *Damalis* consists of Hymenoptera, and over 50% of the order is dominated by Formicidae (supplemental material 3.7). *Holcocephala fusca* prefer Hymenoptera and Diptera prey (Dennis 1979). It is important to note that very few prey records included for this genus are for the included species. All the Trigonomiminae included in this study are known to hunt from the tips of shrubs, grass, or branches (Londt 1994).

Willistonininae

Willistonininae is non-monophyletic in this study (Fig. 3.3). *Sporadothrix gracilis*, *Trichoura pardeos*, and *Willistonina bilineata* predatory habits were all predicted as polyphagous arthropod predators using ancestral state reconstruction (Fig 3.4). *Sporadothrix* and *Ablautus* are known to perch on sandy ground, whereas *Trichoura* and *Willistonina* are found more often perching on tips of grass or twigs and on debris on the ground. All these genera are relatively small-bodied flies and probably prefer smaller and soft-bodied prey. The *Ablautus* included in this study preferred Diptera (supplemental material 3.7).

5.3. Stochastic character mapping (SCM)

The model (*6-rate_ordered*) that performed the best out of the four models tested (Table 3.7) allows for taxa to move from character state 0 to 1, 1 to 2, 2 to 3, and in reverse. This model generally makes sense biologically, in that jumps from a polyphagous arthropod-predator to a specialized arthropod-predator would not happen instantaneously, there would be a transitional state to a more or less specialized diet. The stochastic character map shows where these transitions have the highest probability of happening within the phylogenetic tree. A transition from state 0 (non-predator) to state 1 (polyphagous arthropod predator) happens once at the most recent common ancestor of Asilidae; a transition from state 1 to state 2 (oligophagous arthropod predator) is postulated to have occurred 21 times; and a transition from state 2 to state 3 (specialized arthropod predator) happens eight times.

Most prey specialization transitions happen in a increasing specialization direction, where groups of asilids become more specialized. There are, however, five instances of a reversal from a more specialized prey preference to a more generalist preference. *Sporadothrix gracilis*, *Afroholopogon mauros*, *Trichoura pardeos*, and *Stenopogon albibasis* are optimized to have transitioned from state 2 to state 1, and *Damalis monochaetes* is optimized to have transitioned from state 3 to state 2 (Fig. 3.5). *Sporadothrix gracilis*, *Trichoura pardeos* are both

Willistonininae (a taxon not recovered as monophyletic) and had insufficient prey data to code their prey preference. *Afroholopogon mauros* is a Brachyrhopalinae and was also coded for insufficient prey data.

In the case of *Trichoura pardeos*, this species is the sister to an oligophagous clade consisting of the Stenopogonini. According to the posterior probability at the root node to this clade, there is only a 52% probability that their common ancestor was oligophagous. With such low probability, it could be that with more information the transition to an oligophagous diet would be shifted to be at the base of the Stenopogonini instead.

The reversal for *Stenopogon albibasis* could be due to the fact that this node was coded at the generic level and not an accurate representation of this species. *Damalis monochaetes* also may have this problem. The reversal may have more to do with the data availablility (supplemental material 3.7) rather than the actual biology of these species. This study includes five species of *Damalis*, two of which are unidentified, and only one (*D. monochaetes*) that has enough (N = 18) species-level prey data to warrant a species-level prey preference code. The other four species are all coded at the generic level. Currently, we are unsure how our coding system can help avoid or take into account these potential biases in the ASR analysis, further experimentation of alternative coding schemes is needed.

Afroholopogon mauros and *Sporadothrix gracilis* (together with *Rhabdogaster pedion*) group as sister to the *Damalis* clade. Due to there being so many species of *Damalis* of which, the majority are coded as specialist arthropod predators, the probability of the *Afroholopogon,* *Sporadothrix* group having an oligophagous common ancestor with *Damalis* is the most probable. However, due to the statements above about the biases of generic vs. species-level data, this may not be accurate. Plus, the probability for the oligophagous MRCA is only 49% (Fig. 3.4).

There are two transitions from state 1 through state 2 to state 3 within a branch (*Hoplistomerus nobilis* and *Molobratia teutonus;* Fig 3.4). These are both very specialized species. *Hoplistomerus nobilis* (Fig. 3.1C) is known from southern Africa and feeds almost exclusively on Scarabaeidae (82%; supplemental material 3.7; Londt 2007). They are commonly found in grasslands and perch on piles of dung to wait for the dung-visiting Scarabaeidae (Londt 2007). Londt (2007) mentioned similarities between other Laphriinae typically ovipositing in decaying wood, which is similar to the dung that *Hoplistomerus nobilis* uses. Whereas over 60% of *Molobratia teutonus* diet is Apidae (92% Hymenoptera; supplemental material 3.7). They are striking wasp mimics found in the Palearctic region.

5.4. Elements of prey specificity

The diet of adult assassin flies is entirely composed of arthropod prey. The majority of which are insects, there are some assassin flies (e.g., *Leptogaster* and *Stichopogon*), which have been reported to prey on Arachnida (Alberts Chap II). Many species of Asilidae are known to make foraging flights to assess prey around them (Lavigne and Dennis 1979, Dennis 1979) and will discriminate between potential prey items (Dennis et al., 1975). Many prey characteristics influence the choice of prey, such as size, speed, shape, the toughness of integument, availability, color, or location, such as flying or grounded. The importance of these prey characteristics depends heavily on the asilids' ethology and morphology characteristics, such as their size, hunger, speed, strength, vision, venom potency, proboscis size and density, and foraging perch location (Lavigne and Holland 1969).

Elements like perch location and position seem to be important factors affecting prey selection. For example, *Heteropogon* slightly prefers Coleoptera, and they are often found perching on the tips of dead twigs facing down toward the ground (Lavigne and Bullington 1999). *Laphria* also prefers Coleoptera, and they are often found perching in sunspots on horizontal dead logs, again, a perfect perch to find beetles. The choice of foraging and perch location may also depend strongly on the availability of prey in a particular place or at a specific time. Asilids may appear to be specialists at a particular time because they simply switch to the most abundant prey type (Naskar et al. 2019). Further study is needed for most species with observed prey preference to rule them out as simply opportunistic predators.

The chosen perch location for certain species changes with environmental factors such as the temperature of the perch or wind. Often ground perching asilids will change their perch to low vegetation or debris when the ground temperature rises to a certain level (Lavigne and Dennis 1979, Dennis et al. 1986). The change in perch location throughout the day may affect what prey they hunt. Species like *Saropogon, Stichopogon,* or *Dioctria* which are known to hunt ground-dwelling prey may only do so when the soil temperatures are tolerable. *Holcocephala fusca* was observed to generally hunt from the tips of twigs, but when the wind blew harder than 3.2 km/h. they move their perch closer to the ground (Dennis 1979).

Prey recognition and discrimination towards color has been observed in many species of Asilidae. *Efferia* are known to discriminate between black, orange, and white, with a significant preference for black prey (Dennis et al. 1975).

