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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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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) has inspired the reexamination of the Nearctic species of the globally diverse and taxonomically confounding genus, *Saropogon* Loew, 1847.

Saropogon (Fig. 1) 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; GBIF Secretariat 2021). It is, however, found mainly in temperate and tropical climates. In the Nearctic, *Saropogon* occurs primarily in the southwestern states 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. 2). This manuscript focuses on the species found in Arizona but provides locality information of all specimens examined in the Suppl. material 1.

Figure 1. *Saropogon pyrodes* sp. nov. male in nature at ~0.7 km ENE of Amado in southern Arizona on Sep. 5, 2017 (flicker: [https://www.flickr.com/photos/7432824@N07/45297662671/in/album-72157687317436870/]). Photograph by Jeff Gruber.

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, (VanDyke 2021);
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;
LACMENT	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.; and
USNM	Smithsonian National Museum of Natural History, Washington, D.C., U.S.A.

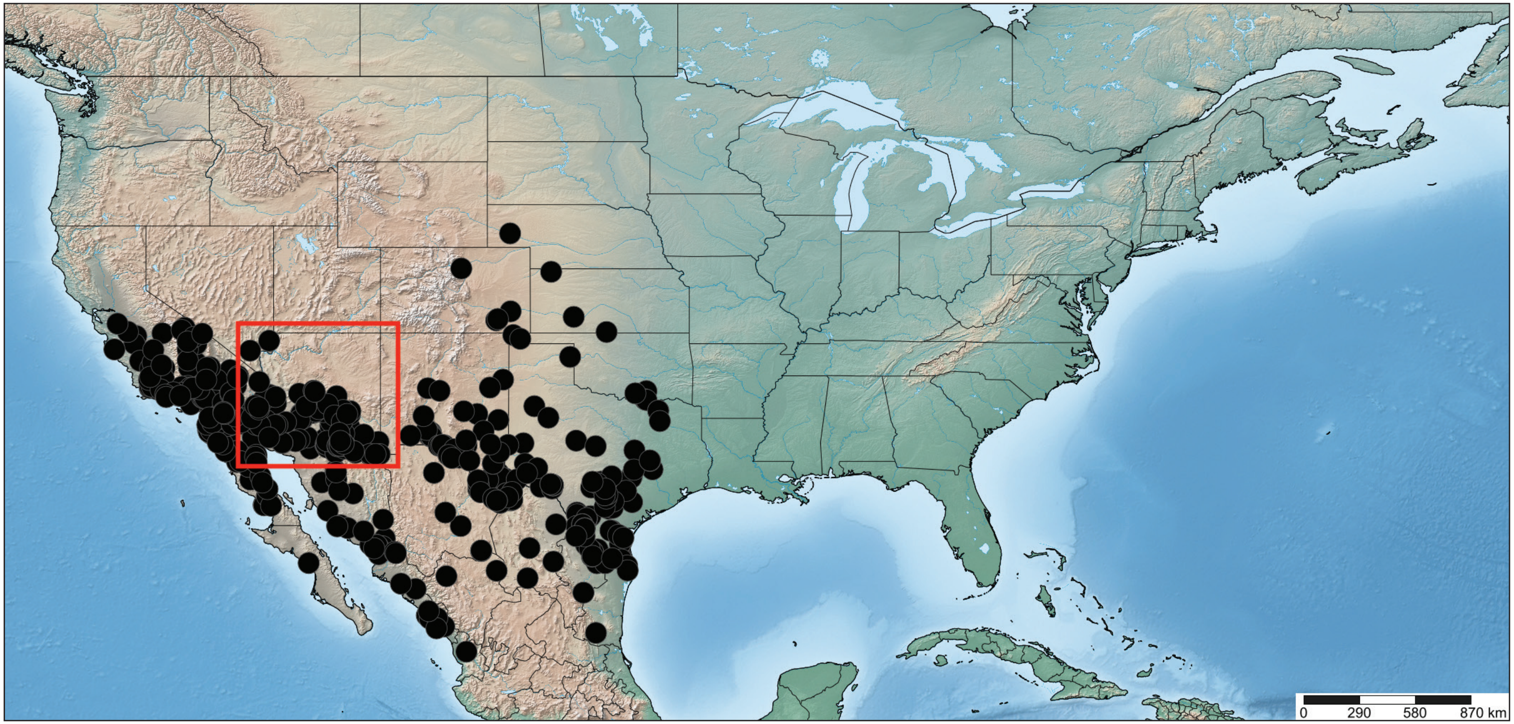

Figure 2. Distribution of Nearctic *Saropogon* (Diptera: Asilidae) examined. Red box indicates focused distribution for Fig. 26. Map created with SimpleMappr on 25 January 2022, and available at: https://www.simplemappr.net/map/17061.

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 (Suppl. material 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. 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 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. The male terminalia were removed, placed in 10% potassium hydroxide (KOH) at 55 °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. 8A–G of the female and male terminalia were taken on a Zeiss SteREO Discovery V12 stereo microscope with a PlanApo S 1.0× lens at 40–95× 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 Suppl. material 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 & Papavero, 1962: 57; junior synonym. Type species: *Oberon velutinus* Carrera & Papavero, 1962: 58.

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

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

Diagnosis. *Saropogon* has a stout and often twisted spur at the antero-ventral apex of the fore tibiae (Fig. 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. 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. 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. 3D) and its face is slightly concave (Fig. 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

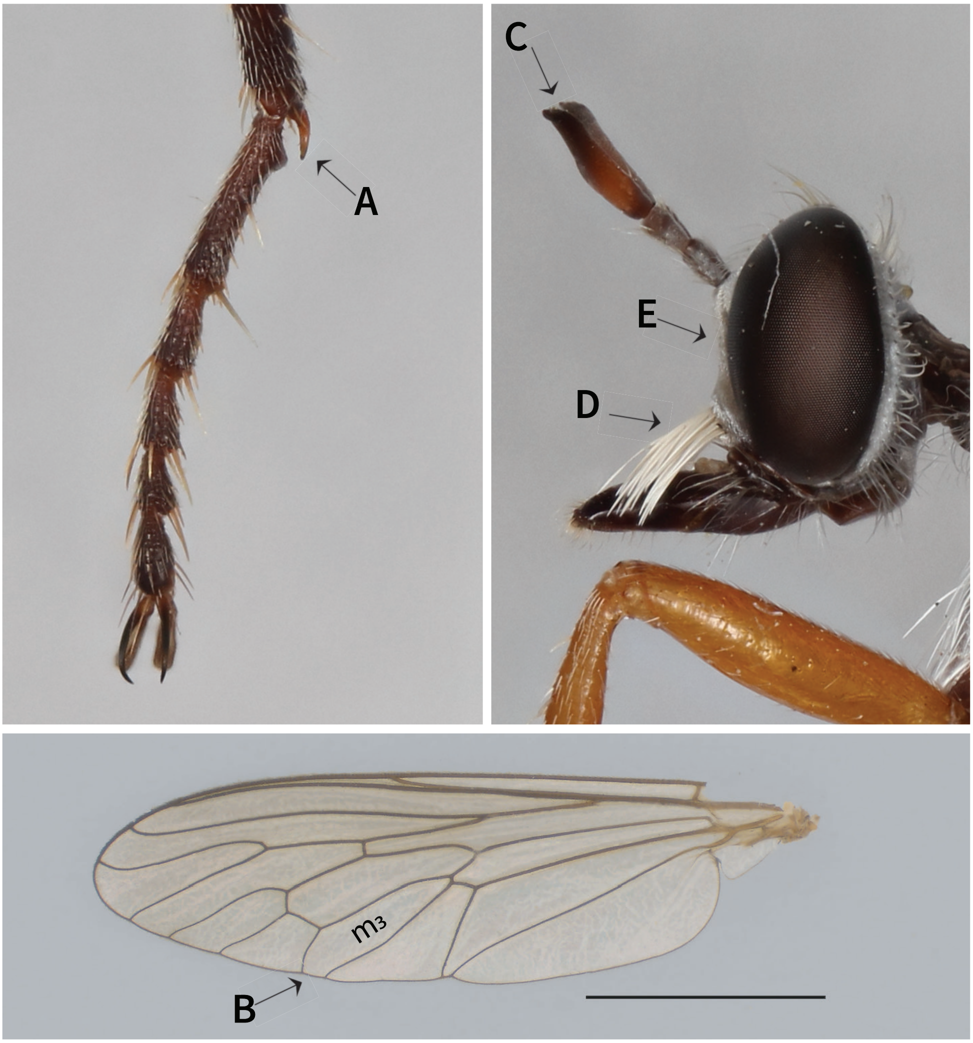

Figure 3. *Saropogon nitidus* illustrating distinguishing characters of the genus **A** fore tibia with a distinct spur. **B** open m_3 cell on wing **C** antennal style **D** mystax of *S. nitidus* restricted to oral margin **E** face slightly concave. Scale bar: 2 mm.

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.

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. 4A, B), *S. combustus* (Fig. 4C, D), *S. purus* (Fig. 4E, F), and *S. senex* (Fig. 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. 5A, B), *S. bryanti* (Fig. 5C, D), *S. combustus* (Fig. 5E, F), *S. dispar* (Fig. 5G, H), *S. hypomelas* (Fig. 5I, J), *S. luteus* (Fig. 5K, L), *S. purus* (Fig. 5M, N), and *S. senex* (Fig. 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.

Biology. Dasypogoninae and *Saropogon* apparently tend to prefer Hymenoptera prey (Lavigne 2016; Pollock 2021; Table 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 (1934) recorded *Diogmites symmachus* Loew, 1872 feeding on *Saropogon dispar* in Texas.

Table 1. Adult *Saropogon* 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. 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)

Predator	Prey order	Prey family	Original source or collection	Country (state)
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	Apidae	BMEC and Thorp 1973	USA (OK)
S. dispar	Hymenoptera	Apidae	USNM, BYU	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	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	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, USNM	USA (TX)
S. mohawki	Coleoptera	Buprestidae	Bellamy 2002, 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)

Predator	Prey order	Prey family	Original source or collection	Country (state)
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. 25D) at the tip of their ovipositor (Londt and Dikow 2017). 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. 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. 6 .... ***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. 29 .... ***S. senex* Osten Sacken**
4 Wings hyaline, without microtrichia or sparse microtrichia apically with no or sometimes slight color staining.. **5**
– Wings infuscate, males with brown or black wings, females paler 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. 16... ***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. 19B, 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 22, 23–27 .... ***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. 19 .... ***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 pale gold pubescence; male legs black with distally red femora, female with reddish legs; wings completely hyaline (USA: California, Arizona; Mexico) Fig. 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. 7 .... ***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. 11 .... ***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. 18... ***S. mohawki* Wilcox**

– Abdomen yellow; two apical scutellar macrosetae; both sexes have entirely reddish legs (USA: New Mexico, Texas; Mexico: Chihuahua, Coahuila) Fig. 14 .... ***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 pale 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. 17 .... ***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. 21....... ***S. purus* Curran**

14 Femora entirely red (e.g., Fig. 13B) **15**

– Femora entirely black or at least with a dorsal black stripe (e.g., Fig. 8B, 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. 13... .... ***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. 20 .... ***S. pritchardi*** **Bromley**

– Wings pale orange stained especially around veins, microtrichia apically; antennae orange (USA: Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas) Fig. 4, 10 .... ***S. combustus*** **Loew - in part (females)**

17 Coxae and katatergite with black setae (USA: Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas) Figs 4, 10........ ***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. 8 .... ***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. 12..***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 sublateral spots (USA: Arizona, New Mexico, Texas; Mexico: Coahuila, Nuevo Leon) Fig. 15 ....***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. 9.. ***S. bryanti*** **Wilcox**

Saropogon abbreviatus **Johnson, 1903**

Figs 4A, B, 5A, B, 6, 26, 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.

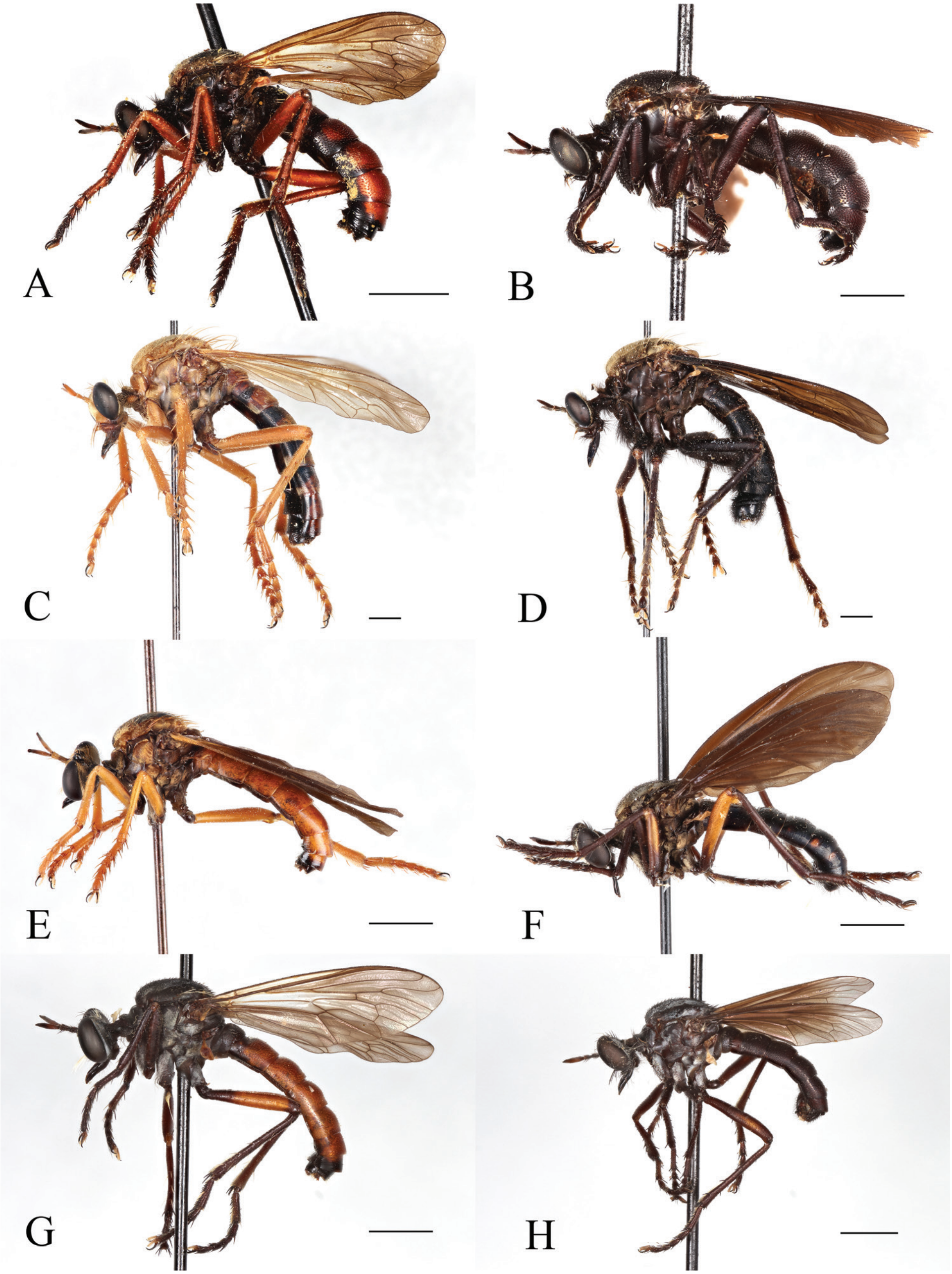

Figure 4. Sexual color dimorphism **A** *Saropogon abbreviatus* female **B** *S. abbreviatus* male **C** *S. combustus* female **D** *S. combustus* male **E** *S. purus* female **F** *S. purus* male **G** *S. senex* female **H** *S. senex* male. Scale bars: 2 mm.

Most similar to *Saropogon 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.