Lavigne and Holland (1969) argue that prey size is the most important character attribute in prey selection. Dennis et al. (1975) found that only the females of *Efferia frewingi* discriminated against larger sized prey. *Genera* like *Ablautus, Holopogon,* and *Lasiopogon* all prefer Diptera, mostly likely because many are small, and soft-bodied, making them easier prey (O-Neill 1992a). These traits refer to the importance of prey suitability, and if the prey and predator physically and biologically compatible. Prey often have defenses against potential predators such as toxins (e.g., Meloidae) or tough cuticle (e.g., Tenebrionidae) that only certain species of Asilidae (e.g., *Ospriocerus* and *Proctacanthus,* respectively) can overcome (Pollock and Lavigne 2019).

Female Asilidae are typically observed capturing prey and collected with prey more than males (Hobby 1931, Dennis and Lavigne 1975, Londt 1999, Londt 2006, Lavigne 2016, Pollock and Lavigne, 2019). They are often seen pursuing prey on a more frequent basis, but females of species like *Efferia frewingi* will eat smaller prey items and more often than males of the same species (Dennis et al. 1975). There are many hypotheses for why females consume more prey than males (1) females have greater nutritional needs in order to produce eggs (Hobby 1931, Londt 2006), (2) males spend less time foraging than females because they spend more time looking for mates (Dennis et al. 2010), (3) there may be populations of asilids that have more females than males (Lavigne 1971), (4) females feed for shorter periods of time and therefore have more time to hunt more individual prey items (Dennis and Lavigne 1975), (5) and lastly, females feed throughout the day and not at particular times, unlike males (Dennis et al. 2010).

5.5. Asilidae prey order preference

The overwhelming majority (65%) of Asilidae prey belong to Diptera (24%) and Hymenoptera (41%), followed by Coleoptera (12%), Hemiptera (10%), Lepidoptera (4%), and Orthoptera (5%) making up a third of their arthropod prey diet (Table 3.6; Alberts Chap 2, Lavigne 2016). The other five orders (Araneae, Blattodea, Neuroptera, Thysanoptera, Trichoptera) make up the remaining 4% of Asilidae prey in this study.

Hymenoptera is the most common order of prey for Asilidae (Table 3.6). Taxa with a preference for Hymenoptera prey are: *Damalis* spp. (62%), *Dasypogon diadema* (91%), *Dioctria atricapilla* (38%), *D. hyalipennis* (55%), *Diogmites angustipennis* (68%), *Lamyra gulo* (67%), *Laphria thoracica* (67%), *Laxenecera albicincta* (45%), *Leptarthrus brevirostris* (60%), *Leptogaster* spp. (49%), *Machimus occidentalis* (52%), *Mallophora* spp. (93%), *Megaphorus pulcher* (94%), *Molobratia teutonus* (92%), *Pegesimallus laticornis* (45%), *Philodicus tenuipes* (36%), *Pilica formidolosa* (86%), *Proctacanthus nearno* (62%), *P. philadelphicus* (72%), *P. rufus* (98%), *Prolatiforceps fulviventris* (87%), *Promachus albifacies* (69%), *P. rufipes* (75%), *Rhabdogaster* spp. (67%), *Saropogon* spp. (78%), *Scylaticus* spp. (58%), *Stenopogon rufibarbis* (62%), *Stiphrolamyra* spp. (57%), and *Trichardis* spp. (50%) (supplemental material 3.7).

Although many species of *Laphria* mimic Hymenoptera, they are mostly known to prefer Coleoptera (Fig. 3.4). However, according to the data collected in this study, *Laphria thoracica* prefers Hymenoptera. *Laphria thoracica* visually mimics a bumblebee very convincingly and greatly prefers prey from the family Apidae (Dennis and Lavigne 2007). Many species of Asilidae mimic Hymenoptera. The most common hypothesis is that it is aggressive mimicry which a diet on Hymenoptera would support, however genera such as *Laphria* that generally prefer Coleoptera could mean that their mimicry is Batesian or Müllerian. A more thorough ASR analysis may help to decipher this. Did Hymenoptera mimicking *Laphria* initially prefer Hymenoptera and eventually move into the woods to feed on Coleoptera? What order of prey did their MRCA prefer?

There are some families of Hymenoptera that have particularly high representation in this dataset. Most of the records for Apidae are asilids feeding on *Apis mellifera* near beehives. This would be an example of opportunistic feeding and may not be a true specialization (Londt 2007). The same may go for the prey family Formicidae. There may be a misleadingly high representation of this family due to emergence events of winged reproductives (O'Neill & Kemp, 1991). Another reason why Hymenoptera may make up the majority of Asilidae prey is due to their availability in the same environments that asilids occupy.

Diptera is the second most common order of prey for Asilidae (Table 3.6). Taxa with a preference for Diptera prey are: *Ablautus* spp. (67%), *Asilus crabroniformis* (47%), *Atomosia puella* (50%), *Cerotainia albipilosa* (36%), *Choerades marginata* (33%), *Cyrtopogon* spp. (51%), *Dasophrys* (38%), *Dioctria rufipes* (48%), *Dysmachus trigonus* (67%), *Efferia aestuans*

(59%), *E. albibarbis* (59%), *E. pogonias* (46%), *Euscelidia* spp. (33%), *Holcocephala abdominalis* (38%), *H. calva* (43%), *Holopogon phaeonotus* (43%), *Laphystia* spp. (58%), *Lasiopogon cinctus* (91%), *Leptogaster cylindrica* (41%), *L. flavipes* (50%), *Machimus callidus* (39%), *Nicocles politus* (63%), *Neoitamus cyanurus* (61%), *Neolophonotus bimaculatus* (38%), *Nusa* spp. (45%), *Ommatius* spp. (28%), *Philodicus tenuipes* (36%), *Philonicus albiceps* (69%), *Psilonyx annulatus* (55%), *Rhipidocephala* spp. (67%), *Stichopogon* spp. (61%), *S. trifasciatus* (51%), and *Tolmerus atricapillus* (69%) (supplemental material 3.7). In this study, Diptera is mostly preferred by smaller Asilidae. This is most likely because of their relatively smaller size, lack of defense (e.g., stinging, or thick cuticle). *Stichopogon* and *Lasiopogon* from a Diptera-specialized clade.

Coleoptera is the third most common order (12%; Table 3.6) of prey represented in this study. *Ceraturgus* spp. (70%), *Choerades* spp. (41%), *Cophinopoda sp.* (43%), *Gonioscelis* spp. (62%), *Heteropogon* spp. (34%), *Hoplistomerus nobilis* (91%), *Laphria grossa* (58%), *Microstylum* spp. (29%), *Ospriocerus aeacus* (90%), and *Pamponerus germanicus* (53%) showed a preference for Coleoptera prey (supplemental material 3.7). Coleoptera are generally seen as difficult prey to overcome due to the strength of their cuticle and defense mechanisms such as cantharidin (Pollock and Lavigne 2019). Asilids that prey on Coleoptera may have morphological or behavioral adaptations to help them overcome such formidable prey. For example, *Ospriocerus* is well known to predate on beetles from the Meloidae and Cantharidae families (Dennis and Lavigne 1975, Lavigne 2016) which both produce defensive cantharidin toxins. The adaptation that *Ospriocerus* has to detoxify such toxic prey is still unknown (Pollock and Lavigne 2019).