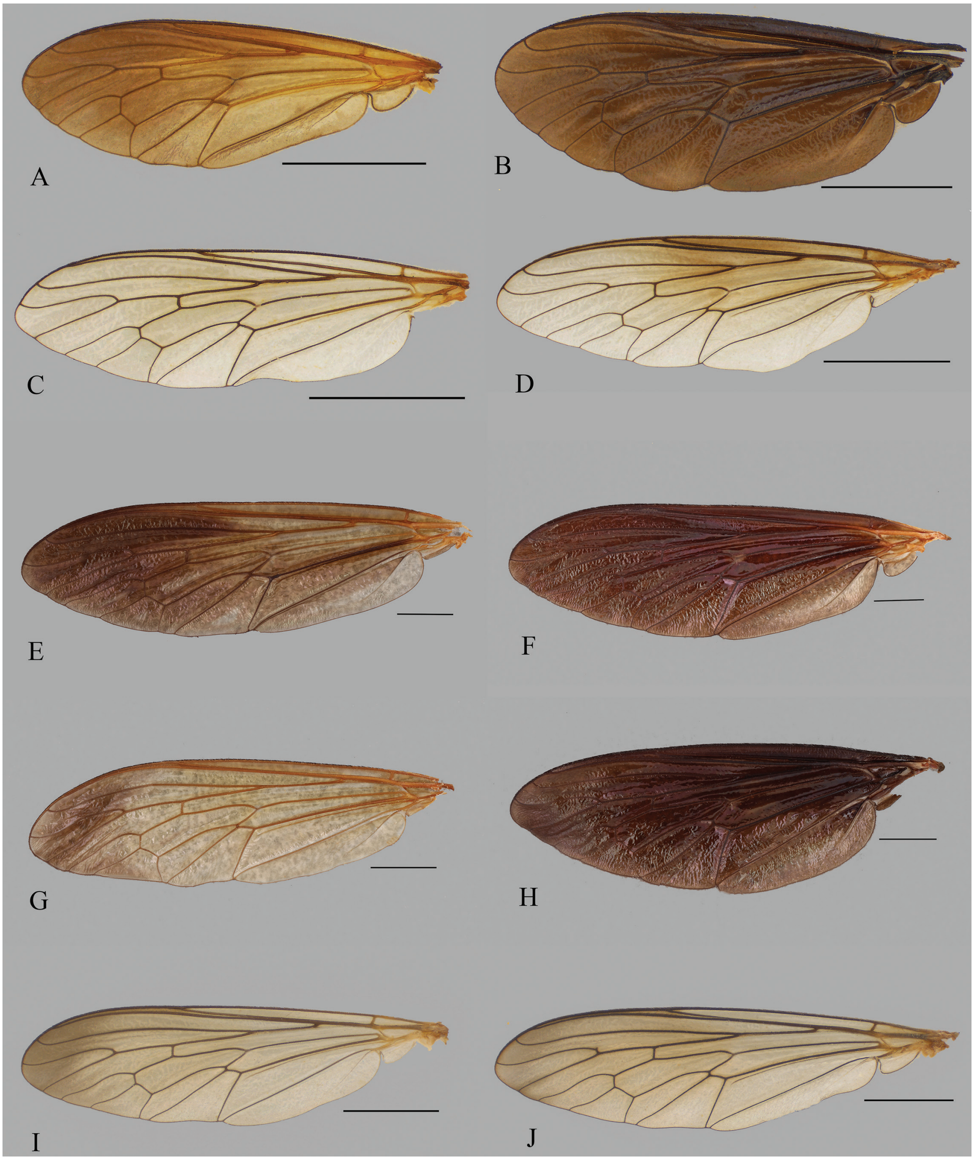

Figure 5. Representative *Saropogon* wings of **A** *S. abbreviatus* female **B** *S. abbreviatus* male **C** *S. bryanti* female **D** *S. bryanti* male **E** *S. combustus* female **F** *S. combustus* male **G** *S. dispar* female **H** *S. dispar* male **I** *S. hypomelas* female **J** *S. hypomelas* male **K** *S. luteus* female **L** *S. luteus* male **M** *S. purus* female **N** *S. purus* male, and **O** *S. senex* female **P** *S. senex* male. 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. Suppl. material 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 pro-

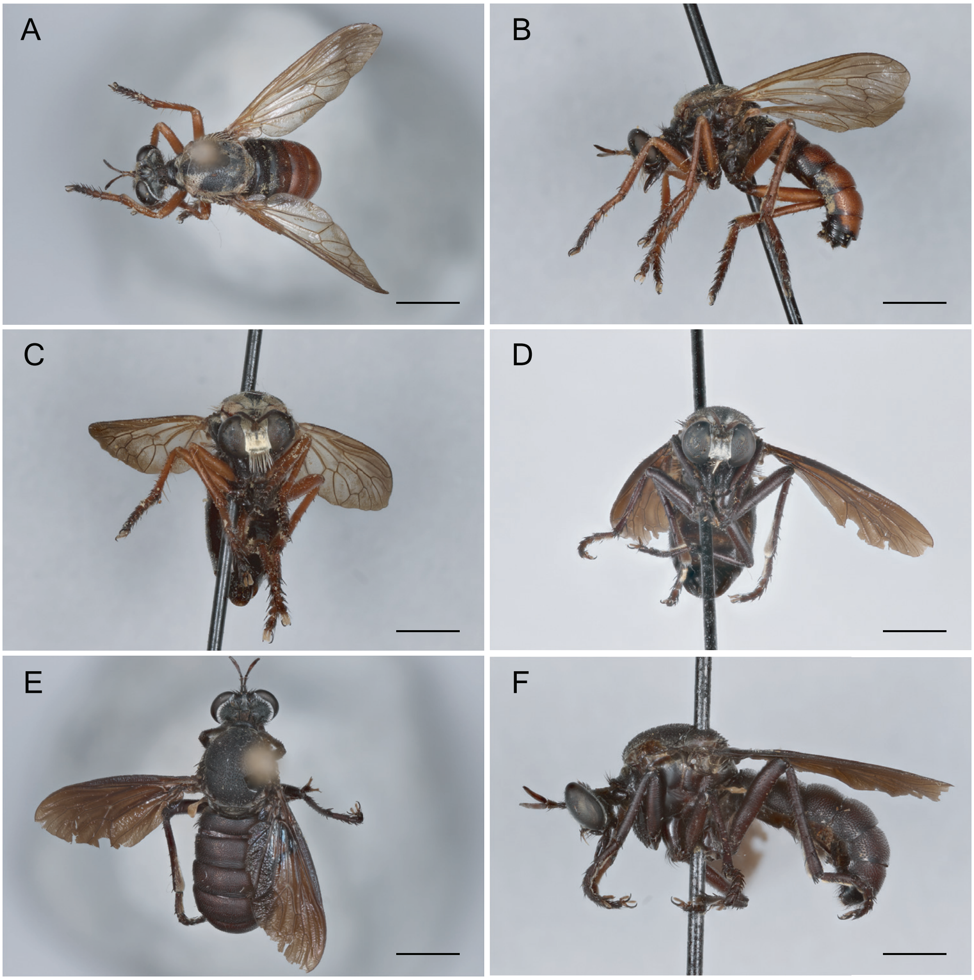

Figure 6. *Saropogon abbreviatus* Johnson, 1903 Female (USNMENT01830071): **A** dorsal view **B** lateral view **C** anterior view; Male (USNMENT01830070): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

vides 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 7, 26, 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.

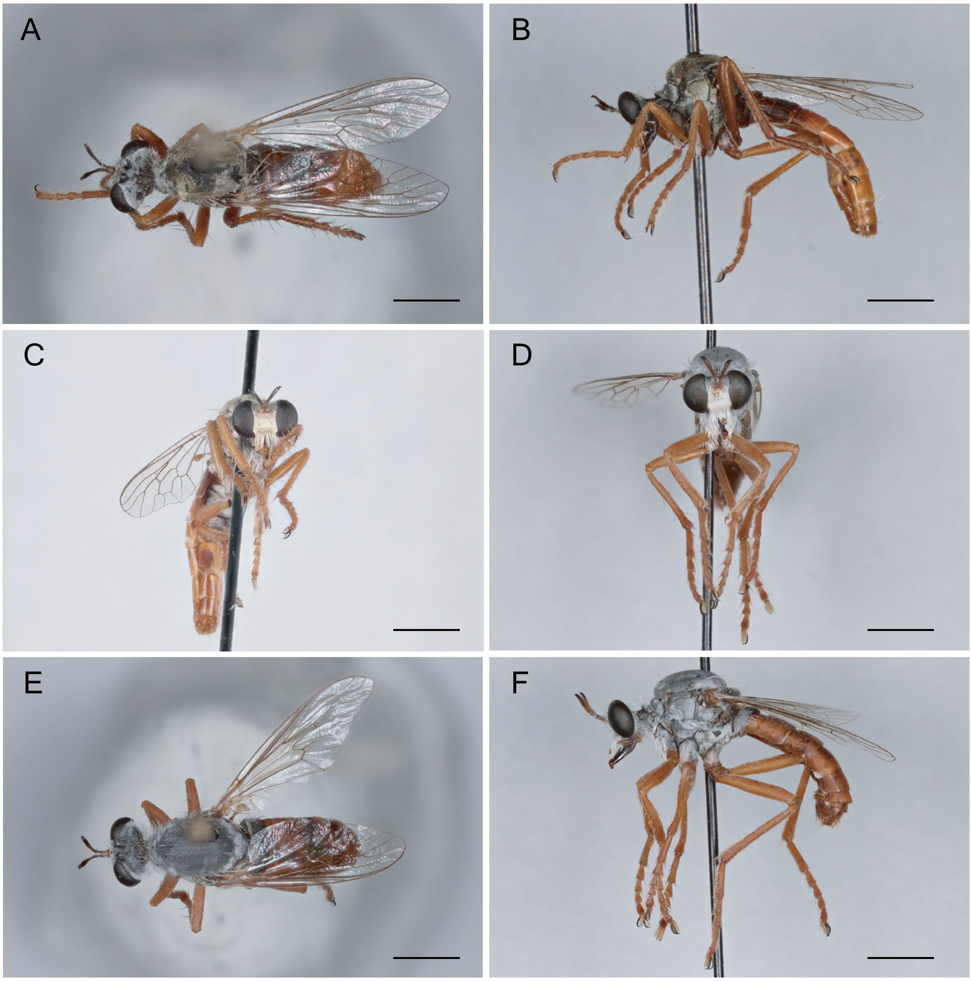

Figure 7. *Saropogon albifrons* Back, 1904 Female (USNMENT01819164): **A** dorsal view **B** lateral view **C** anterior view; Male (USNMENT01830072): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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. Suppl. material 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/.

Saropogon birdi Curran, 1931

Figs 8, 26, 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 *Saropogon 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.

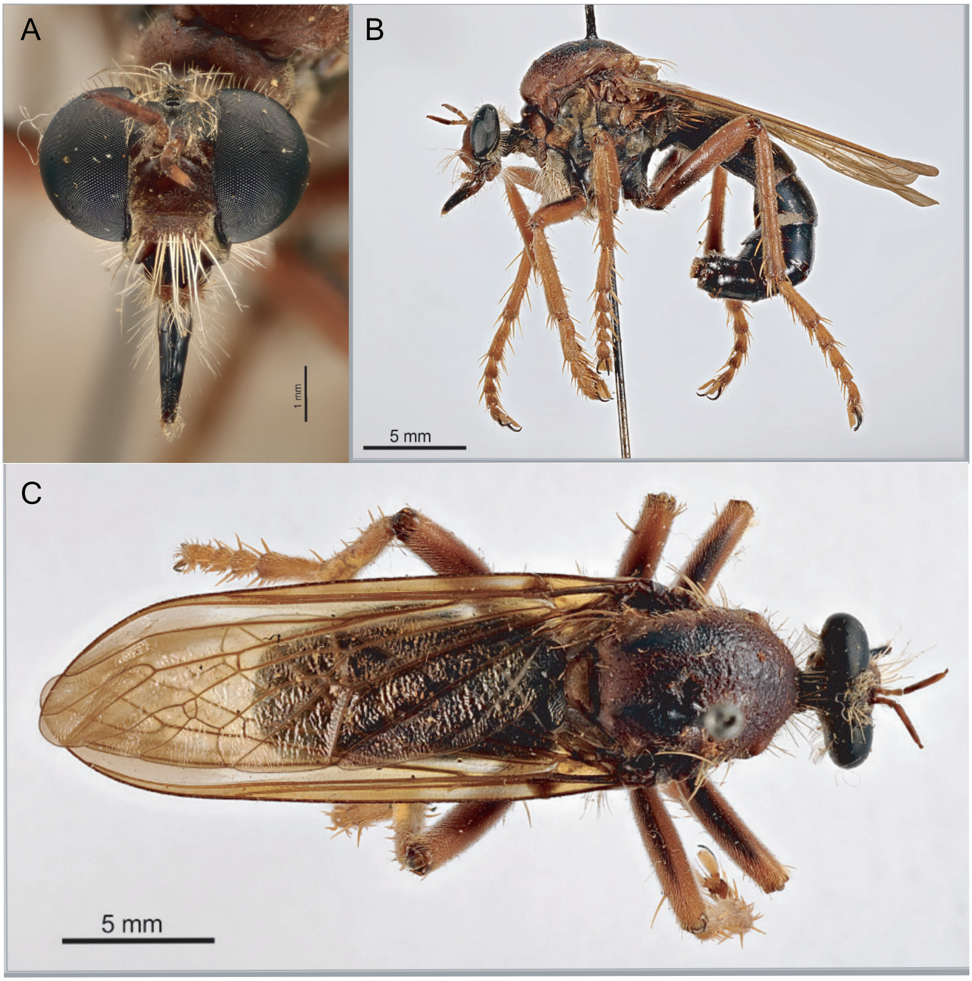

Figure 8. *Saropogon birdi* Curran, 1931 Female holotype **A** anterior view **B** lateral view **C** dorsal view. Photograph provided by American Museum of Natural History.

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.

Saropogon bryanti Wilcox, 1966

Figs 5C, D, 9, 26, 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.

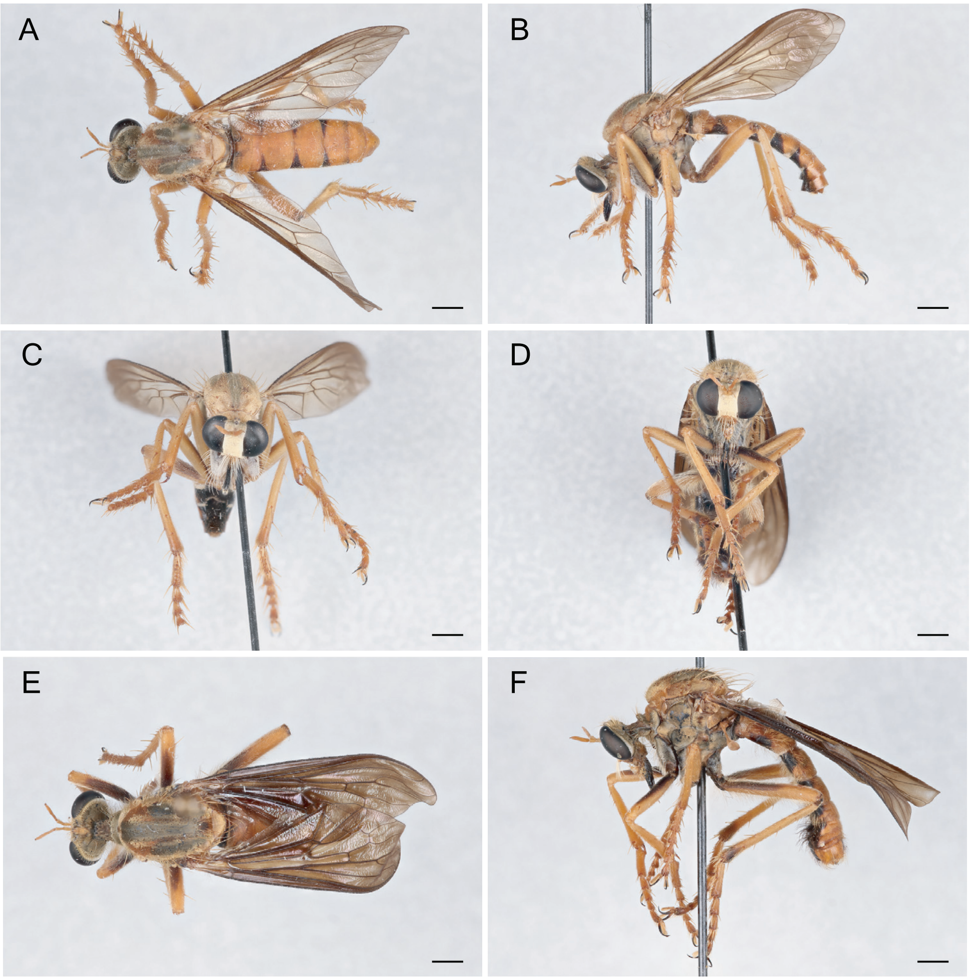

Figure 9. *Saropogon bryanti* Wilcox, 1966 Female (USNMENT01830074): **A** dorsal view **B** lateral view **C** anterior view; Male (USNMENT01830073): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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. Suppl. material 1.

Comments. One specimen we examined was from Iowa (CASENT8427218, Suppl. material 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, 10, 26, 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.

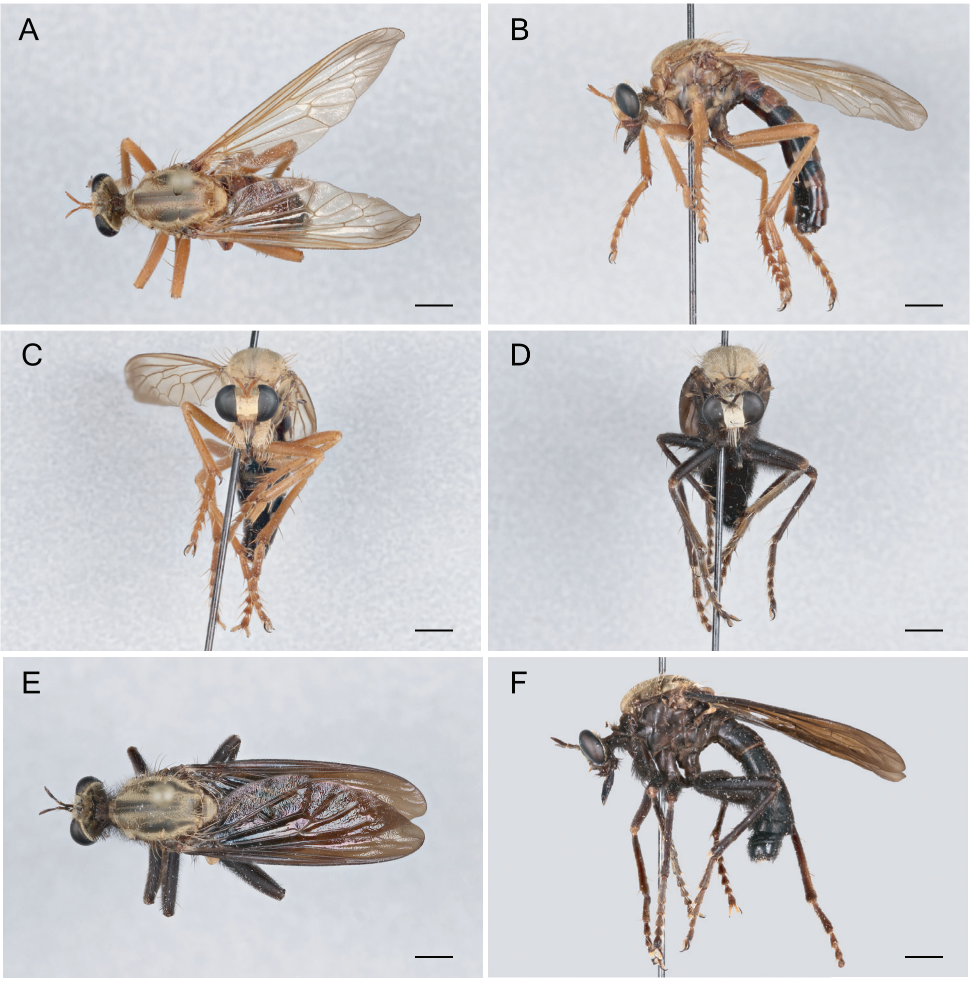

Figure 10. *Saropogon combustus* Loew, 1874 Female (USNMENT01819131): **A** dorsal view **B** lateral view **C** anterior view; Male (USNMENT01819138): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

The male is easily distinguished from *Saropogon 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 pale brown and darker apically.