Hemiptera made up 10% of the prey records for this analysis (Table 3.6; supplemental material 3.7) *Proctacanthella cacopiloga* and *Eudioctria* spp. are the only taxa in this analysis that slightly prefer Hemiptera (54% and 47% respectively). However, neither percentage is high enough to qualify them as oligophagous in this analysis. Like Diptera, Hemiptera are known to have relatively weak cuticle and therefore potentially make suitable prey for smaller asilids (Melin 1923; Dennis and Lavigne 1975; Scarbrough 1978).

Lepidoptera is not a common preferred prey item in this analysis (4%) despite them being available in many shared environments with Asilidae (Table 3.6; supplemental material 3.7). The best representation of Lepidoptera as prey is in Asilinae with only 7% of their diet (Table 3.6). Only *Asilus sericeus* prefers Lepidoptera over other orders in this study. This may seem surprising because Lepidoptera are generally seen as “easy” prey for asilids due to them being slow fliers with soft integument. *Alcimus sp.* in this study are polyphagous arthropod predators (preferring both Orthoptera and Lepidoptera), however Londt (1999) found them to be one of the only genera (and in particular *Alcimus mimus*) who had a particular preference for Lepidoptera.

There are a few potential reasons for this lack of Lepidoptera as assassin fly prey. First, most of Lepidoptera (~75%) are moths and fly at night whereas Asilidae forage during the day (Dennis et al. 2012). Another potential reason is that asilids and Lepidoptera occupy different habitat niches. Assassin flies are found primarily in arid to semi-arid regions, whereas Lepidoptera are known to occur in more humid and tropical areas (Dennis et al. 2012). The most likely reason in our point of view, is that many Lepidoptera, especially day-flying butterflies seem considerably large to a foraging assassin fly due to their wingspan. Size discrimination has been well documented across Asilidae (Lavigne and Holland 1969, Dennis and Lavigne 1975).

5.6. Elements of sampling bias

The size of predator and prey species is one of the more apparent sampling biases within this dataset and likely others. Smaller asilids are more difficult to find and collect than larger ones. It is even more challenging to collect a small asilid with the prey because, most likely, the prey is much smaller than the predator. Often when an asilid is caught with prey, it immediately drops the prey in the net. The collector can sometimes rummage on the ground and find the prey item. However, if it is small, the chances of locating it and associating it with the assassin fly are much less. Also, larger asilids are flashier and have a greater chance of ending up in a museum collection with amateur donations.

The habitat of specific genera can often require other methods of collecting than hand net collecting one specimen at a time, like how the majority of Asilidae are collected. Genera such as *Leptogaster* and *Afroholopogon* are often only collected while sweep netting (Londt 1994). This collecting method means that prey associations are most likely lost in the collecting event. Species that dwell within the grass or difficult-to-reach places will most likely have poor prey representation within museum collections. Most likely, only collectors targeting these asilids with prey, will be successful.

6. Conclusions

A maximum likelihood analysis of six genes (*18S, 28S, COI, AATS, EF1-a,* and *CAD*) for 211 Asiloidea and outgroup species recovered Bombyliidae as sister to the rest of Asiloidea, Mydidae plus Apioceridae as sister to Asilidae, and Laphriinae as sister to the rest of Asilidae. Within Asilidae, six of the twelve subfamilies were recovered as monophyletic. The other six were either polyphyletic or paraphyletic. *Plesiomma* most likely is a Dasypogoninae based on our phylogenetic hypothesis and feeding behavior, whereas the placement of *Molobratia* within Dasypogoninae may need to be investigated further. Trigonomiminae is split into two main clades (*Damalis* and *Holcocephala*). Willistonininae, Stenopogoninae, and Brachyrhopalinae are scattered throughout the center of the phylogeny. Further examination of their classification may be needed.

With ancestral state reconstruction, we were able to find that the most recent common ancestor of Asilidae was a polyphagous arthropod predator, as well as the most recent common ancestor of the major clades within Asilidae. Most of the species are polyphagous arthropod predators. Oligophagous, and specialist arthropod predators independently evolved 20 times within Asilidae. With the visualization of the stochastic character map, we found eight occurrences of asilids evolving from a more specialized state to a less specialized state. However, many of these reversals show that more work must be done to gather prey preference data.

Some species, like *Ospriocerus aeacus, Molobratia teutonus, Dasypogon diadema,* and *Hoplistomerus nobilis* show an exceptionally high level of specialization. Hymenoptera is the most common order of prey for Asilidae, followed by Diptera. Prey choice depends on many variables, such as availability, size, predator sex, niche, weather, and time of day. More species level data is needed to understand how these variables effect the asilids prey preference.

There is a great need for more ethology and ecological studies concerning the predatory habits of Asilidae. Asilidae are top aerial predators in most natural environments and are essential for the health of an ecosystem. Until now, most Asilidae literature are taxonomy-related with occasional ecological and behavioral notes included. Formal ecological studies are needed to reduce the amount of bias and uncontrolled variables to better understand the role Asilidae have in their environments. Though the information presented in this study is interesting and revealing about some biological patterns within the family, the amount of missing data (absence of a sufficient number of prey records) show that more information is needed! This was an important first step to understanding the evolution of prey specificity and preference within Asilidae.

Author contributions

Alberts – Conceptualization, Data collection and curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing, and Editing
Dikow – Molecular data acquisition, Supervision, Visualization, Review, and Editing

Funding statement

This project was partially funded with the Williston Diptera Research Fund, the University of California, Davis Travel Award, the Lewis and Clark Fund for Exploration and Field Research, the Smithsonian 10-week Graduate Student Fellowship, and the Law Family Award for the Study of Systematic Entomology, with Matching Support from the CA&ES Dean's Circle Fund.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Ziad Khouri for helping with fixing many computer issues and the analyses. Jessica Gillung helped with the development of the idea for this project. Madi Alderman helped with compiling and cross referencing a lot of literature for the predator-prey data. We would like to thank Edson Guilherme for letting us include reference to his iNaturalist photo of *Plesiomma.* We would also like to thank David Mozzoni, Tamara Szentivanyi, Paul Reeves Photography, Rose Payne, and Jeff Gruber for their photographs reproduced in Fig. 3.1. Lastly, the first author would like to thank her husband George Alberts and her family for supporting her while she finished her Ph.D. with two young children.

References

Artigas, J.N., Papavero, N., 1997. The American genera of Asilidae (Diptera): keys for identification with an atlas of female spermathecae and other morphological details. IX. 5. Subfamily Asilinae Leach (including Apocleinae Lehr): key to generic group. Universidade de São Paulo; Museu de Zoologia. 34(1-4), 57–63. https://doi.org/10.11606/issn.2176-7793.v34i1-4p57-63.

Bartlett, T., 2004. BugGuide: Order Coleoptera – Beetles. https://bugguide.net/node/view/60 [accessed on August 14, 2022].

Barahona-Segovia, R.M., Pañinao-Monsálvez L., 2020. Desolation comes from the sky: Invasive Hymenoptera species as prey of Chilean giant robber flies (Diptera: Asilidae) through field observations and citizen science. Journal of Asia-Pacific Entomology. 23(3), 840–844. https://doi.org/10.1016/j.aspen.2020.07.012.

Bernasconi, M.V., Pawlowski, J., Valsangiacomo, C., Piffaretti, J-C., Ward, P.I., 2000. Phylogeny of the Scathophagida (Diptera, Calyptretae) Based on Mitochondrial DNA Sequences. Molecular Phylogenetics and Evolution. 16(2), 308–315. https://doi.org/10.1006/mpev.2000.0825.

Bertone, M.A., Coutney, G.W., Wiegmann, B.M., 2008. Phylogenetics and temporal diversification of the earliest true flies (Insecta: Diptera) based on multiple nuclear genes. Systematic Entomology. 33, 668–687. https://doi.org/10.1111/j.1365-3113.2008.00437.x.

Borowiec, M.L., 2016. AMAS: a fast tool for alignment manipulation and computing of summary statistics. PeerJ. 4, e1660. https://doi.org/10.7717/peerj.1660.

Broek R.V.D., Smit, J.T., Bree, E.D., Beentjes, K., 2018. *Tolmerus calceatus* (Meigen) confirmed as a valid species separate from *Tolmerus atricapillus* (Fallén) (Diptera: Asilidae). Zootaxa. 4508(2), 249–258. ISSN: 1175-5326.

Bromley, S.W., 1945. Robber fly and Japanese Beetle. Bulletin of the Brooklyn Entomological Society. 40, 44–47. ISSN: 1051-8932

Bromley, S.W., 1945b. Insect enemies of the house fly, *Musca domestica* L. Journal of the New York Entomological Society. 53(2), 145–152. https://www.jstore.org/stable/25005105.

Bromley, S.W., 1950. Florida Asilidae (Diptera) with description of one new species. Annals Entomological Society of America. 43, 227–239. https://doi.org/10/1093/aesa/43.2.227.

Bronte, D., Dekoninck, W., Grootaert, P., 2002. A contribution to the distribution and ecology of asilid flies in the sandy regions of Flanders (Diptera Asilidae) with a focus on the paucity in the Flemish coastal dunes. Bulletin S RBE/KB VE. 138, 20–28.

Brues, C.T., 1946. Insect dietary. An account of the food habits of insects. Harvard University press. Cambridge, Massachusetts, 266–267.

Bullington, S.W., Beck, A.F., 1991. A new species of *Machimus* Loew (Diptera: Asilidae) from Burrows of *Gopherus polyphemus* (Testudines: Testudinidae). Annals of the Entomological Society of America. 84(6), 590–595. https://doi.org/10.1093/aesa/84.6.590.

Bybee, S.M., Taylor, S.D., Nelson, C.R., Whiting, M.F., 2004. A phylogeny of robber flies (Diptera: Asilidae) at the subfamily level: molecular evidence. Molecular Phylogenetics and Evolution. 30, 789–797. https://doi.org/10.1016/S1055-7903(03)00253-7.

Çaliskan, H., 2019. Contributions to the records of *Dysmachus preamorsus* (Loew, 1854) (Diptera, Asilidae) In Turkey and some notes on its seasonal activity. Biological Diversity and Conservation. 12(3), 20–27. https://doi.org/10.5505/biodicon.2019.48658.

Capinera, J.L., Scott, R.D., Walker, T.J., 2004. Field guide to grasshoppers, katydids, and crickets of the United States. Cornell University Press. 280 pp. ISBN: 0801442605.

Cannings, R.A. 2014. The Robber Flies (Diptera: Asilidae) of Western Canadian Grasslands. *In.* Arthropods of Canadian Grasslands (Volume 4): Biodiversity and Systematics Part 2. (eds.) Giberson DJ, Cárcamo HA. Biological Survey of Canada. 269–297. http://dx.doi.org/10.3752/9780968932179.ch7.

Chernomor, O., Haeseler, Av., Minh, B.Q., 2016. Terrace aware data structure for phylogenomic inference from supermatrices. Systematic Biology. 65, 997–1008. https://doi.org/10.1093/sysbio/syw037.

Cicero, J. M., Adair, M. M., Adair, R. C., Hunter, W. B., Avery, P. B., Mizell R. F., 2017. Predatory behavior of long-legged flies (Diptera: Dolichopodidae) and their potential negative effects on the parasitoid biological control agent of the Asian citrus psyllid (Hemiptera: Liviidae). Florida Entomologist. 100(2), 485–487. https://doi.org/10.1653/024.100.0243.

Cohen, C. M., 2020. Robber flies of the world. Version 0.5. https://www.robberfliesoftheworld.com/Catalog/Catalog.php [accessed Oct 4, 2022].

Cohen, C. M., Nobel, K., Cole, J., Brewer, M.S., 2021. The phylogeny of robber flies (Asilidae) inferred from ultraconserved elements. Systematic Entomology. 46(4), 812–826. https://doi.org/10.1111/syen.12490.

Cole, F. R., 1969. The flies of western North America. University of California Press, Berkeley and Los Angeles. 11: 184–217.

Collins, K.P., Wiegmann, B.M., 2002. Phylogenetic relationships and placement of the Empidoidea (Diptera: Brachycera) based on 28S rDNA and *EF-1*α sequences. Insect Systematics & Evolution. 33, 421–444. https://doi.org.10.1163/187631202X00226.

Danforth, B. N., Sauquet, H., Packer, L., 1999. Phylogeny of the bee genus *Halictus* (Hymenoptera: Halictidae) based on parsimony and likelihood analyses of nuclear *EF-1 alpha* sequence data. Molecular Phylogenetics and Evolution. 13, 605–618. https://doi.org/10.1006/mpev.1999.0670.

Dennis, S.D., 1979. Ethology of *Holcocephala fusca* in Virginia (Diptera: Asilidae). Proceedings of the Entomological Society of Washington. 81(3), 366–378. ISSN: 0013-8797.

Dennis, S.D., 2012. Ethology of *Proctacanthus brevipennis* (Wiedemann, 1828) (Diptera: Asilidae) in Northeastern Florida, U.S.A. Journal of the Entomological Research Society. 14(3), 91–109. ISSN: 1302-0250.

Dennis, S.D., Lavigne, R.J., 1975. Comparative behavior of Wyoming robber flies II (Dipter a: Asilidae). University of Wyoming Agricultural Experimental Station Science Monograph. 30, 68 pp. OCLC: 10795887.