Distribution. USA: Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas, SimpleMappr: https://www.simplemappr.net/map/16981.

Type material examined. United States of America • 1 ♂, holotype; Loew; photographed pinned specimen; MCZ; Type 12819 • 1 ♀; Loew; MCZ; Type 12818.

Other material examined. Suppl. material 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 11, 26, 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 Flor-

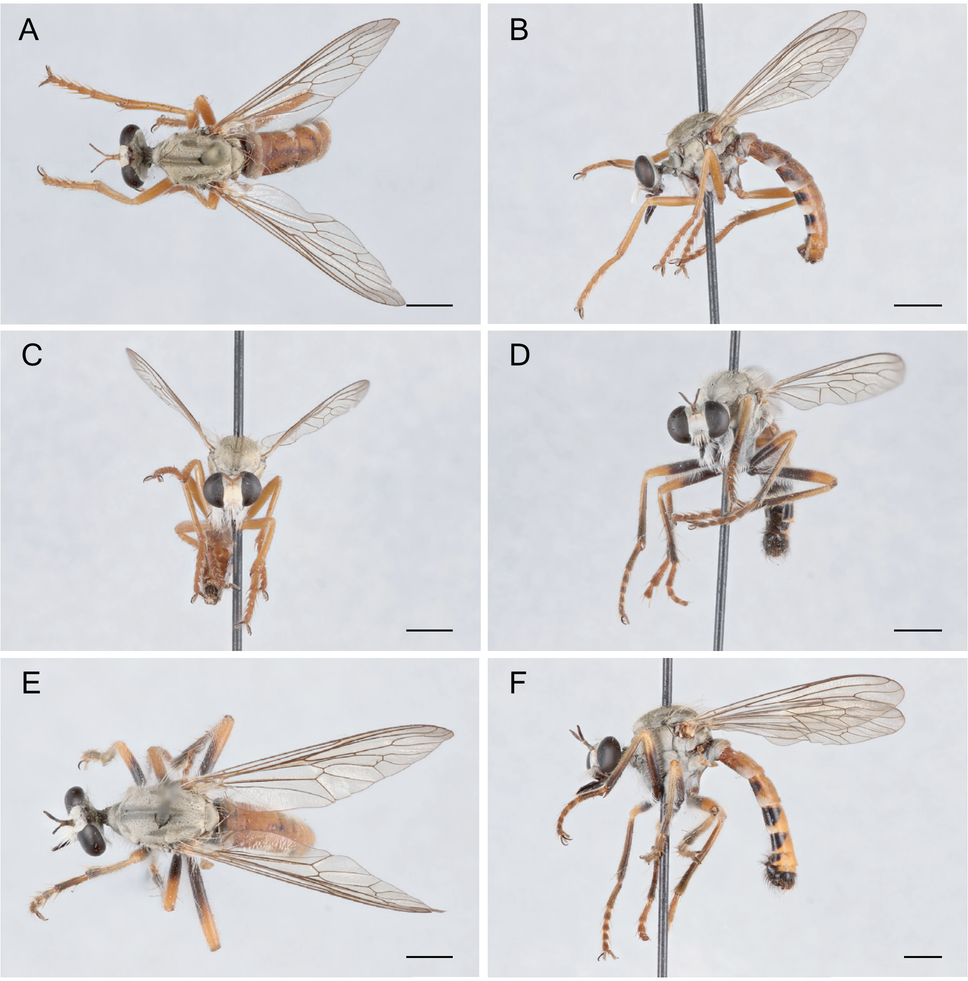

Figure 11. *Saropogon coquillettii* Back 1909 Female (USNMENT01830076): **A** dorsal view **B** lateral view **C** anterior view; Male (USNMENT01830075): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

ence; 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. Suppl. material 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.

Saropogon dispar Coquillett, 1902

Figs 5G, H, 12, 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.

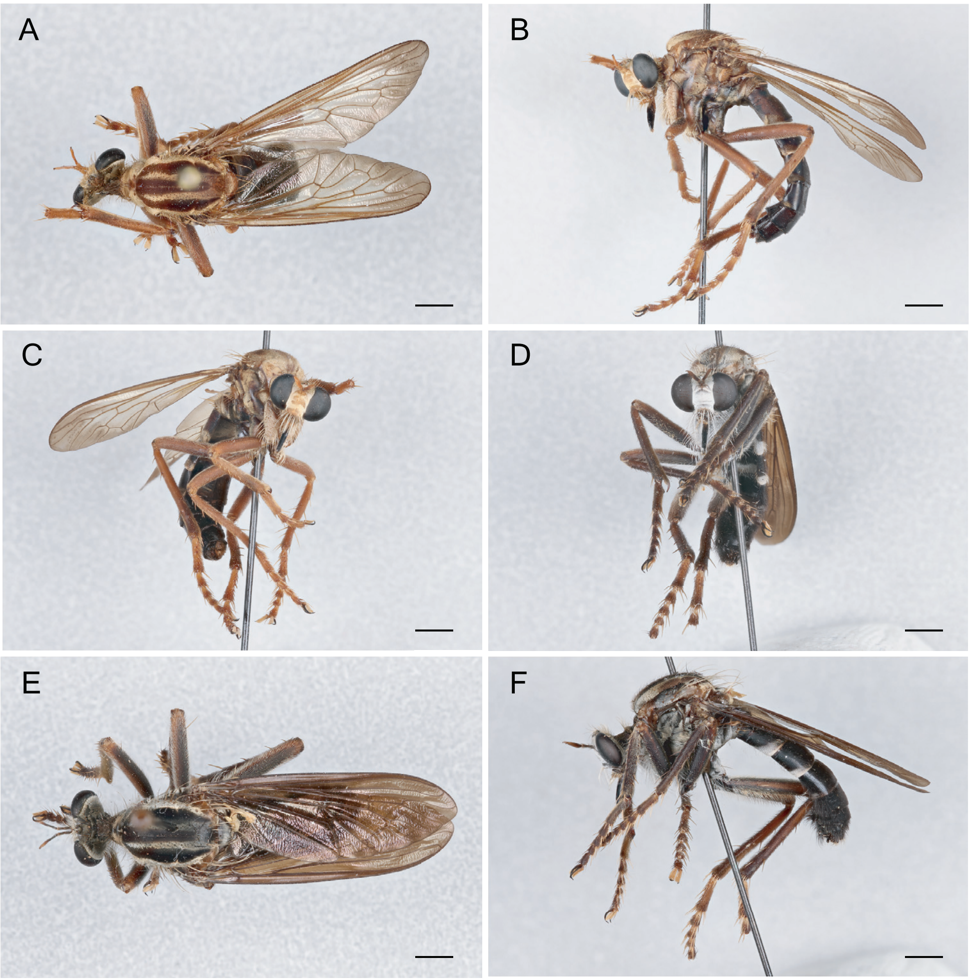

Figure 12. *Saropogon dispar* Coquillett, 1902 Female (UCBMEP0280509): **A** dorsal view **B** lateral view **C** anterior view; Male (UCBMEP0280508): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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. Suppl. material 1.

Comments. Bromley (1934) states "*Saropogon dispar* is by far the most noxious species in bee-yards in the San Antonio region." See Table 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 13, 26, 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. Suppl. material 1.

Saropogon hyalinus Coquillett, 1904

Figs 14, 26, 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).

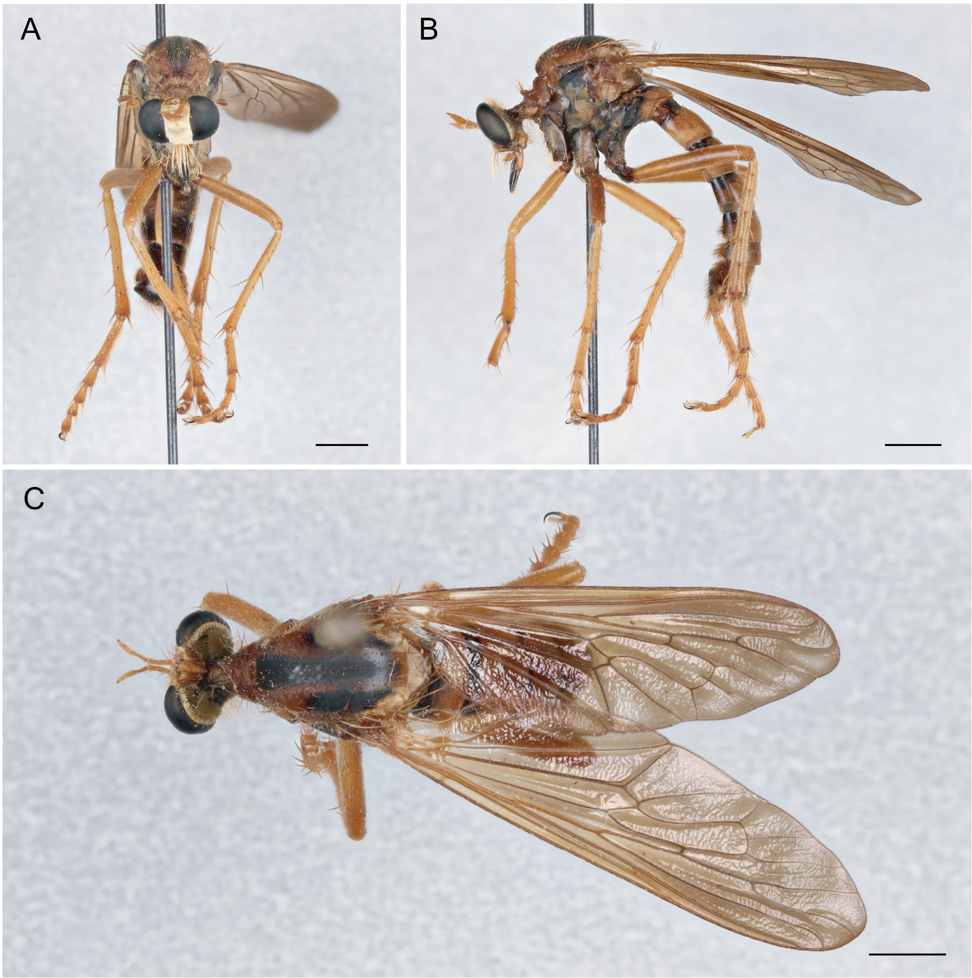

Figure 13. *Saropogon fletcheri* Bromley, 1934 Male (UCBMEP0280504): **A** anterior view **B** lateral view **C** dorsal view. Scale bars: 2 mm.

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. Suppl. material 1.

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

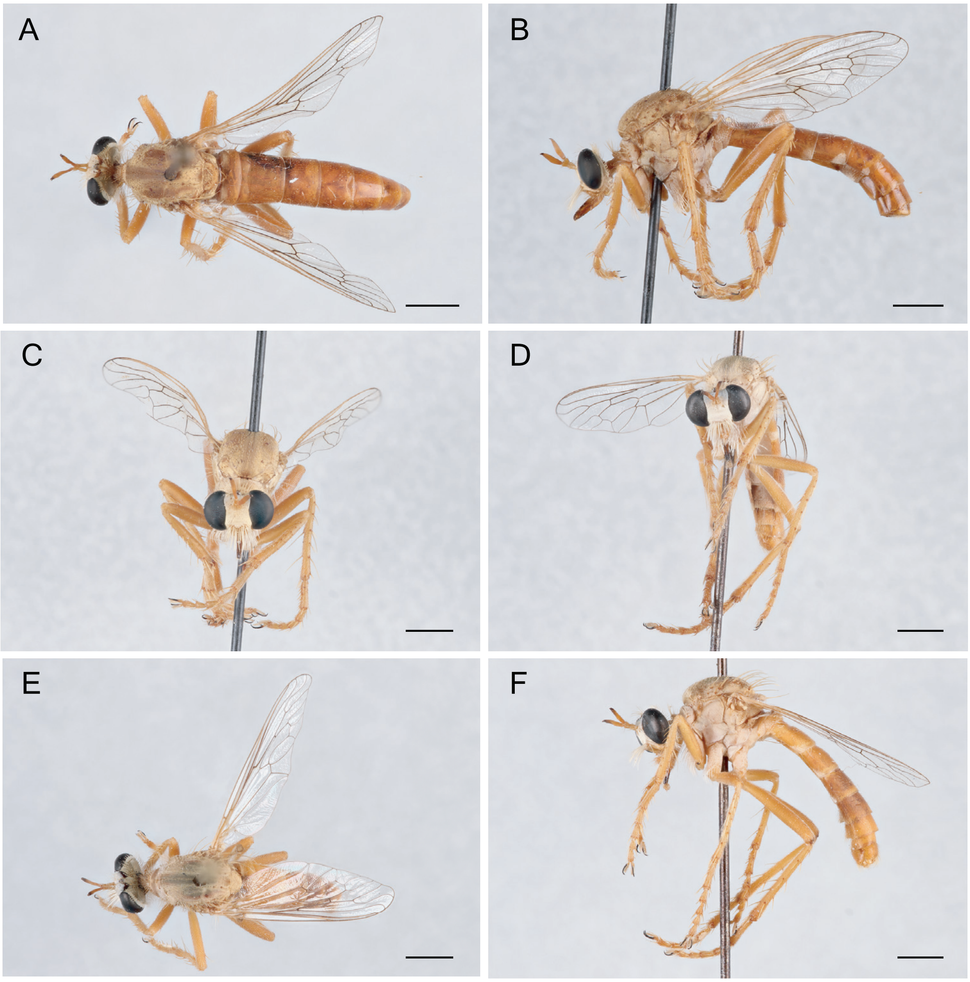

Figure 14. *Saropogon hyalinus* Coquillett, 1904 Female (USNMENT01830078): **A** dorsal view **B** lateral view **C** anterior view; Male (UCBMEP0280500): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

Saropogon hypomelas (Loew, 1866)

Figs 5I, J, 15, 26, 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

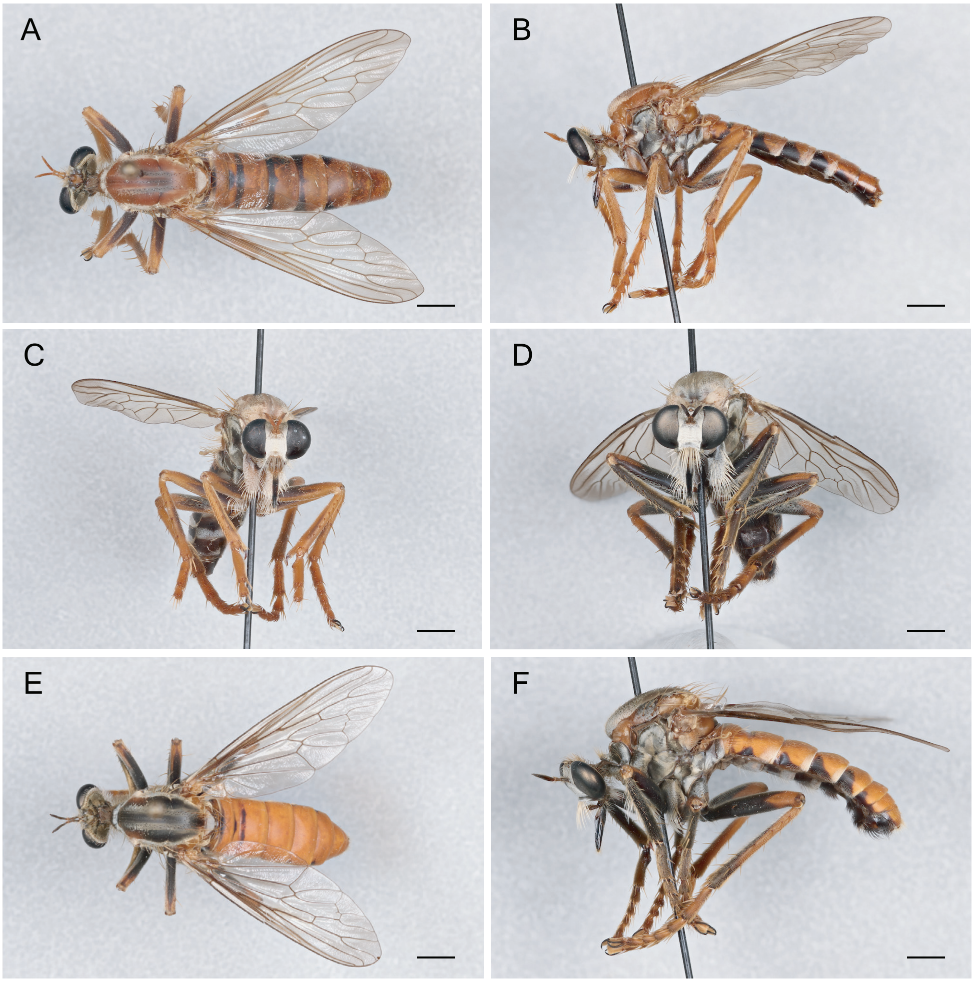

Figure 15. *Saropogon hypomelas* Loew, 1866 Female (USNMENT01830080): **A** dorsal view **B** lateral view **C** anterior view; Male (UCBMEP0280599): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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. Suppl. material 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.

***Saropogon laparoides* Bromley, 1951**

Figs 16, 26, 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. Suppl. material 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)).

***Saropogon luteus* Coquillett, 1904**

Figs 5K, L, 17, 26, 33

Saropogon luteus Coquillett, 1904: 185.
Saropogon rufus Back 1904: 290, junior synonym.