Dennis, S.D., Lavigne, R.J., Bullington, S.W., 1986. Ethology of *Efferia cressoni* with a review of the comparative ethology of the genus (Diptera: Asilidae). Proceedings of the Entomological Society of Washington. 88(1), 42–55. BHL: 16264743.

Dennis, S.D., Lavigne, R.J., Dennis, J.G., 2010. Hemiptera (Heteroptera/Homoptera) as prey of robber flies (Diptera: Asilidae) with unpublished records. Journal of the Entomological Research Society. 12(1), 27–47. ISSN: 1302-0250.

Dennis, S.D., Roehrkasse, G.P., and Lavigne, R.J., 1975. Prey Recognition by *Efferia frewingi* (Diptera: Asilidae). Annals of the Entomological Society of America. 68(3), 404–408. https://doi.org/10.1093/aesa/68.3.404.

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 coquillettii* (Insecta: Diptera: Asilidae) and 16 representative transcriptomes. PeerJ. 5, e2951. https://doi.org/10.7717/peerj.2951.

Dikow, T., 2009a. Phylogeny of the Asilidae inferred from morphological characters of imagines (Insecta: Diptera: Brachycera; Asiloidea). Bulletin of the American Museum of Natural History. 319, 1–175. http://hdl.handle.net/2246/5949.

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. https://www.doi.org/10.1016/j.ode.2009.02.004.

Douglass, J.K., Wehling, M.F., 2016. Rapid mapping of compound eye visual sampling parameters with FACETS, a highly automated wide-field goniometer. Journal of Comparative Physiology A. 202, 839–851. https://doi.org/10.1007/s00359-016-1119-7.

Drukewitz, S.H., Fuhrmann, N., Undheim, E.A.B., Blanke, A., Giribaldi, J., Mary, R., Laconde, G., Dutertre, S., and Reumont, B.M.v., 2018. A dipteran's novel sucker punch: evolution of arthropod atypical venom with a neurotoxic component in robber flies (Asilidae: Diptera). Toxins. 10(1), 29 https://doi.org/10.3390/toxins10010029.

Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research. 32(5), 1792–1797. https://www.doi.org/10.1093/nar/gkh340.

Fattig P.W., 1945. The Asilidae or robber flies of Georgia. Emory University Museum Bulletin. 3, 1–33. https://doi.org/10.1093/aesa/38.3.440.

Fidalgo, P.A., van den Broek, R., Pires, F., 2019. A new contribution to the knowledge of the distribution of the asilids of Spain and Portugal (Diptera: Asilidae), including a new species for the Iberian Peninsula. Boletin de la Sociedad Entomológica Aragonesa. 65, 45–52. https://www.researchgate.net/publication/339136656.

Fisher, E.M. 2012. Asilidae Classification. Available from http://buigguide.net/node/view/151. [accessed 29 September 2022].

Folmer, O., Black, M., Hoeh, W., Lutz, R., and Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology. 3(5), 294–299. PMID: 7881515.

Freudenstein, J.V., Pickett, K.M., Simmons, M. P., Wenzel, J. W., 2003. From basepairs to birdsongs: phylogenetic data in the age of genomics. Cladistics. 19, 333–347. https://doi.org/10.1111/j.1096-0031.2003.tb00377.x.

Göbbeler, K., Klussmann-Kolb, A., 2011. Molecular phylogeny of the Euthyneura (Mollusca, Gastropoda) with species focus on Opisthobrachia as a framework for reconstruction of evolution of diet. Thalassas. 27, 121–54. https://doi.org/10.1093/oxfordjournals.molbev.a025573.

Goulet, H., Huber, J. T., 1993. Hymenoptera of the world: an identification guide to families. Centre for Land and Biological Resources Research. Ottawa, Ontario. 680 pp. ISBN: 0-660-14933-8.

Giribet, G., Carranza, S., Baguñà, J., Riutort, M., Ribera, C., 1992. First molecular evidence for the existence of a Tardigrada + Arthropoda clade. Molecular Biology and Evolution. 13, 76–84. https://doi.org/10.1093/oxfordjournals.molbev.a025573.

Harmston, F.C., 1948. Dipterous predators of the mosquito in Utah and Wyoming. The Great Basin Naturalist. 9(1/2), 21–23. https://www.jstor.org/stable/41710863.

Hebert, P.D.N., deWaard, J.R., Zakharov, E.V., Prosser, S.W.J., Sones, J.E., McKeown, J.T.A., Mantle, B., Salle, J.L., 2013. A DNA 'Barcode Blitz': rapid digitization and sequencing of a natural history collection. PLOS ONE. 8(7), e68535–e68535. https://doi.org/10.1371/journal.pone.0068535.

Hobby, B.M., 1931. The British species of Asilidae (Diptera) and their prey. Transactions of the Entomological Society of South England. 6, 1–42.

Holston, K.C., Irwin, M. E., Wiegmann, B.M., 2007. Monophyly and phylogenetic relationships of *Thereva* and therevine genus-groups (Insecta: Diptera: Therevidae) based on *EF-1*α, 28S rDNA and mitochondrial 16S rDNA sequences. Invertebrate Systematics. 21, 279–296. https://doi.org/10.1071/ISO6005.

Holt, R.D., Polis, G.A., 1997. A theoretical framework for intraguild predation. American Naturalist. 149, 45–64. https://www.jstor.org/stable/2463547.

Hoang, D.T., Chernomor, O., Haeseler, A.v., Minh, B.Q., Vinh, L.S., 2018. UFBoot2: Improving the ultrafast bootstrap approximation. Molecular Biology and Evolution. 35, 518–522. https://doi.org/10.1093/molbev/msx281.

Höhna, S., Landis, M.J., Heath, T.A., Boussau, B., Lartillot, N., Moore, B.R., Huelsenbeck, J.P., Ronquist, F., 2016. RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. Systematic Biology. 65(4), 726–736. https://doi.org/10.1093/sysbio/syw021.

Ivanova, N.V., deWaard, J.R., Hebert, P.D.N., 2006. An inexpensive, automation-friendly protocol for recovering high-quality DNA. Molecular Ecology Notes. 6(4), 998–1002. https://doi.org/10.1111/j.1471-8286.2006.01428.x.

Jeffreys, H., 1961. The Theory of Probability. Oxford University Press. 470 pp. https://doi.org/10.1038/109132a0.

Joern, A., Rudd, N.T., 1982. Impact of predation by robber fly *Proctacanthus milbertii* (Diptera: Asilidae) on grasshopper (Orthoptera: Acrididae) populations. Oecologia. 55, 42–46. https://doi.org/10.1007/BF00386716.

Joseph, A.N.T., Parni, P., 1976. Some ecological observations on *Clephydroneura brevipennis* Oldroyd (Diptera: Asilidae). Newsletter of the Zoological Survey of India. 2(3), 119–120. Accession: 023623899.

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., Haeseler, A.v., Jermiin, L.S., 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods. 14, 587–589. https://doi.org/10.1038/nmeth.4285.