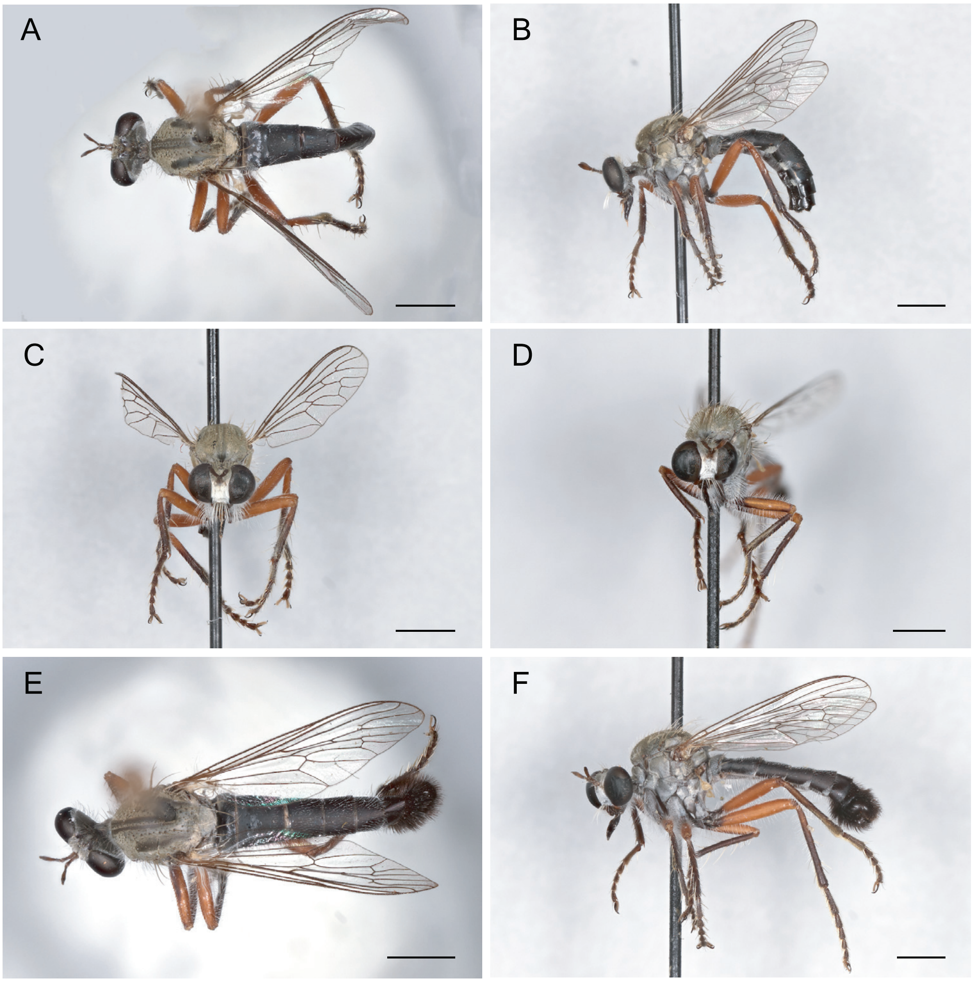

Figure 16. *Saropogon laparoides* Bromley, 1951 Female (USNMENT01819592): **A** dorsal view **B** lateral view **C** anterior view; Male (USNMENT01819567): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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.

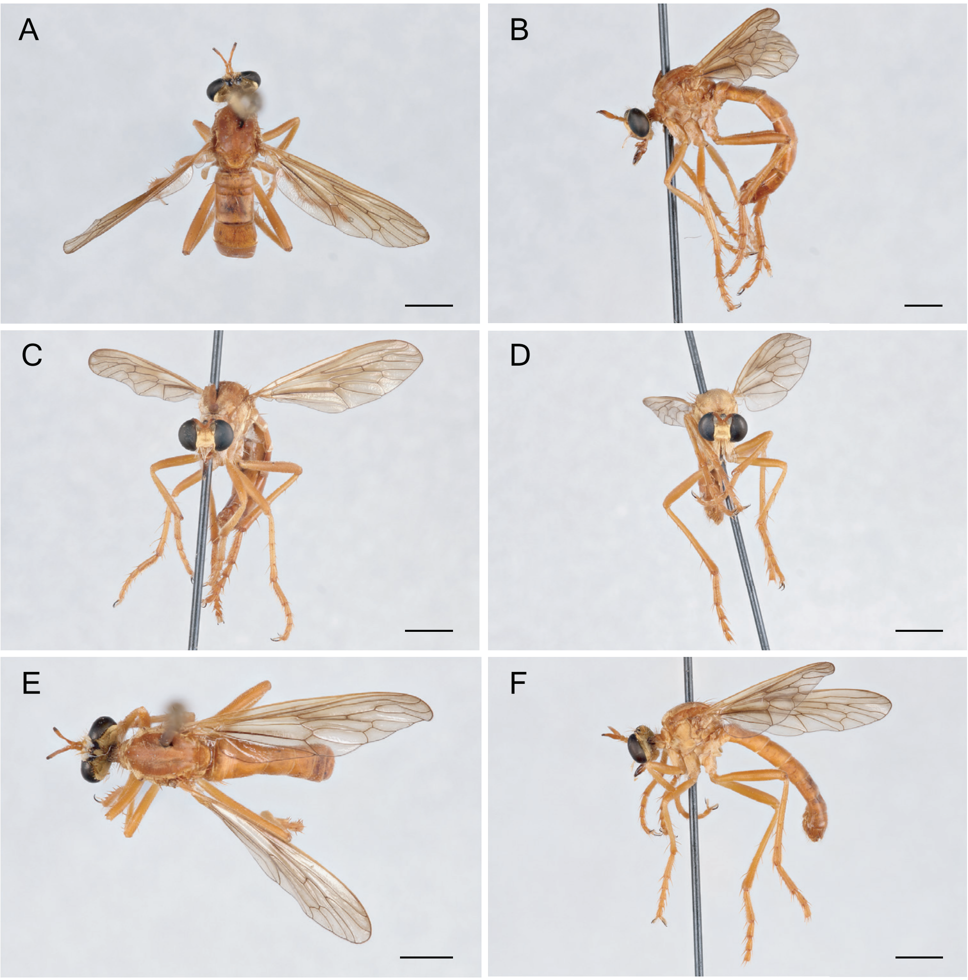

Figure 17. *Saropogon luteus* Coquillett, 1904 Female (UCBMEP0073792): **A** dorsal view **B** lateral view **C** anterior view; Male (UCBMEP0073760): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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. Suppl. material 1.

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 18, 26, 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 pale-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

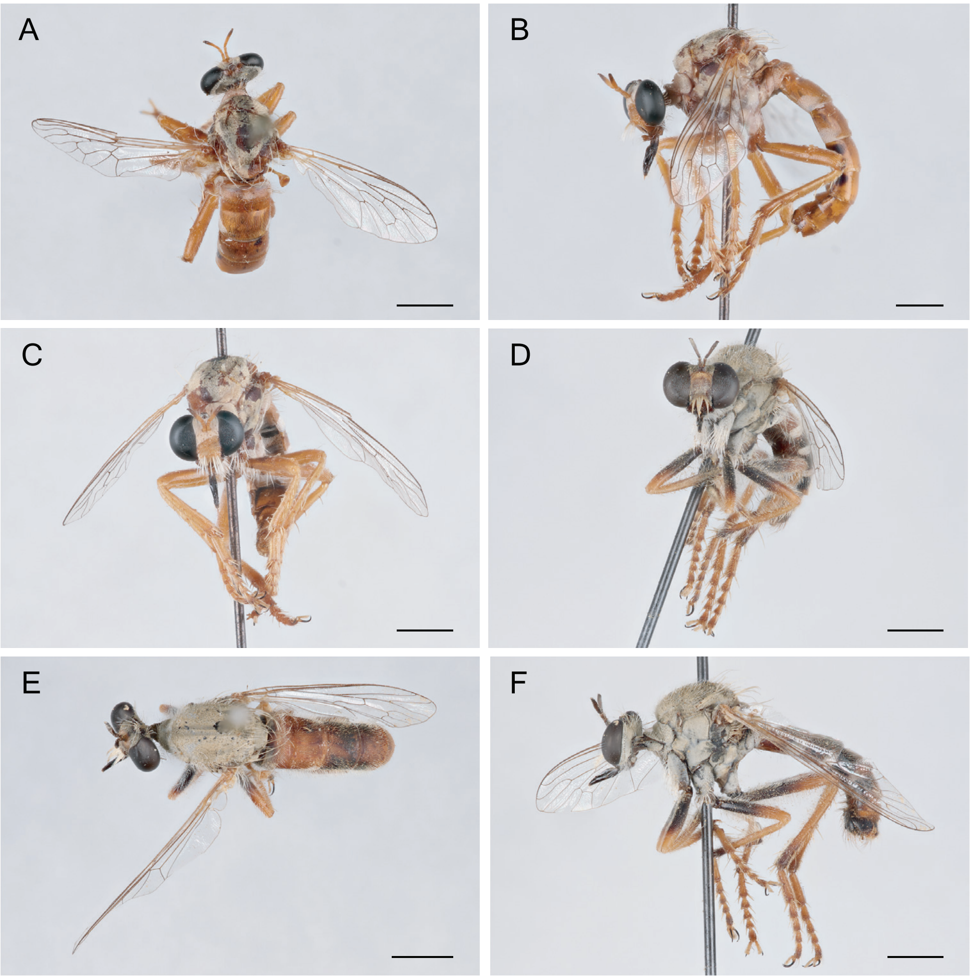

Figure 18. *Saropogon mohawki* Wilcox, 1966 Female paratype (UCBMEP0003173): **A** dorsal view **B** lateral view **C** anterior view; Male (UCBMEP0003175): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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. Suppl. material 1.

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

Saropogon nitidus Wilcox, 1966

Figs 19, 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 katepis-

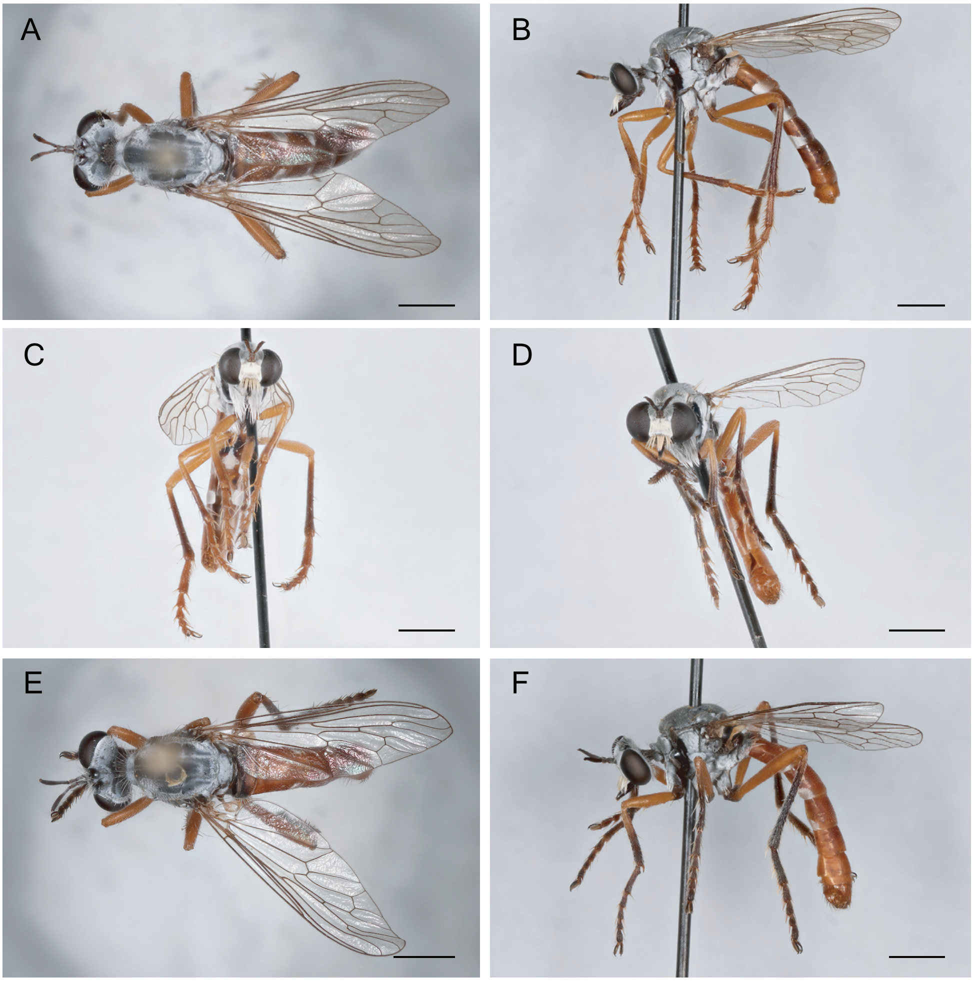

Figure 19. *Saropogon nitidus* Wilcox, 1966 Female (USNMENT01830081): **A** dorsal view **B** lateral view **C** anterior view; Male (UCBMEP0280497): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

ternum. 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. Suppl. material 1.

Comments. Photographs of holotype can be found at: https://monarch.calacademy.org/taxa/index.php?tid=679457.

Saropogon pritchardi **Bromley, 1934**

Figs 20, 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 *S. 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 pale-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. Suppl. material 1.

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

Saropogon purus **Curran, 1930**

Figs 4E, F, 5M, N, 21, 26, 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).

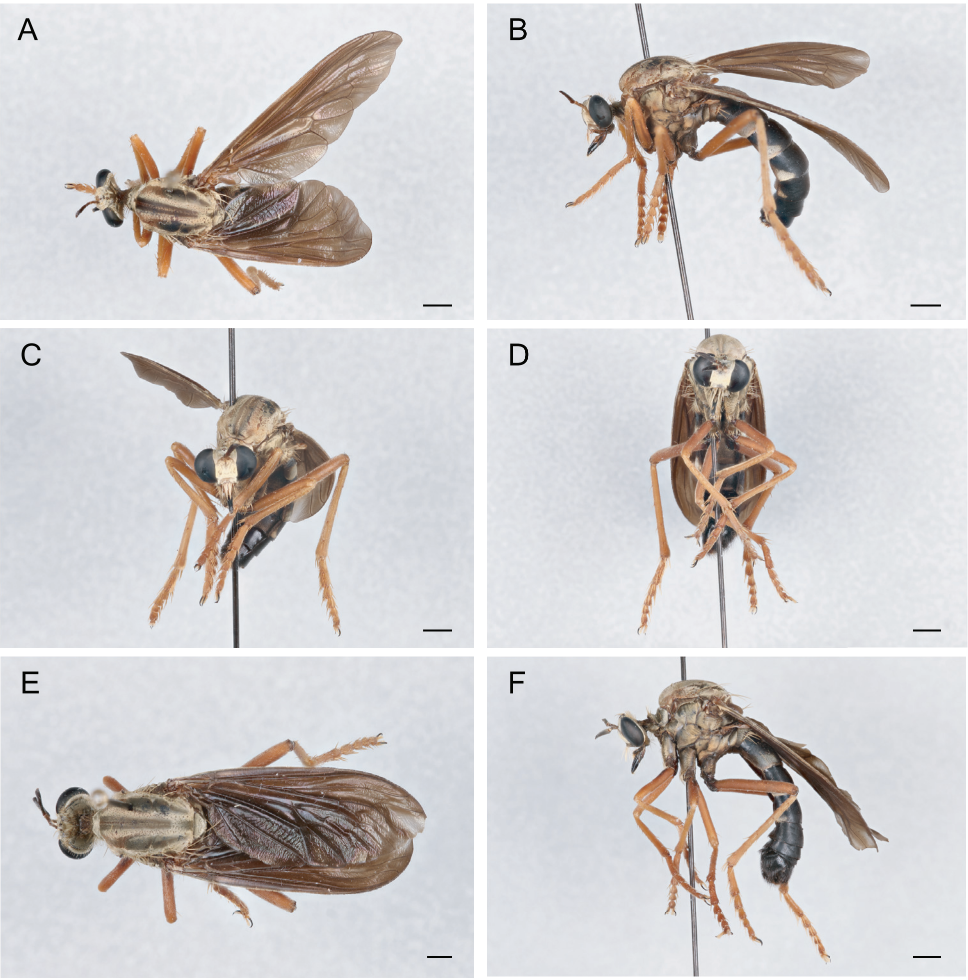

Figure 20. *Saropogon pritchardi* Bromley, 1934 Female (UCBMEP0280596): **A** dorsal view **B** lateral view **C** anterior view; Male (UCBMEP0280595): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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.