Larsson, A., 2014. AliView: a fast and lightweight alignment viewer and editor for large data sets. Bioinformatics. 30(22), 3276–3278. https://dx.doi.org/10.1093/bioinformatics/btu531.

Lavign, R.J., 1968. Notes on two species of *Asilus* (Diptera: Asilidae) associated with animal burrows, with a redescription of *Asilus gilvipes* Hine. Journal of the Kansas Entomological Society. 41, 334–339. https://www.jstor.org/stable/25083718.

Lavigne, R.J., 1969. A new species of Lasiopogon from Wyoming (Diptera: Asilidae). Journal of the Kansas Entomological Society. 42(4), 363–365. https://www.jstor.org/stable/25083811.

Lavigne, R.J., 1970a. Courtship and predatory behavior of *Cyrtopogon auratus* and *C. glarealis* (Diptera, Asilidae). Journal of the Kansas Entomological Society. 43(2), 163–171. https://jstor.org/stable/25082312.

Lavigne, R.J., 1970b. Courtship and predatory behavior of *Heteropogon maculinervis* (Diptera: Asilidae). Journal of the Kansas Entomological Society. 43(3), 270–273. https://www.jstor.org/stable/25082329.

Lavigne, R.J., 1971. *Backomyia seminoensis* sp. n. from Wyoming with ethological notes on *B. limpidipennis*. Journal of the Kansas Entomological Society. 44(3), 337–342. https://www.jstor.org/stable/25082428.

Lavigne, R.J., 1972. Ethology of *Ablautus rufotibialis* on Pawnee Grasslands IBP site. Journal of the Kansas Entomological Society. 45(3), 271–274. https://www.jstor.org/stable/25082499.

Lavigne, R.J., 1982. Ethology of *Neoitamus vittipes* (Diptera: Asilidae) in South Australia. Proceedings of the Entomological Society of Washington. 84(3), 617–627. https://biostor.org/reference/73671.

Lavigne, R.J., 2016. Predator-prey database. https://www.gellergrimm.de/catalog/lavigne.htm. [accessed 14 July 2022].

Lavigne, R.J., Bullington, S.W., 1984. Ethology of *Laphria fernaldi* (Back) (Diptera: Asilidae) in Southeast Wyoming. Proceedings of the Entomological Society of Washington. 86(2), 326–336. ISSN: 0013-8797.

Lavigne, R.J., Bullington, S.W., Stephens, G., 1993. Ethology of *Holopogon seniculus* (Diptera: Asilidae). Annals of the Entomological Society of America. 86(1), 91–95. https://doi.org/10.1093/aesa/86.1.91.

Lavigne, R.J., Bullington, S.W., 1999. Ethology of *Heteropogon paurosomus* Pritchard (Diptera: Asilidae) in Mexico. Journal of the Entomological Research Society. 1(3), 9–19. ISSN:1302-0250

Lavigne, R.J., Dennis, S.D., 1979. Notes of the Ethology of *Proctacanthus nearno* (Diptera: Asilidae) in Mexico. Proceedings of the Entomological Society of Washington. 81(3), 438–442. BHL: 25209289.

Lavigne, R.J., Holland, F.R., 1969. Comparative behavior of eleven species of Wyoming robber flies (Diptera: Asilidae). University of Wyoming Science monograph. 18, 3–61.

Linsley E. G., 1960. Ethology of some bee-and wasp-killing robber flies of southeastern Arizona and western New Mexico (Diptera: Asilidae). University of California Publications in Entomology. 16: 357–381. https://digitalcommons.usu.edu/bee_lab_all/11.

Londt, J.G.H., 1980. The genus *Synolcus* Loew (Diptera: Asilidae). Journal of the Entomological Society of South Africa. 43(1), 23–40. https://doi.org/10.5733/afin.053.0206.

Londt, J.G.H., 1981. Afrotropical Asilidae (Diptera) 5. The genus *Dasophrys* Loew, 1858 (= *Hobbyus* Bromley, 1952) (Asilinae: Asilini). Annals of the Natal Museum. 24, 635–699. https://hdl.handle.net/10520/AJA03040798_542.

Londt, J.G.H., 1991. Afrotropical Asilidae (Diptera) 21. Notes on the biology and immature stages of *Damalis femoralis* Ricardo, 1925 (Trigonomiminae). Annals of the Natal Museum. 32, 149–162. http://dx.doi.org/10.5281/zenodo.523759.

Londt, J.G.H., 1993. Afrotropical robber fly (Diptera: Asilidae) predation of honey bees, *Apis mellifera* Linnaeus (Hymenoptera: Apidae). African Entomology. 1(2), 167–173. https://hdl.handle.net/10520/AJA10213589_57.

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. https://hdl.handle.net/10520/AJA03040798_241.

Londt, J.G.H., 1999. Butterfly predation by robber flies (Diptera: Asilidae). Metamorphosis, Journal of the Lepidopterists' Society of Southern Africa. 10, 24–30.

Londt, J.G.H., 2005a. An annotated key to the genera of Afrotropical Apocleinae, with descriptions of six new genera. Tijdschrift Voor Entomologie. 148, 39–62. https://doi.org/10.1163/22119434-900000166.

Londt, J.G.H., 2005b. A review of Afrotropical *Afroholopogon* Londy,1994 with the description of a new genus and new species (Diptera: Asilidae: Stenopogoninae). African Invertebrates. 46, 203–252. https://hdl.handle.net/10520/EJC84542.

Londt, J.G.H., 2006. Predation by Afrotropical Asilidae (Diptera): an analysis of 2000 prey records. African Entomology. 14(2), 317–328. https://hdl.handle.net/0520/EJC32691.

Londt, J.G.H., 2007. A review of the genus *Hoplistomerus* Macquart, 1838 (Diptera: Asilidae: Laphriinae). African Invertebrates. 48(2), 167–198. https://hdl.handle.net/10520/EJC84604.

Londt, J.G.H., 2019. A revision of Afrotropical *Astochia* Becker, 1913 with descriptions of three new species (Diptera, Asilidae, Asilini). African Invertebrates. 60(2), 215–237. https://doi.org/10.3897/AfrInvertebr.60.38432.

Londt, J.G.H., Dikow, T., 2017. Chapter 48. Asilidae (assassin flies or ribber flies). *In:* Kirk-Spriggs, A. H., Sinclaire, B. J., (Eds.). Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. Suricata 5. Pretoria: South African National Biodiversity Institute. pp. 1097-1182. ISBN: 9781828224129.

Londt, J.G.H., Harris, M.S., 1984. Notes on the biology and immature stages of *Neolophonotus dichaetus* Hull in South Africa (Diptera: Asilidae). 50(2), 427–434. https://hdl.handle.net/10520/AJA00128789_4312.

McAlpine, J. F., Peterson, B. V., Shewell, G. E., Teskey, H. J., Vockeroth, J. R., Wood, D. M. (Eds). 1981. Manual of Nearctic Diptera Volume 1. Research Branch Agriculture Canada. 573 pp. ISBN: 0-660-10731-7.

Melin, D., 1923. Contributions to the knowledge of the biology, metamorphosis, and distribution of the Swedish asilids in relation to the whole family of asilids. Zoologiska Bidrag Från Uppsala. 8, 1–317.

Mengual, X., Ståhls, G., Rojo, S., 2008. First phylogeny of predatory flower flies (Diptera, Syrphidae, Syrphinae) using mitochondrial COI and nuclear 28S rRNA genes: conflict and congruence with the current tribal classification. Cladistics. 24(4), 543–562. https://doi.org/10.1111/j.1096-0031.2008.00200.x.

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., Haeseler, A.v., Lanfear, R., 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution. 37(5), 1530–1534. https://doi.org/10.1093/molbev/msaa015.

Moulton, J.K., 2003. Can the current molecular arsenal adequately track rapid divergence events within Simuliidae (Diptera)? Molecular Phylogenetics and Evolution. 27, 45–57. https://doi.org/10.1016/s1055-7903(02)00397-4.

Moulton, J.K., Wiegmann, B. M., 2004. Evolution and phylogenetic utility of *CAD* (rudimentary) among Mesozoic-aged Eremoneuran Diptera (Insecta). Molecular Phylogenetics and Evolution. 31, 363–378. https://doi.org/10.1016/S1055-7903(03)00284-7.

Moulton, J. K., Wiegmann, B.M., 2007. The phylogenetic relationships of flies in the superfamily Empidoidea (Insecta: Diptera). Molecular Phylogenetics and Evolution. 43, 701–713. https://doi.org/10.1016/j.ympev.2007.02.029.

Naskar, A., Maity, A., Homechaudhuri, S., Banerjee, D., 2019. New distributional records of robber flies (Insecta: Diptera: Asilidae) from the Darjeeling Himalaya of West Bengal. Munis Entomology & Zoology Journal. 14(2), 412–426. https://www.researchgate.net/publication/334223074.

Neuwirth, E., 2022. RColorBrewer: ColorBrewer Palettes. v. 1.1-3. https://cran.r-project.org/web/packages/RColorBrewer/index.html

Newkirk, M.R., 1963. The feeding and mating of *Leptogaster annulatus* (Diptera: Asilidae). Annals of the Entomological Society of America. 56(2), 234–236. https://doi.org/10.1093/aesa/56.2.234.

Oldroyd, H., 1964. Chapter 10: Robber Flies *In.* The Natural History of Flies. Norton, New York. 324 pp.

O'Neill, K.M., Kemp, W.P., 1991. Foraging of *Stenopogon inquinatus* (Loew) (Diptera: Asilidae) on Montana rangeland sites. Pan-Pacific Entomologist. 67, 177–180.

O'Neill, K.M. 1992a. Body size asymmetries in predatory interactions among robber flies (Diptera: Asilidae). Annals of the Entomological Society of America. 85(1), 34–38. https://doi.org/10.1093/aesa/85.1.34.

O'Neill, K.M. 1992b. Temporal and spatial dynamics of predation in a robber fly (*Efferia staminae*) population (Diptera: Asilidae). Canadian Journal of Zoology. 70(8), 1546–1552. https://doi.org/10.1139/z92-213.

Papavero, N., 1973. Studies of Asilidae (Diptera) systematics and evolution. I. A preliminary classification in subfamilies. Arquivos de Zoologia. 23(3), 217–274. https://doi.org/10.11606/issn.2176-7793.v23i3p217-274.

Papavero, N., Artigas, J. N., Lamas, C. J. E., 2009. Manual of Neotropical Diptera. Asilidae. Neotropical Diptera. 18, 1–320. ISSN: 1982-7121.

Pape, T., Blagoderov, V., Mostovski, M. B., 2011. Order Diptera Linnaeus, 1758. *In*: Z.-Q. (Ed.) Animal Biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa. 3148(1), 224. https://doi,org/10.11646/zootaxa.3148.1.42.

Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics. 35, 526–528. https://doi.org/10.1093/bioinformatics/bty633.

Pollock, D.A. (2021) Robber flies (Diptera: Asilidae) as predators of harvester ant workers (Hymenoptera: Formicidae: Pogonomyrmex) in Eastern New Mexico and West Texas. The Southwestern Naturalist. 65(1), 19–27. https://doi.org/10.1894/0038-4909-65.1.3.

Pollock, D.A., Davidson, R.L., 2020. New records of ground and tiger beetles (Coleoptera: Carabidae) as prey for Asilidae (Diptera) in the high plains of New Mexico and Texas. The Coleopterists Bulletin. 74(1), 15–23. https://doi.org/10.1649/0010-065X-74.1.15.

Pollock, D.A., Lavigne, R.J., 2019. Records of Coleoptera as Prey of Robber Flies (Diptera: Asilidae) in Eastern New Mexico and West Texas. BioOne. 121(1), 81–102. https://doi.org/10.4289/0013-8797.121.1.81.

Pollock, D.A., Reichert, L.A., 2019. Review of the Nearctic genus *Wilcoxia* James (Diptera: Asilidae: Stenopogoninae), with descriptions of three new species. Zootaxa. 4695(5), 401–437. https://doi.org/10.11646/zootaxa.4695.5.1.

Prosser, S.W.J., deWaard, J.R., Miller, S.E., Hebert, P.D.N., 2015. DNA barcodes from century-old type specimens using next-generation sequencing. Molecular Ecology Resources. 16(2), 287–487. https://doi.org/10.1111/1755-0998.12474.

Rambaut, A., 2018. Molecular evolution, phylogenetics and epidemiology: FigTree v1.4.4. http://tree.bio.ed.ac.uk/software/figtree/ (accessed Oct. 2022).

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology. 67(5), 901–904. https://doi.org/10.1093/sysbio/syy032.

Resh, V.H., Cardé, R.T. (Eds), 2009. Encyclopedia of Insects. Academic Press. 1168 pp. https://doi.org/10.1016/B978-0-12-374144-8.X0001-X.

Revell, L.J., 2012. phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution. 3, 217–223.

Ricardo, G., 1920. A Persian asilid attacking house-flies. The Entomologist's Monthly Magazine. 56, 278–280.

Robins, J., 2008. "Bark beetles kill millions of acres of trees in West. The New York Times. [accessed: October 1, 2022]. https://www.nytimes.com/2008/11/18/science/18trees.html.

Sakhvon, V.V., 2020. Review of the genus *Saropogon* Loew, 1847 (Diptera: Asilidae) from Russia, Transcaucasia and Central Asia, with description of three new species. Zootaxa. 4860(4), 577–591. https://doi.org/10.11.646/zootaxa.4860.4.7.

Scarbrough, A.G., 1978. Ethology of *Cerotainia albipilosa* Curran (Diptera: Asilidae) in Maryland: predatory behavior. Proceedings Entomological Society of Washington. 80, 113–127.

Scarbrough, A.G., 1981. Ethology of *Eudioctria tibialis* Banks (Diptera: Asilidae) in Maryland: prey, predator behavior, and enemies. Proceedings Entomological Society of Washington. 83(2), 258–268. BHL: 16364599.