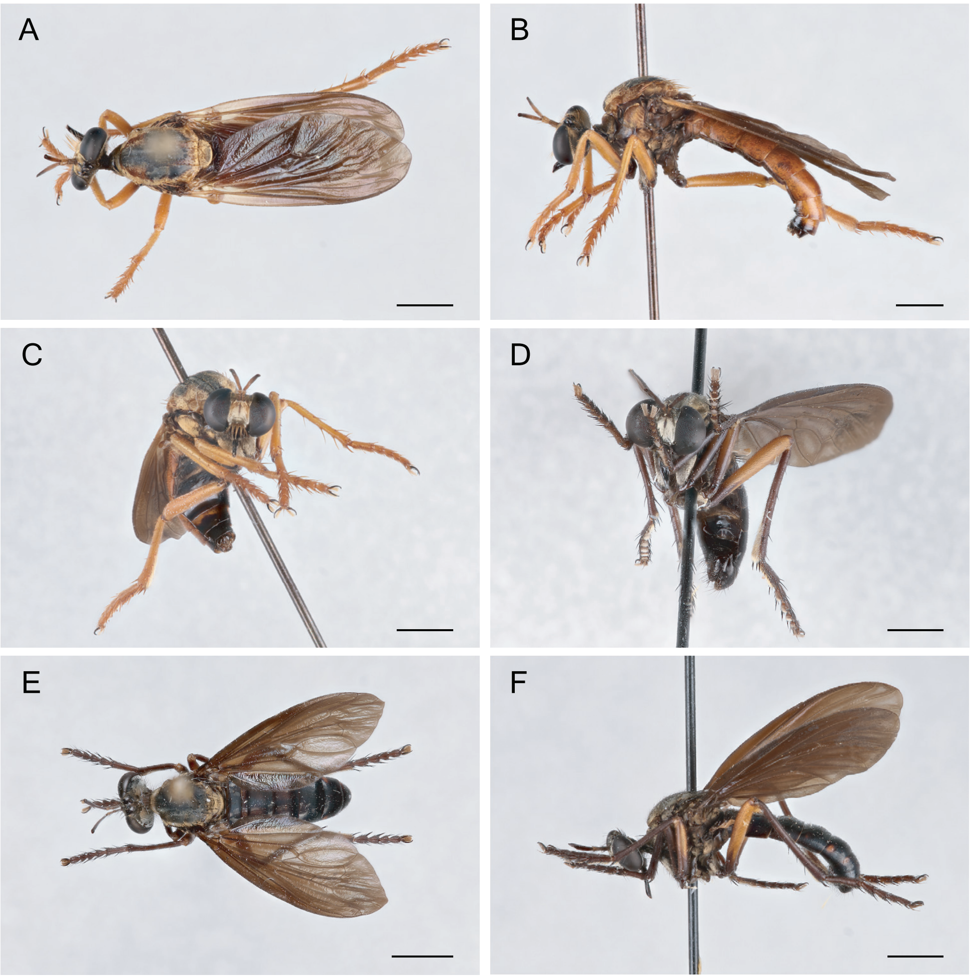

Figure 21. *Saropogon purus* Curran, 1930 Female (UCBMEP0280564): **A** dorsal view **B** lateral view **C** anterior view; Male (USNMENT01830082): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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. Suppl. material 1.

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

Saropogon pyrodes **sp. nov.**

https://zoobank.org/3B057DFB-5B32-445D-AE22-037E7FD4C0C8
Figs 1, 22, 23, 24, 25, 26, 27, 34

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).

Description. Male. Holotype (Figs 22, 23D–F).

Head. (Fig. 23) Wider than high; vertex slightly depressed (less than 60° 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.

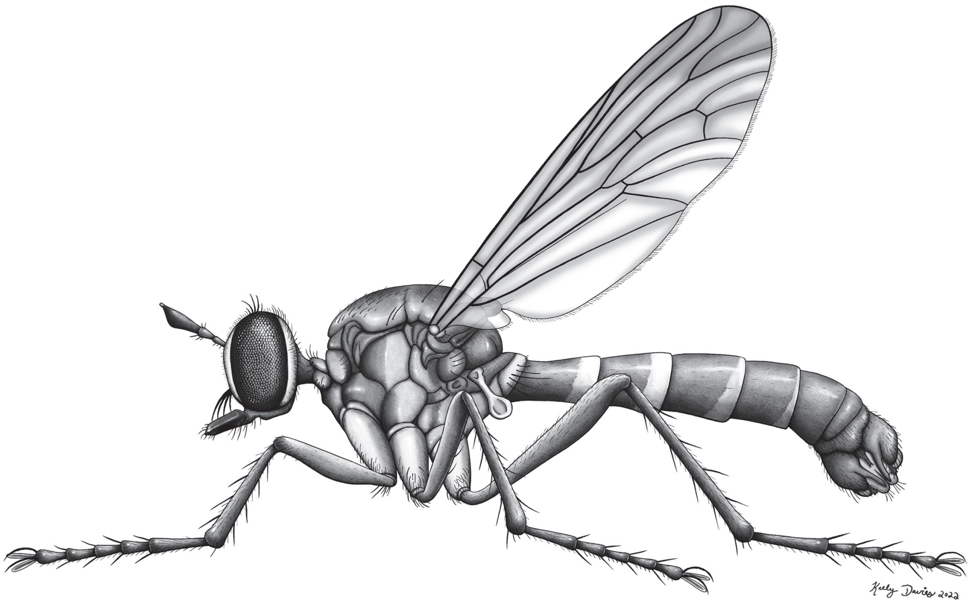

Figure 22. Habitus drawing of male *Saropogon pyrodes* sp. nov. by Keely Davies.

Proboscis and maxillary palpus. (Fig. 23) Proboscis straight, subequal in length to an eye when viewed from the front, pale brown to dark brown distally; postmentum with white setae ventrally; prementum with white setae proximo-ventrally; labella reduced, apex blunt; maxillary palpus pale brown to orange, with yellow setae and macrosetae, non-pubescent.

Antenna. (Fig. 23) Pale brown to dark brown distally, with pale gray pubescence; scape approximately as long as pedicel, short white setae dorsally and long white macrosetae ventrally; pedicel white and pale 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. 23) Pale 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

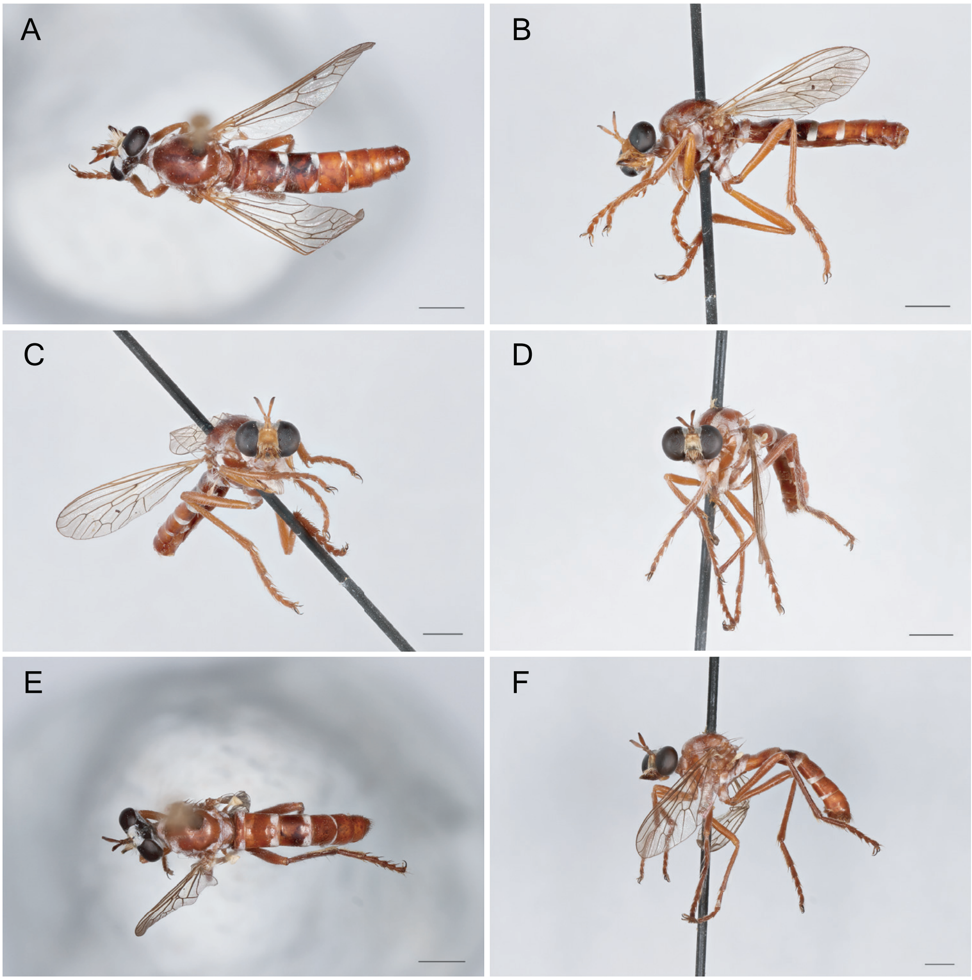

Figure 23. *Saropogon pyrodes* sp. nov. paratype female: **A** dorsal view **B** lateral view **C** anterior view; holotype male: **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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. 23) Pale brown to orange, non-pubescent, at least some setae dorsoventrally 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. 24) 8 mm. Hyaline, without microtrichia; posterior wing margin with microtrichia arranged in a single plane.

Abdomen. (Figs 6, 25) Pale 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 pale 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 pale gray pubescence.

Male abdomen. (Fig. 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

Figure 24. *Saropogon pyrodes* sp. nov. wing. Scale bar: 2 mm.

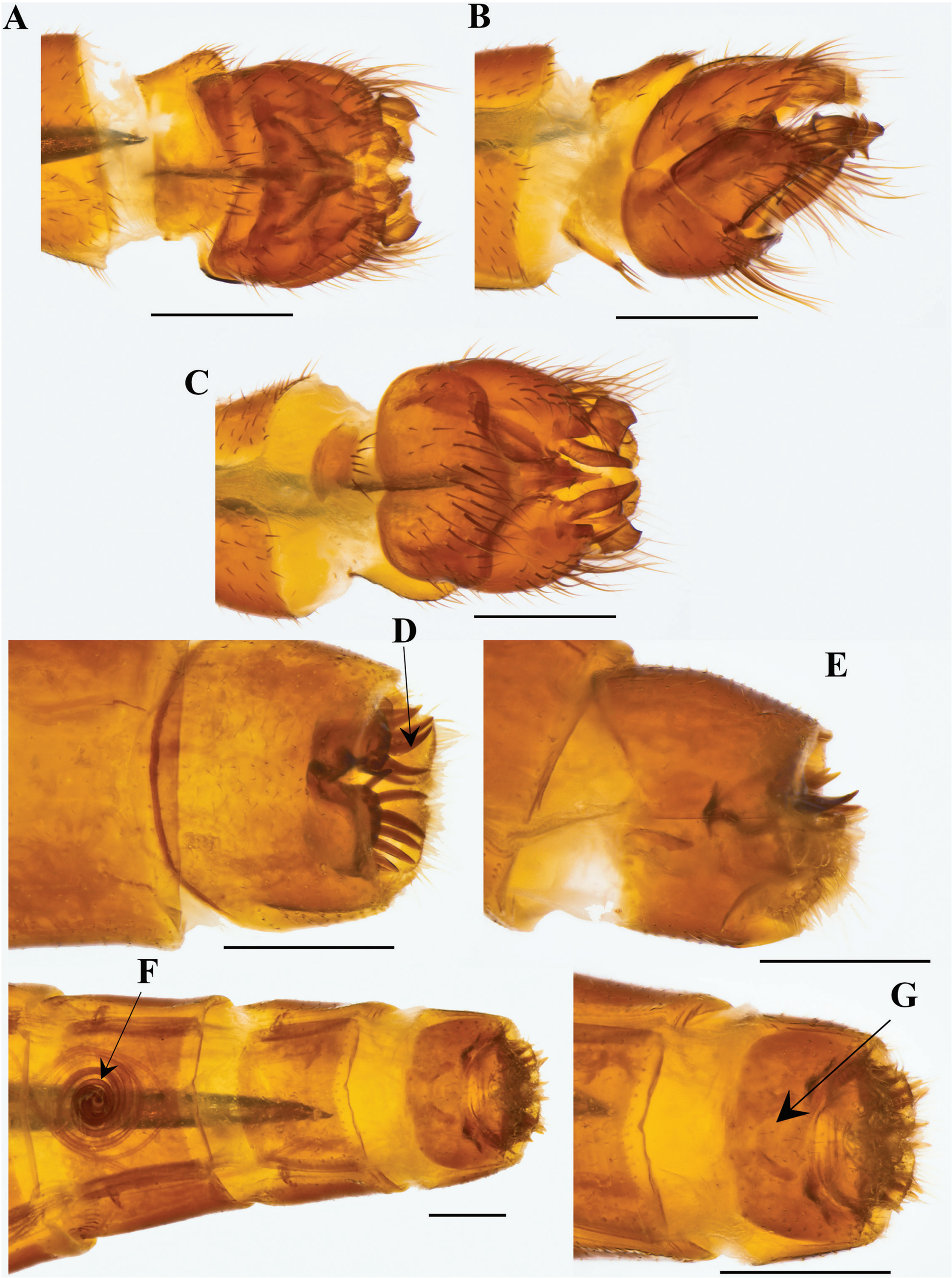

Figure 25. *Saropogon pyrodes* sp. nov. terminalia. Male (USNMENT01819155): **A** dorsal view 75× **B** lateral view 75× **C** ventral view 75×; female (UAIC1128818): **D** dorsal view 80×, arrow indicating acanthophorites (spines) **E** lateral view 95× **F** ventral view of T6–9 40×, arrow indicating spiral spermathecal reservoir **G** ventral view of T8–9 80×, arrow indicating "X" shaped furca. Scale bars: 1 mm.

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. 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.

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♂). Information and pictures of the holotype are available on the Smithsonian National

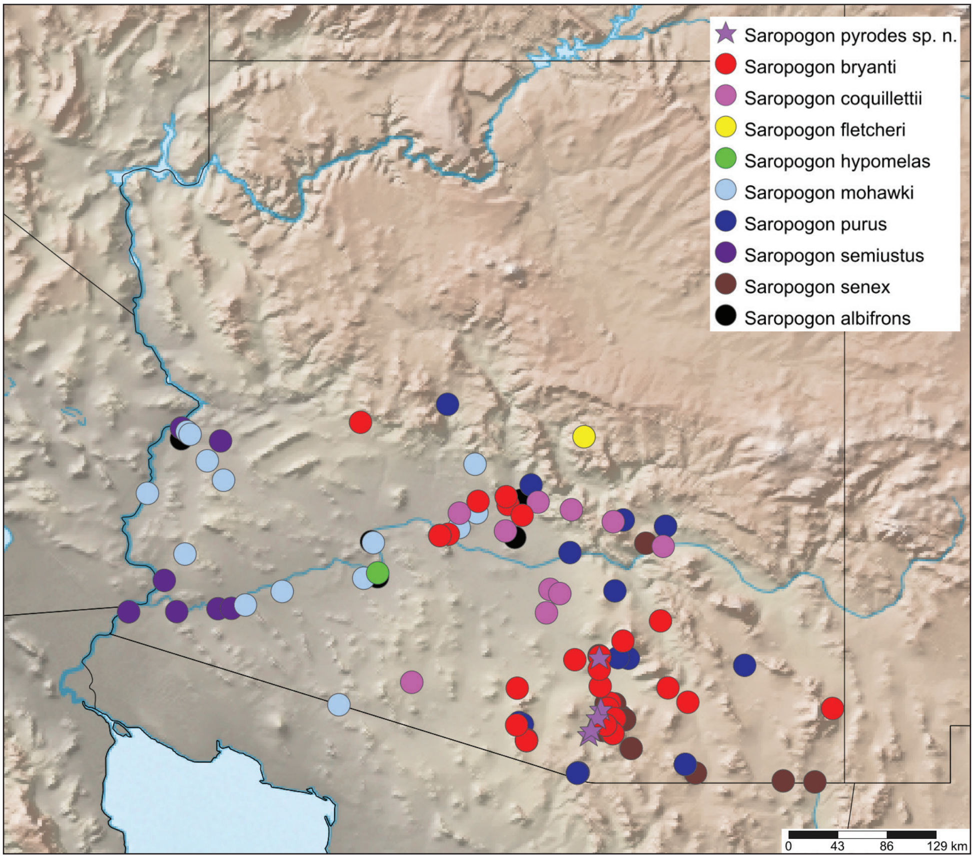

Figure 26. Focused map of the Arizona distribution of Nearctic *Saropogon* (Diptera: Asilidae). Map created with SimpleMappr on January 25, 2022, and available at: https://www.simplemappr.net/map/17143.

Museum of Natural History Search the Department of Entomology Collections website: http://n2t.net/ark:/65665/36f568a66-098a-4932-8900-92113e4b58b9.

Distribution. USA: Arizona (Fig. 26) https://www.simplemappr.net/map/17143.

Biology. Jeff Gruber photographed specimens of *Saropogon pyrodes* sp. nov. and its habitat (Fig. 27A, B). *S. pyrodes* sp. nov. is seen here perching/hunting on a grass, most likely *Bouteloua aristidoides* (Poaceae; Fig. 27C), on the edge of a sandy clearing as well as consuming its prey (Fig. 27D) in the typical hanging position observed in other Dasypogoninae species.

Jeff Gruber described some behavior (Figs 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

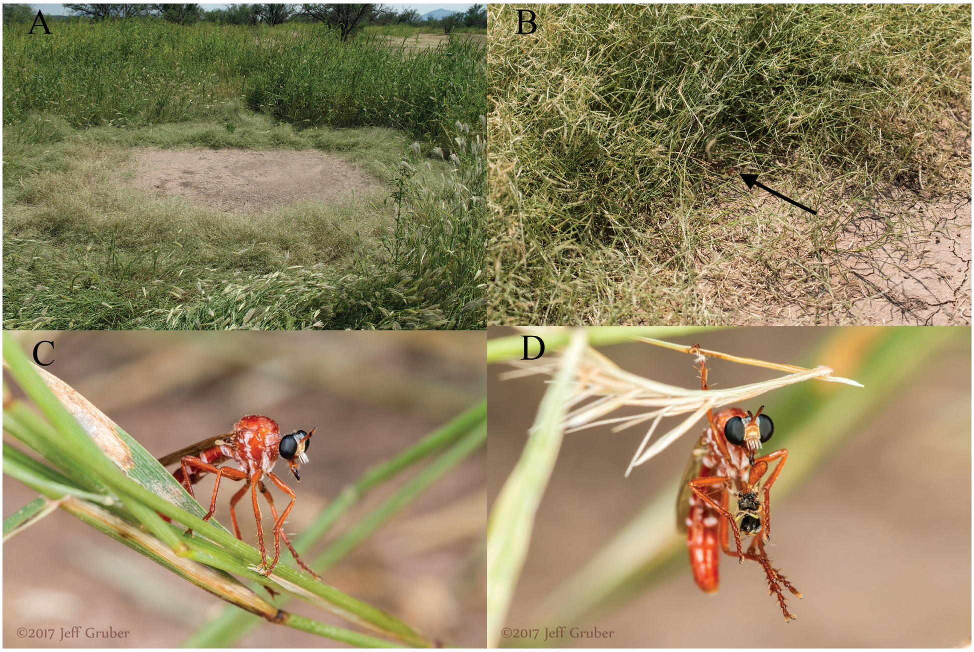

Figure 27. *Saropogon pyrodes* sp. nov. in natural habitat at ~ 0.7 km ENE of Amado in southern Arizona on September 5, 2017 **A** habitat overview **B** habitat detail with *S. pyrodes* included (arrow) **C** close-up of male perching **D** close-up of male consuming a bee (Hymenoptera: Apidae). Photographs by Jeff Gruber.

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. 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. 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 26, 28, 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; AS-

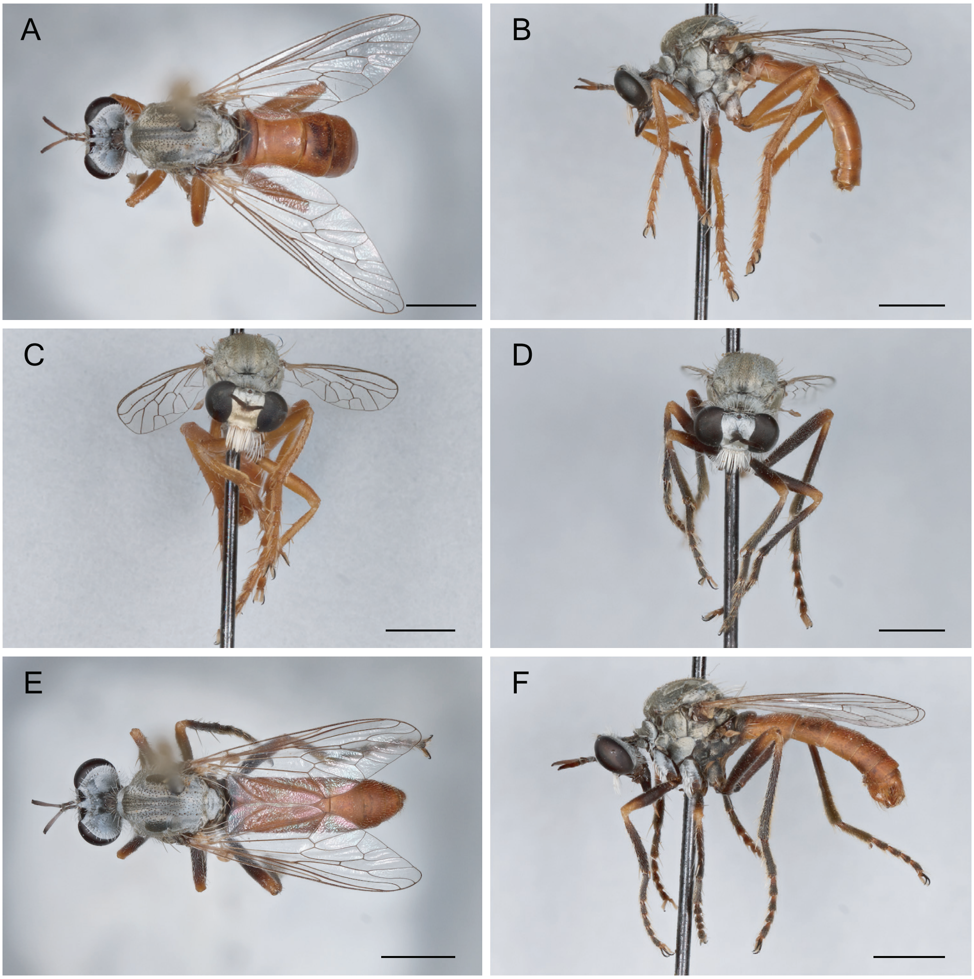

Figure 28. *Saropogon semiustus* Coquillett, 1904 Female (USNMENT01830085): **A** dorsal view **B** lateral view **C** anterior view; Male (USNMENT01830084): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

UHIC0139665, 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. Suppl. material 1.

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

Saropogon senex Osten Sacken, 1887

Figs 4G, H, 5O–P, 26, 29, 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,

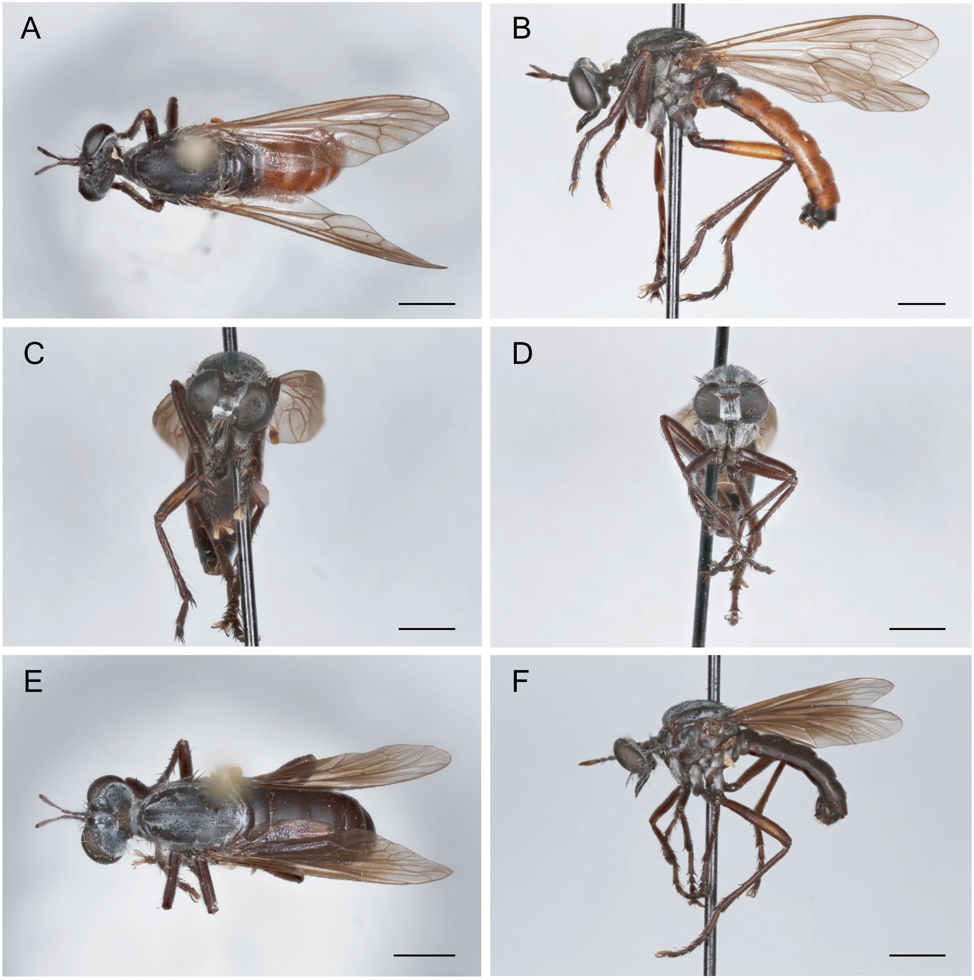

Figure 29. *Saropogon senex* Osten Sacken, 1887 Female (UCBMEP0280483): **A** dorsal view **B** lateral view **C** anterior view; Male (UCBMEP0280489): **D** anterior view **E** dorsal view **F** lateral view. Scale bars: 2 mm.

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. Suppl. material 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.

Saropogon solus **Bromley, 1951**

Figs 30, 31

Saropogon solus Bromley, 1951: 15.

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

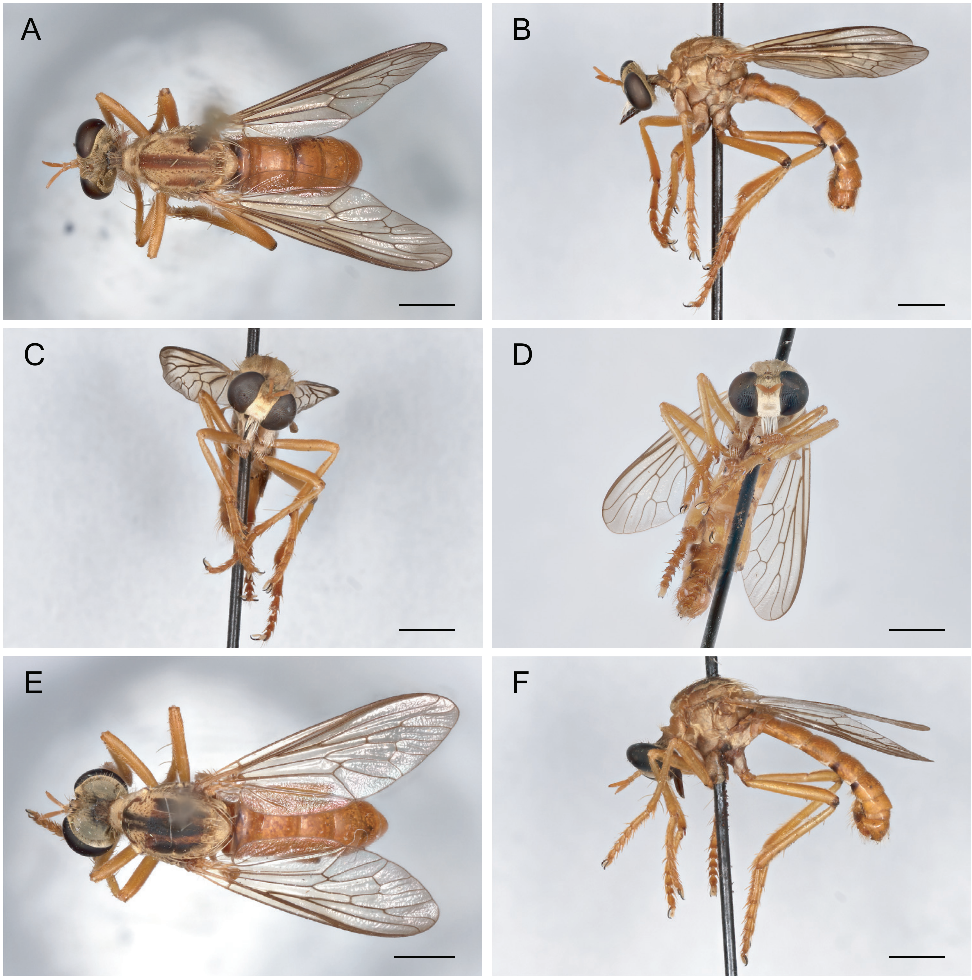

Figure 30. *Saropogon solus* Bromley, 1951 Female (USNMENT01819178): **A** dorsal view **B** lateral view **C** anterior view; Male (USNMENT01819132): **D** anterior view **E** dorsal view **F** lateral view. Scale bars 2 mm.

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. Suppl. material 1.

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

Discussion

The description of the unique species *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 collections, 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* Osten Sacken (~ 34 spp.) and *Diogmites* Loew 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 pale 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 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.

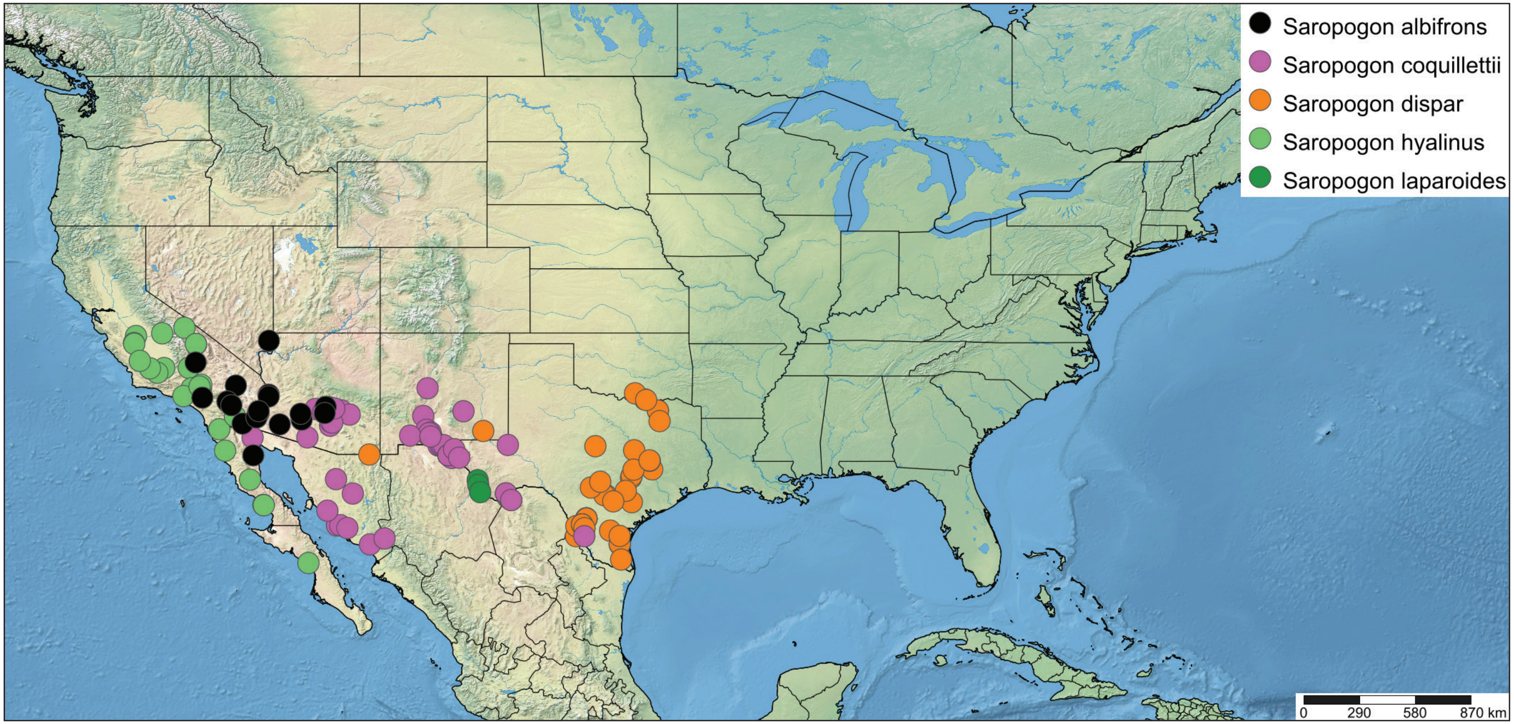

Figure 32. Distribution of *Saropogon* (Diptera: Asilidae) specimens studied for *S. albifrons*, *S. coquillettii*, *S. dispar*, *S. hyalinus*, and *S. laparoides*. Map created with SimpleMappr on July 25, 2022, and available at: https://www.simplemappr.net/map/18317.

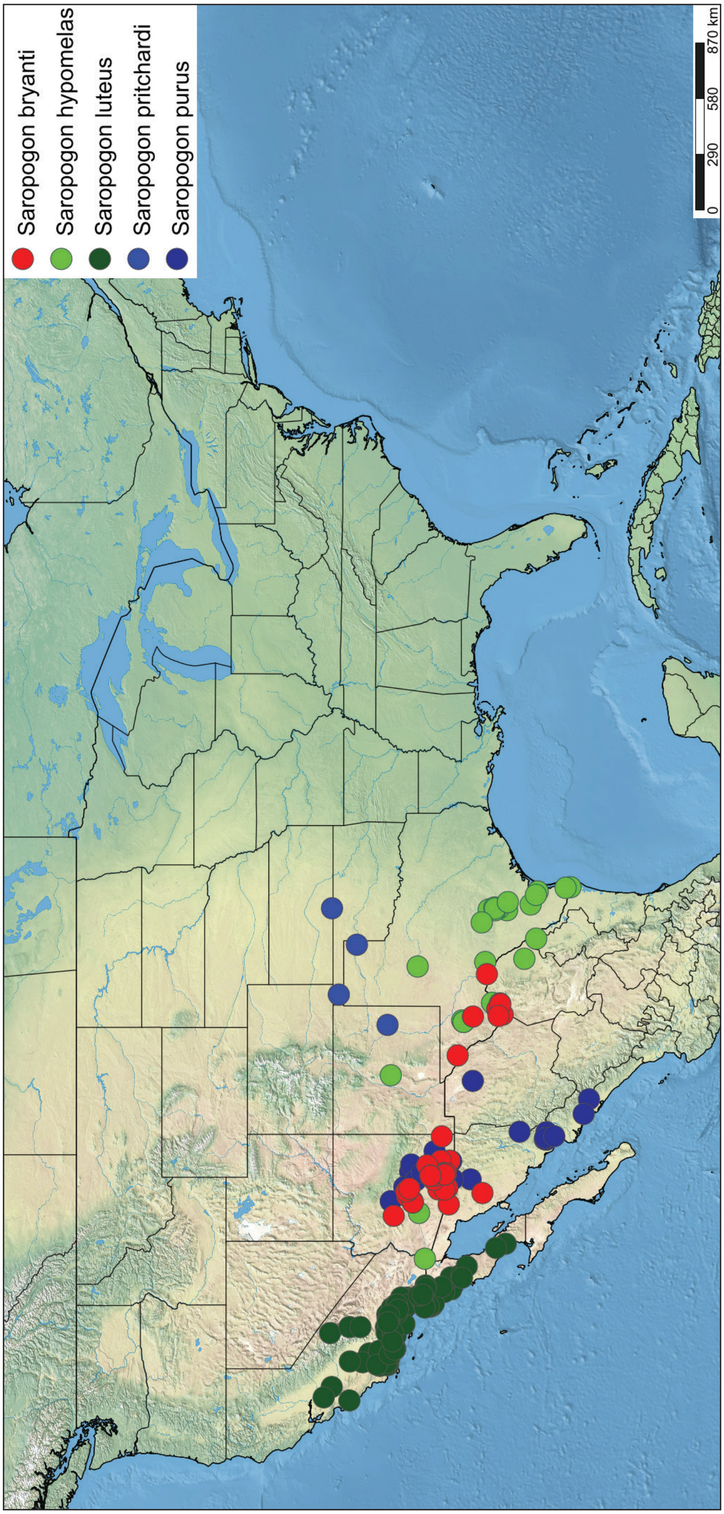

Figure 33. Distribution of *Saropogon* (Diptera: Asilidae) specimens studied for *S. bryanti*, *S. hypomelas*, *S. luteus*, *S. pritchardi*, and *S. purus*. Map created with SimpleMappr on July 25, 2022, and available at: https://www.simplemappr.net/map/18318.