Shelly T.E., 1984. Comparative foraging behavior of Neotropical robber flies (Diptera: Asilidae). Oecologia. 62, 188–195. https://doi.org/10.1007/BF00379012.

Shelly T.E., Pearson, D.L., 1980. Predatory behavior of *Proctacanthella leucopogon* (Diptera: Asildiae): Prey recognition and prey records. Environmental Entomology. 9(1), 7–9. https://doi.org/10.1093/ee/9.1.7.

Shin, S., Bayless, K.M., Winterton, S.L., Dikow, T., Lessard, B.D., Yeates, D.K., Wiegmann, B.M., Trautwein, M.D., 2018. Taxon sampling to address an ancient rapid radiation: a supermatrix phylogeny of early brachyceran flies (Diptera). Systematic Entomology. 43, 277–289. https://doi.org/10.1111/syen.12275.

Simon, C., Frati, F., Beckenback, A., Crespi, B., Liu, H., Flook, P. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and computation of conversed polymerase chain reaction primers. Entomological Society of America. 8, 651–701 https://doi.org/10.1093/aesa/87.6.651.

Sommerfeld, A., Rammer, W., Heurich, M., Hilmers, T., Mueller, J., Seidl, R., 2020. Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe? Journal of Ecology. 109(2), 737–749. https://doi.org/10.1111/1365-2745.13502.

Stange, L. A., 1992. The bumble bees of Florida (Hymenoptera: Apidae). Florida Department of Agriculture & Consumer Services, Division of Plant Industry, Gainesville. Entomology Circular. 353. 2 pp.

Suludere, Z., Lavigne, R., Bayrakdar, F. 2018. First Record of Accidental Contamination of Asilidae (Insecta: Diptera) with Brochosomes. BioOne. 127(5), 413–417. https://doi.org/10.3157/021.127.0504.

Tamsyn, W., Hendrix, J., Boeraeve, M., Mortelmans, J., Opdekamp, W., 2020. The discovery of three spectacular robber flies new to Belgium (Diptera: Asilidae). Bulletin de la Société royale belge d'Entomologie. 117–123. https://www.researchgate.net/publication/338792211.

Trautwein, M.D., Wiegmann, B.M., Yeates, D.K., 2010. A multigene phylogeny of the fly superfamily Asiloidea (Insecta): Taxon sampling and additional genes reveal the sister-group to all higher flies (Cyclorrhapha). Molecular Phylogenetics and Evolution. 56(3), 918–930. https://doi.org/10.1016/j.ympev.2010.04.017.

Vaughan, T.G., 2017. IcyTree: Rapid browser-based visualization for phylogenetic trees and networks. Bioinformatics. https://doi.org/10.1093/bioinformatics/btx155.

Vega, F.E., Hofstetter, R.W. (Eds), 2015. Bark Beetles. Academic Press. 640 pp. https://doi.org/10.1016/C2013-0-04752-4.

Werner, D., Pont, A.C. 2003. Dipteran predators of Simuliid blackflies: a worldwide review. Medical and Veterinary Entomology. 17(2), 115-132. https://doi.org/10.1046/j.1365-2915.2003.00431.x.

Whiting, M. F., 2002. Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and Siphonaptera. Zoologica Scripta. 31, 93–104. https://doi.org/10.1046/j.0300-3256.2001.00095.x.

Wiegmann, B.M., Trautwein, M.D., Winkler, I.S., Barr, N.B., Kim, J., Lambkin, C., Bertone, M.A., Cassel, B.K., Bayles, K.M., Heimberg, A.M., Wheeler, B.M., Peterson, K.J., Pape, T., Sinclair, B.J., Skevington, J.H., Blagoderov, V., Caravas, J., Kutty, S.N., Schmidt-Ott, U., Kampmeier, G.E., Thompson, F.C., Grimaldi, D.A., Beckenbach, A.T., Courtney, G.W., Friedrich, M., Meier, R., Yeates, D.K., 2011. Episodic radiations in the fly tree of life. PNAS. 1-6. www.pnas.org/cgi/doi/10.1073/pnas.1012675108.

Wiegmann, B.M., Trautwein, M.D., Kim, J.W., Cassel, B.K., Bertone, M.A., Winterton, S.L., Yeates, D.K., 2009. Single-copy nuclear genes resolve the phylogeny of the holometabolous insects. BMC Biology. 7, 34. https://doi.org/10.1186/1741-7007-7-34.

Wiegmann, B.M., Tsaur, S.-C., Webb, D. W., Yeates, D.K., Cassel, B.K., 2000. Monophyly and relationships of the Tabanomorpha (Diptera: Brachycera) based on 28S ribosomal gene sequences. Annals of the Entomological Society of America. 93, 1031–1038. https://doi.org/10.1603/0013-8746(2000)093[1031:MAROTT]2.0.CO;2.

Winterton, S.L., Ware, J.L., 2015. Phylogeny, divergence times and biogeography of window flies (Scenopinidae) and the therevoid clade (Diptera: Asiloidea). Systematic Entomology. 40, 491–519. https://doi.org/10.1111/syen.12117.

Winterton, S.L., Hardy, N.B., Gaimari, S.D., Hauser, M., Hill, H.N., Holston, K.C., Irwin, M.E., Lambkin, C.L., Metz, M.A., Turco, F., Webb, D., Yang, Longlong., Yeates, D.K., Wiegmann, B.M., 2015. The phylogeny of stiletto flies (Diptera: Therevidae). Systematic Entomology. 41(1), 144-161. https://doi.org/10.1111/syen.12147.

Winterton, S.L., Wiegmann, B.M., Schlinger, E.I., 2007. Phylogeny and Bayesian divergence time estimations of small-headed flies (Diptera: Acroceridae) using multiple molecular markers. Molecular Phylogenetics and Evolution. 43, 808–832. https://doi.org/10.1016/j.ympev.2006.08.015.

Wood, G. C., 1981. Asilidae. *In.* McAlpine, J. F., Peterson, B. V., Shewell, G. E., Teskey, H. J., Vockeroth, J. R., Wood, D. M. (Eds). Manual of Nearctic Diptera Volume 1. Research Branch Agriculture Canada. 549–573. ISBN: 0-660-10731-7.

Yang, L., Wiegmann, B. M., Yeates, D.K., Irwin, M.E., 2000. Higher-level phylogeny of the Therevidae (Diptera: Insecta) based on 28S ribosomal and Elongation Factor-1alpha gene sequences. Molecular Phylogenetics and Evolution. 15, 440–451. https://www.doi.org/10.1006/mpev.1999.0771.

Zhang, B., Liu, Y.H., Wu, W.X., Wang, Z.L., 2010. Molecular phylogeny of Bactrocera species (Diptera: Tephritidae: Dacini) inferred from mitochondrial sequences of 16S rDNA and COI sequences. The Florida Entomologist. 93(3), 369–377.