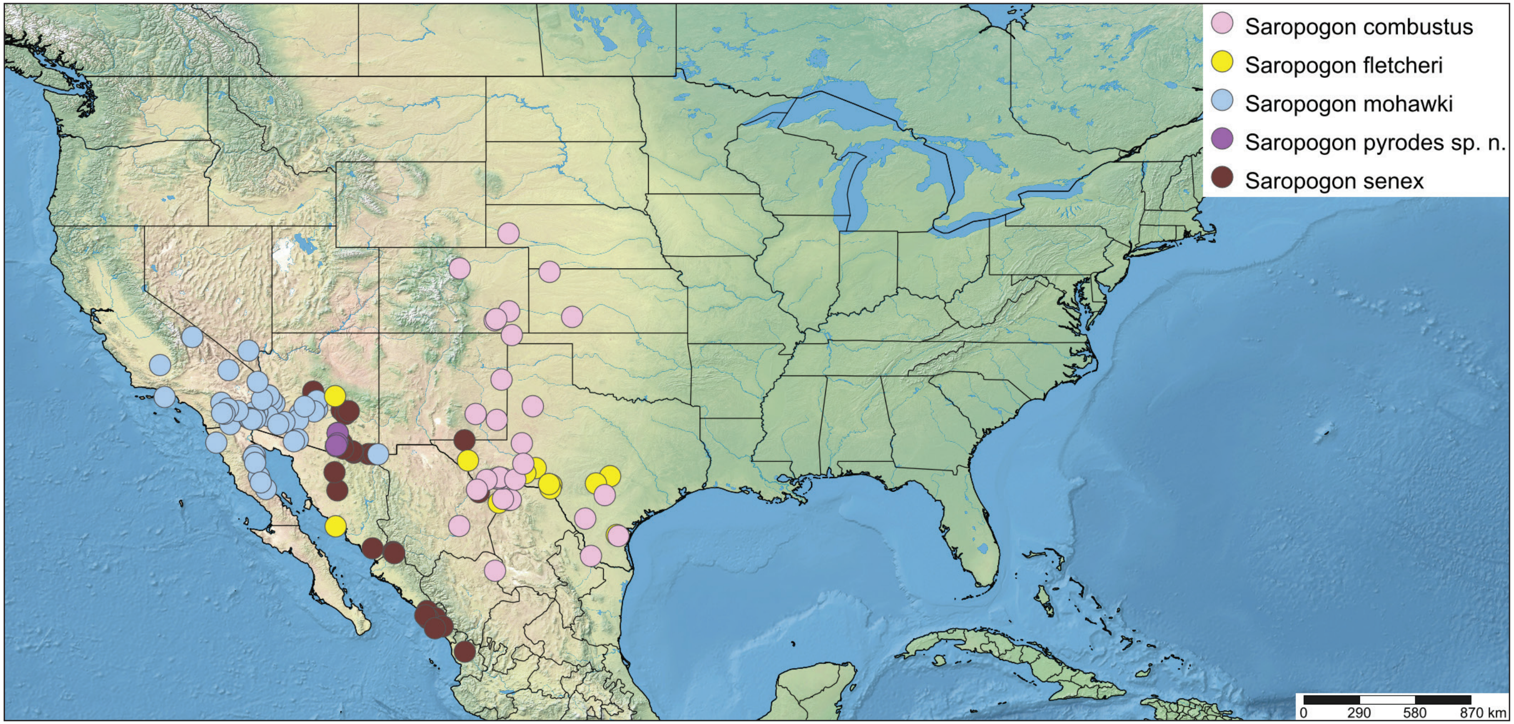

Figure 34. Distribution of *Saropogon* (Diptera: Asilidae) specimens studied for *S. combustus*, *S. fletcheri*, *S. mohawki*, *S. pyrodes* sp. nov., and *S. senex*. Map created with SimpleMappr on July 25, 2022, and available at: https://www.simplemappr.net/map/18362.

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Supplementary material 1

Locality information of all specimens examined

Authors: Charlotte H. E. Alberts, Eric M. Fisher

Data type: excel file

Explanation note: Locality information of all specimens examined.

Link: https://doi.org/10.3897/zookeys.1130.81874.suppl1

ZooKeys 1130: 65–78 (2022)
doi: 10.3897/zookeys.1130.91325
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The complete mitochondrial genome of the terrestrial snail *Monacha cartusiana* (O.F. Müller, 1774) (Gastropoda, Eupulmonata, Hygromiidae)

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Abstract

The mitochondrial genome of *Monacha cartusiana* is the first complete mitochondrial sequence described for the pulmonate snail genus *Monacha* and for the family Hygromiidae. The identified mitogenome has a length of 13,894 bp and encodes 13 proteins, 22 tRNAs, and two rRNAs. A phylogenetic analysis of available mitogenomes from representatives of helicoid families shows a sister group relationship of Hygromiidae and Geomitridae, which have been recently recognised as separate families.

Keywords

Carthusian snail, Helicoidea, mitogenome, phylogeny, Stylommatophora

Introduction

Mollusca is the second largest animal phylum after Arthropoda in terms of the number of named species, with the class Gastropoda as the most speciose group with approximately 95,000 species (Ponder et al. 2020). Stylommatophoran pulmonates constitute the most species-rich gastropod order with an estimated number of about 30,000 species (Mordan and Wade 2008). Although the monophyly of Stylommatophora within panpulmonate heterobranchs is relatively well established (Jörger et al. 2010; Ponder et al. 2020), the phylogenetic relationships between stylommatophoran families are still debated (White et al. 2011; Gaitán-Espitia et al. 2013; Razkin et al. 2015; Doğan et al. 2020; Ponder et al. 2020).

Mitogenome sequences are of great importance in molecular phylogenetic studies (Moritz et al. 1987), especially to infer evolutionary relationships at species level (Avise et al. 1987); this is also the case within Mollusca (Boore 1999). The analysis of mitogenomes may thus provide additional evidence related to stylommatophoran phylogeny (White et al. 2011; Parmakelis et al. 2013; Minton et al. 2016a). The number of available stylommatophoran mitogenomes has increased in the last two decades, from three at the end of the 20th century (Hatzoglou et al. 1995; Terrett et al. 1996; Yamazaki et al. 1997) to 35 in recent years (Yang et al. 2019; Doğan et al. 2020). However, considering the number of recognised extant families within the Stylommatophora (117 according to Bouchet et al. 2017), the number of stylommatophoran mitogenomes still is very small and new mitogenomes, especially from families for which no, or very few, mitogenomes are available, are worth publishing. Hitherto, two mitogenomes were available for the Hygromiidae, viz. *Cernuella virgata* (Da Costa, 1778) and *Helicella itala* (Linnaeus, 1758), published by Lin et al. (2016) and Romero et al. (2016), respectively. However, these two species have recently been transferred from the Hygromiidae to the Geomitridae (Razkin et al. 2015; Neiber et al. 2017; Bouchet et al. 2017), so that the Hygromiidae, very rich in species, is left without any available mitogenome.

The hygromiid genus *Monacha* Fitzinger, 1833 is widespread in the western Palaearctic from western Europe to North Africa, Iran, and Arabia. It includes a large number of nominal species and shows its highest diversity in south-eastern Europe and Turkey (Hausdorf 2000a, 2000b; Welter-Schultes 2012). Although most of the *Monacha* species occur in rather narrow areas (Welter-Schultes 2012; Neiber and Hausdorf 2017), *Monacha cartusiana* (O.F. Müller, 1774), the type species of the genus, is widely distributed and can be found in almost the whole of Europe excluding its north-eastern fringes (Scandinavia, Russia, Baltic States, Belarus, northern Ukraine) (Welter-Schultes 2012; Pieńkowska et al. 2018). The mitogenome of this species will facilitate the future identification of species within the genus and the understanding of their phylogenetic relationships, as is the case with other families of terrestrial pulmonate snails (González et al. 2016; Groenenberg et al. 2017; Korábek et al. 2019; Doğan et al. 2020). Hence, in this paper, we present the complete mitogenome of *M. cartusiana* and analyse its phylogenetic position within the superfamily Helicoidea.

Material and methods

The specimen of *Monacha cartusiana* used for this research was collected in Ostrowiec Świętokrzyski (Poland) by Mariusz Gwardjan on 03.07.2015. It was identified by the sequence of the cytochrome c oxidase subunit I gene fragment (*coI*) of *M. cartusiana* in GenBank (KX258398) deposited by Pieńkowska et al. (2016). Total genomic DNA was extracted following Pieńkowska et al. (2015). The sequencing of the *M. cartusiana* mitogenome (for gene acronyms see Table 3) was started using four pairs of primers complementary to the conservative regions of *coI* (Folmer et al. 1994), *16S rRNA* (Palumbi et al. 1991), *coII* (Hugall et al. 2002) and *cytb* (Merritt et al. 1998), the missing fragments between them were identified by primer walking (Lin et al. 2016). The primers used for the amplification of mtDNA are listed in Table 1.

The mitogenome was annotated using the MITOS Web Server (Bernt et al. 2013). For the phylogenetic analysis we used a concatenated sequence alignment of 12 protein coding genes (PCGs; excluding *atp8*), and 2 rRNAs (*12S rRNA* and *16S rRNA*). Every set of 14 sequences was separately aligned using CLUSTAL W (Thompson et al. 1994) implemented in BIOEDIT v. 7.0.6 (Hall 1999; BioEdit 2017). The length of the alignment after combining the 14 gene sequences was for each species 14,287 bp. For the phylogenetic analysis we used all mitogenome sequences deposited in GenBank for species of the superfamily Helicoidea (Table 2). The mitogenome of *Theba pisana* (MH362760) was not annotated, so we designated the individual PCGs and rRNAs by aligning the whole *T. pisana* sequence with the extracted sequences of species belonging to the family Helicidae. Each of the *T. pisana* PCGs was tested for start and stop codons with ORF FINDER (2004). Mitogenomes of two arionoid species (*Arion vulgaris* and *Meghimatium bilineatum*, Table 2) were used as the outgroup.

Phylogenetic analysis was performed using maximum likelihood (ML) as implemented in the online version of IQ-TREE (Trifinopoulos et al. 2016). ML analysis

Table 1. List of primers used for the amplification of *Monacha cartusiana* mitochondrial DNA.

Primer	Sequence 5' – 3'	References
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
HC02198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. 1994
16Sar-L	CGCCTGTTTATCAAAAACAT	Palumbi et al. 1991
16Sbr-H	CCGGTCTGAACTCAGATCACGT	Palumbi et al. 1991
144F	TGAGSNCARATGTCNTWYTG	Merritt et al. 1998
272R	GCRAANAGRAARTACCAYTC	Merritt et al. 1998
FCOII	AAATAATGCTATTTCATGAYCAYG	Hugall et al. 2002
RCOII	GCTCCGCAAATCTCTGARCAYTG	Hugall et al. 2002
1F_556 Os	TACCTGTACTAGCGGGGGCT	this paper
1R_75 Os	CAGTCAGGGTACTGCGGCTA	this paper
2F_342 Os	TTGTGACCTCGATGTTGGACT	this paper
2R_83 Os	CCGCCTCAGACCCAACTAAC	this paper
3F_320 Os	GGCCTAACTTGTTCACTGATCCT	this paper
3R_50 Os	TTTCTAGGGTCTGCGCTTCA	this paper
4F_429 Os	TTGTGGGGGTTTATTACGGGC	this paper
4R_110 Os	ATCACTCAACACCCCTGAAGT	this paper
seqF_F1	ACGGTTTCCTGTTCTATTATTTG	this paper
seqF_R1	CAAATAATAAGCTCCTAATGTAATC	this paper
seqF_R2	ATAAACTTTCCACTTCAGGGAAT	this paper
seqF_R3	GTAAAACATTTATTGGGGCCCAG	this paper
seqF_R4	AACTAATTAACAACCTATATAGGG	this paper
seqF_R5	TAGTCCCGTGCTGGCTAGTATT	this paper
seqH_F2	CTATTGTAACTCGCCTTAACTCTAA	this paper
seqH_R2	GAAATAAACACCTAAAATTACTGTA	this paper
seqH_R3	GATGTACCTGATATTAAACCTA	this paper
seqH_F4	CTACTAAACAGAAAAAGCGAACCC	this paper
seqH_R4	GCAGCCACAATTTACTTCTT	this paper

Table 2. Mitogenomes from GenBank used in the phylogenetic analysis and their lengths.

species	GenBank Accession No.	Mitogenome length (bp)	References
Camaenidae: *Aegista aubryana* (Heude, 1882)	KT192071	14238	Yang et al. 2016
Camaenidae: *Aegista diversifamilia* Huang, Lee, Lin & Wu, 2014	KR002567	14039	Huang et al. 2016
Camaenidae: *Camaena cicatricosa* (O. F. Müller, 1774)	KM365408	13843	Wang et al. 2014
Camaenidae: *Camaena poyuensis* Zhou, Wang & Ding, 2016	KT001074	13798	Lin et al. 2016
Camaenidae: *Dolicheulota formosensis* (Adams, 1866)	KR338956	14237	Huang et al. 2016
Camaenidae: *Fruticicola koreana* (L. Pfeiffer, 1850)	KU237291	13979	Hwang 2015
Camaenidae: *Mastigeulota kiangsinensis* (Martens, 1875)	KM083123	14029	Deng et al. 2016
Geomitridae: *Cernuella virgata* (Da Costa, 1778)	KR736333	14147	Lin et al. 2016
Geomitridae: *Helicella itala* (Linnaeus, 1758)	KT696546	13967	Romero et al. 2016
Helicidae: *Cylindrus obtusus* (Draparnaud, 1805)	JN107636	14610	Groenenberg et al. 2012
Helicidae: *Cepaea nemoralis* (Linnaeus, 1758)	U23045	14100	Terrett et al. 1996
Helicidae: *Cornu aspersum* (O. F. Müller, 1774)	JQ417194	14050	Gaitán-Espitia et al. 2013
Helicidae: *Helix pomatia* Linnaeus, 1758	MK347426	14070	Korabek et al. 2019
Helicidae: *Helix pomatia* Linnaeus, 1758	MK488030	14072	Groenenberg and Duijm 2019
Helicidae: *Helix pomatia* Linnaeus, 1758	MK488031	14070	Groenenberg and Duijm 2019
Helicidae: *Theba pisana* (O. F. Müller, 1774)	MH362760	14795	Wang et al. 2018
Hygromiidae: *Monacha cartusiana* (O. F. Müller, 1774)	MW485067	13894	This paper
Polygyridae: *Practicolella mexicana* Perez, 2011 [1]	KX278421	14008	Minton et al. 2016a
Polygyridae: *Practicolella mexicana* Perez, 2011 [2]	KX240084	14153	Minton et al. 2016b
Arionidae: *Arion vulgaris* Moquin-Tandon, 1855	MN607980	14548	Doğan et al. 2020
Philomycidae: *Meghimatium bilineatum* (Benson, 1842)	MG722906	14347	Yang et al. 2019

[1] Deposited in GenBank as mitogenome of *Polygyra cereolus* (Megerle von Mühlfeldt, 1818) but according to Minton et al. (2016a) it represents *Practicolella mexicana* Perez, 2011.

[2] Mitogenome not mentioned in the paper by Minton et al. (2016a) but directly submitted to GenBank (Minton et al. 2016b).

was done using 14 partitions. Best substitution models were inferred according to the Bayesian information criterion (BIC) for each of the partitions by MODELFINDER (Kalyaanamoorthy et al. 2017) implemented in IQ-TREE. The TVM+F+I+G4 model was selected for *nd1*, *nd2*, *nd4*, *nd5*, *atp6*, and *16S rRNA*; TPM3u+F+I+G4 for *nd3*; K3Pu+F+G4 for *nd4l*; TPM3+F+I+G4 for *nd6*; K3Pu+F+I+G4 for *cytb*, and *coII*; TIM+F+I+G4 for *coI*; GTR+F+I+G4 for *coIII*, and *12S rRNA*. ML trees were constructed under 1,000 ultrafast bootstrap replicates (Minh et al. 2013) and with Shimodaira-Hasegawa-like approximate likelihood ratio test with 1,000 replicates (SH-aLRT; Guindon et al. 2010). A Bayesian inference (BI) analysis was performed with MRBAYES v. 3.2.6 (Ronquist et al. 2012). Four Monte Carlo Markov chains were run for 1 million generations, sampling every 100 generations (the first 25% of trees were discarded as "burn-in"). Ultrafast bootstrap support, SH-aLRT support (both expressed in percentages) and posterior probability (PP) values obtained on 50% majority rule consensus Bayesian tree were mapped on the ML tree of concatenated sequences. The ML tree was visualized using FIGTREE v. 1.4.3 (Rambaut 2016).

Results and discussion

The complete mitogenome of *M. cartusiana* was deposited in GenBank under accession number MW485067. With 13,894 bp in length, it was one of the shortest mito-

Table 3. Organisation of the mitogenome of *Monacha cartusiana.*

Type	Gene product	Gene acronym	Start	End	Length (bp)	Direction	Start codon	Stop codon
PCG	cytochrome c oxidase subunit I	*coI*	0	1552	1552	+	ATG	TAA[1]
tRNA	valine transfer RNA	*tRNA Val*	1525	1585	61	+		
rRNA	16S ribosomal RNA	*16S rRNA*	1242	2652	1410	+		
tRNA	leucine transfer RNA	*tRNA Leu*	2593	2657	65	+		
tRNA	proline transfer RNA	*tRNA Pro*	2654	2718	60	+		
tRNA	alanine transfer RNA	*tRNA Ala*	2716	2778	63	+		
PCG	NADH dehydrogenase subunit 6	*nd6*	2777	3263	451	+	ATT	TAA
PCG	NADH dehydrogenase subunit 5	*nd5*	3316	4915	1657	+	ATA	TAG
PCG	NADH dehydrogenase subunit 1	*nd1*	4896	5799	901	+	ATA	TAA[1]
PCG	NADH dehydrogenase subunit 4L	*nd4l*	5843	6076	233	+	TTG	TAT
PCG	cytochrome b	*cytb*	6054	7192	1097	+	GTC	TAA[1]
tRNA	aspartic acid transfer RNA	*tRNA Asp*	7192	7263	71	+		
tRNA	cysteine transfer RNA	*tRNA Cys*	7250	7310	61	+		
tRNA	phenylalanine transfer RNA	*tRNA Phe*	7310	7369	60	+		
PCG	cytochrome c oxidase subunit II	*coII*	7370	8052	672	+	ATG	TAA[1]
tRNA	tyrosine transfer RNA	*tRNA Tyr*	8040	8102	55	+		
tRNA	tryptophan transfer RNA	*tRNA Trp*	8094	8158	65	+		
tRNA	glycine transfer RNA	*tRNA Gly*	8158	8223	66	+		
tRNA	histidine transfer RNA	*tRNA His*	8216	8274	58	+		
tRNA	glutamine transfer RNA	*tRNA Gln*	8274	8331	57	-		
tRNA	leucine transfer RNA	*tRNA Leu*	8320	8392	73	-		
PCG	ATP synthase F0 subunit 8	*atp8*	8385	8544	104	-	ATG	TAA[1]
tRNA	asparagine transfer RNA	*tRNA Asn*	8544	8602	59	-		
PCG	ATP synthase F0 subunit 6	*atp6*	8582	9242	661	-	ATG	TAA
tRNA	arginine transfer RNA	*tRNA Arg*	9241	9304	62	-		
tRNA	glutamic acid transfer RNA	*tRNA Glu*	9303	9367	65	-		
rRNA	12S ribosomal RNA	*12S rRNA*	9412	10120	798	-		
tRNA	metionine transfer RNA	*tRNA Met*	10118	10180	63	-		
PCG	NADH dehydrogenase subunit 3	*nd3*	10160	10493	307	-	ATT	TAA[1]
tRNA	serine transfer RNA	*tRNA Ser*	10523	10576	53	-		
tRNA	serine transfer RNA	*tRNA Ser*	10648	10700	52	+		
PCG	NADH dehydrogenase subunit 4	*nd4*	10721	12005	1210	+	ATT	TAG
tRNA	threonine transfer RNA	*tRNA Thr*	11996	12058	63	-		
PCG	cytochrome c oxidase subunit III	*coIII*	12046	12833	776	-	ATG	TAA[1]
tRNA	isoleucine transfer RNA	*tRNA Ile*	12877	12937	61	+		
PCG	NADH dehydrogenase subunit 2	*nd2*	12899	13872	833	+	ATA	TAA[1]
tRNA	lysine transfer RNA	*tRNA Lys*	13842	13894	60	+		

[1] Stop codons completed by the addition of 3' A residues to mRNA.

genomes known in Helicoidea, which ranged from 13,798 bp (*Camaena poyuensis*) to 14,795 bp (*Theba pisana*) (Table 2). The mitogenome included: 13 PCGs, 22 tRNA genes and two rRNA genes (Fig. 1, Table 3), typical for most metazoan mitogenomes. The base composition of the *M. cartusiana* mitogenome was: 30.26% A, 37.95% T, 16.94% G and 14.85% C, i.e. with a bias towards A and T (68.21% content of A-T). These values differ from other helicoid species, but fit into the range previously reported for helicoids, especially when compared with the A-T values for *C. virgata* (65.96%) and *H. itala* (66.22%) (Doğan et al. 2020: table S3). The total length of all PCGs was 10,404 bp (74.88% of the entire mitogenome), and they had different start and stop codons, which also vary among helicoid mitogenomes (Table 4). Some of the stop codons TAA were generated by posttranscriptional polyadenylation (as in Groenenberg et

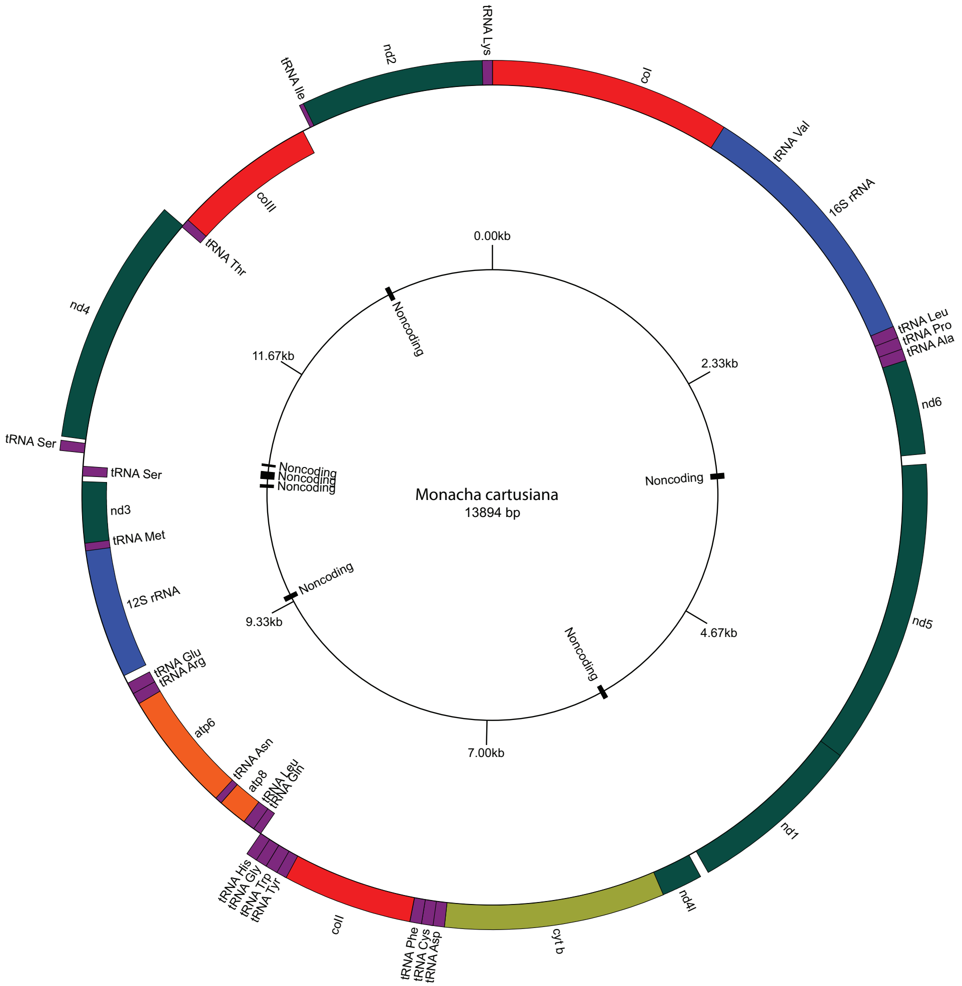

Figure 1. Circular diagram of the mitochondrial genome of *Monacha cartusiana* (GenBank acc. no. MW485067). Genes encoded in the "plus" and the "minus" directions are shown outside and inside the circle, respectively. Particular gene types are marked with different colours: red – PCGs coding I, II, and III subunits of cytochrome c oxidase; green – PCGs coding NADH dehydrogenase family; orange – PCGs coding ATPase family; yellow – sequence coding cytochrome b; purple – tRNAs coding sequences; blue – rRNA coding genes. Noncoding sequences are mapped on a small inner circle. The circular diagram was created with GENOMEVX (Conant and Wolfe 2008).

al. 2012 and Yang et al. 2016). Nine PCGs were encoded in the "plus" direction (*nd1*, *nd2*, *nd4*, *nd4l*, *nd5*, *nd6*, *cytb*, *coI*, *coII*) and four in the "minus" direction (*coIII*, *atp6*, *atp8*, *nd3*). Furthermore, 14 tRNA and one rRNA were encoded in the "plus" direction and eight tRNA and one rRNA in the "minus" direction (Table 3). Additionally, seven intergenic regions (with noncoding sequences) were identified with a total length of 295 bp (the longest was 70 bp while the shortest 19 bp) (Fig. 1). The gene order in

Table 4. Start and stop codons in the mitogenome protein coding genes of helicoid species.

Species	Start codons	Stop codons
Monacha cartusiana	ATA – 3; ATG – 5; ATT – 3; GTC – 1; TTG – 1	TAA – 10; TAG – 2; TAT – 1
Cernuella virgata	ATA – 4; ATG – 4; ATT – 5	TAA – 9; TAG – 4
Helix pomatia	ATA – 1; ATC – 1; ATG – 6; GTG – 3; TTG – 2	TAA – 8; TAG – 5
Cepaea nemoralis	ATA – 5; ATG – 2; ATT – 6	TAA – 2; TAG – 4; TA – 7
Cornu aspersum	ATA – 5; ATG – 6; TTG – 2	TAA – 5; TAG – 5; T – 3
Theba pisana	ATA – 2; ATC – 1; ATG – 2; ATT – 8	TAA/TAG – 12; T – 1
Cylindrus obtusus	ATA – 5; ATG – 4; ATC – 1; GTG – 1; TTG – 2	TAA – 4; TAG – 5; T – 4
Practicolella mexicana	ATC – 1; ATG – 5; ATT – 2; GTG – 2; TTG – 3	TAA – 3, TAG – 4; T – 6
Aegista aubryana	ATA – 6; ATG – 7	TAA/TAG – 11; T – 2
Aegista diversifamilia	ATG – 5; ATT – 3; TTG – 3; TTA – 2	TAA – 5; TAG – 2; TA – 2; T – 4
Camaena cicatricosa	ATA – 5; ATG – 4; ATT – 3; GTG – 1	TAA – 11; TAG – 2
Dolicheulota formosensis	ATG – 4; ATA – 3; ATT – 3; TTG – 2; GTG – 1	TAA – 5; TAG – 2; TA – 6
Mastigeulota kiangsinensis	ATA – 4; ATG – 7; ATT – 1; GTG – 1	TAA – 7; TAG – 6

For references see Table 2.

M. cartusiana mitogenome was exactly the same as in *C. virgata* and *H. itala* (geomitrid species). Yet, the polygyrid *Practicolella mexicana* differed in four places and helicid species in seven (Table 5). The species representing the Camaenidae formed three groups with the same order of genes, but each of these groups differed in gene order from species from Hygromiidae, Geomitridae, Helicidae, and Polygyridae (Table 5).

Phylogenetic analyses of the stylommatophoran mitogenomes (González et al. 2016; Romero et al. 2016) showed them in a well-supported clade among Panpulmonata (with PP and bootstrap values 1 and 99, respectively). Previous mitogenome phylogenies of stylommatophoran superfamilies (Groenenberg et al. 2017; Harasewych et al. 2017; Yang et al. 2019; Doğan et al. 2020) showed a clade of Helicoidea separate from other superfamilies, although mitogenomes of only 11 stylommatophoran superfamilies (Yang et al. 2019) out of 26 listed by Bouchet et al. (2017) are represented in GenBank. According to Bouchet et al. (2017), Helicoidea includes 17 families but hitherto phylogenetic relationships could be analysed only for three or four of them, namely Helicidae, Camaenidae, Geomitridae, and Polygyridae (González et al. 2016; Lin et al. 2016; Minton et al. 2016a; Harasewych et al. 2017; Doğan et al. 2020).

For the phylogenetic analysis, a concatenated alignment of 12 PCGs (excluding *atp8*, because it was too short, too variable, and not annotated in the mitogenome of *Cernuella virgata*) and 2 rRNAs (12S and 16S) was used. The dataset included 19 helicoid species (Table 2) yielding the ML tree shown in Fig. 2. The Bayesian tree (not shown) had the same topology.

The mitogenome of *M. cartusiana* allows to add Hygromiidae to the previous analyses of Helicoidea families. It shows up in a clade with mitogenomes of the geomitrid species, *Cernuella virgata* and *Helicella itala*, confirming the close relationships of two families, i.e., Hygromiidae and Geomitridae (Razkin et al. 2015). The mitogenome of the helicid *Cylindrus obtusus* of the subfamily Ariantinae forms a branch separated from the subfamily Helicinae (Fig. 2). This was also noted in previous phylogenetic analyses (Korábek et al. 2019; Doğan et al. 2020). Moreover, Camaenidae are separated into

Table 5. Gene order in known mitogenomes of helicoid species.

	M. cartusiana	***coI***	***Val***	***16S***	***Leu***	***Pro***	***Ala***	***nd6***	***nd5***	***nd1***	***nd4l***	***cytb***	***Asp***	***Cys***	***Phe***	***coII***	***Tyr***	***Trp***	***Gly***	***His***	***Gln***	***Leu***	***atp8***	***Asn***	***atp6***	***Arg***	***Glu***	***12S***	***Met***	***nd3***	***Ser***	***Ser***	***nd4***	***Thr***	***coIII***	***Ile***	***nd2***	***Lys***
🟩	*C. virgata*	*coI*	*Val*	*16S*	*Leu*	*Pro*	*Ala*	*nd6*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Tyr*	*Trp*	*Gly*	*His*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Ser*	*nd4*	*Thr*	*coIII*	*Ile*	*nd2*	*Lys*
🟩	*H. itala*	*coI*	*Val*	*16S*	*Leu*	*Pro*	*Ala*	*nd6*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Tyr*	*Trp*	*Gly*	*His*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Ser*	*nd4*	*Thr*	*coIII*	*Ile*	*nd2*	*Lys*
🟫	*P. mexicana*	*coI*	*Val*	*16S*	*Leu*	*Pro*	*Ala*	*nd6*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Gly*	*His*	*Tyr*	*Trp*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Ser*	*nd4*	*Thr*	*coIII*	*Ile*	*nd2*	*Lys*
🟥	*H. pomatia*	*coI*	*Val*	*16S*	*Leu*	*Ala*	*nd6*	*Pro*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Tyr*	*Trp*	*Gly*	*His*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Thr*	*coIII*	*Ser*	*nd4*	*Ile*	*nd2*	*Lys*
🟥	*C. aspersum*	*coI*	*Val*	*16S*	*Leu*	*Ala*	*nd6*	*Pro*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Tyr*	*Trp*	*Gly*	*His*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Thr*	*coIII*	*Ser*	*nd4*	*Ile*	*nd2*	*Lys*
🟥	*C. nemoralis*	*coI*	*Val*	*16S*	*Leu*	*Ala*	*nd6*	*Pro*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Tyr*	*Trp*	*Gly*	*His*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Thr*	*coIII*	*Ser*	*nd4*	*Ile*	*nd2*	*Lys*
🟥	*C. obtusus*	*coI*	*Val*	*16S*	*Leu*	*Ala*	*nd6*	*Pro*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Tyr*	*Trp*	*Gly*	*His*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Thr*	*coIII*	*Ser*	*nd4*	*Ile*	*nd2*	*Lys*
🟦	*Ae. aubryana*	*coI*	*Val*	*16S*	*Leu*	*Pro*	*Ala*	*nd6*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Gly*	*His*	*Tyr*	*nd3*	*Trp*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*Ser*	*Ser*	*nd4*	*Thr*	*coIII*	*Ile*	*nd2*	*Lys*
🟦	*Ae. diversifamilia*	*coI*	*Val*	*16S*	*Leu*	*Pro*	*Ala*	*nd6*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Gly*	*His*	*Tyr*	*nd3*	*Trp*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*Ser*	*Ser*	*nd4*	*Thr*	*coIII*	*Ile*	*nd2*	*Lys*
🟦	*D. formosensis*	*coI*	*Val*	*16S*	*Leu*	*Pro*	*Ala*	*nd6*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Gly*	*His*	*Tyr*	*Trp*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Ser*	*nd4*	*Thr*	*coIII*	*Ile*	*nd2*	*Lys*
🟦	*F. koreana*	*coI*	*Val*	*16S*	*Leu*	*Pro*	*Ala*	*nd6*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Gly*	*His*	*Tyr*	*Trp*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Ser*	*nd4*	*Thr*	*coIII*	*Ile*	*nd2*	*Lys*
🟦	*M. kiangsinensis*	*coI*	*Val*	*16S*	*Leu*	*Pro*	*Ala*	*nd6*	*nd5*	*nd1*	*nd4l*	*cytb*	*Asp*	*Cys*	*Phe*	*coII*	*Gly*	*His*	*Tyr*	*Trp*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Ser*	*nd4*	*Thr*	*coIII*	*Ile*	*nd2*	*Lys*
🟦	*C. cicatricosa*	*coI*	*Val*	*16S*	*Leu*	*Pro*	*Ala*	*nd6*	*nd5*	*nd1*	*nd4l*	*cytb*	*Cys*	*Phe*	*coII*	*Asp*	*Tyr*	*Gly*	*His*	*Trp*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Ser*	*nd4*	*Thr*	*coIII*	*Ile*	*nd2*	*Lys*
🟦	*C. poyuensis*	*coI*	*Val*	*16S*	*Leu*	*Pro*	*Ala*	*nd6*	*nd5*	*nd1*	*nd4l*	*cytb*	*Cys*	*Phe*	*coII*	*Asp*	*Tyr*	*Gly*	*His*	*Trp*	*Gln*	*Leu*	*atp8*	*Asn*	*atp6*	*Arg*	*Glu*	*12S*	*Met*	*nd3*	*Ser*	*Ser*	*nd4*	*Thr*	*coIII*	*Ile*	*nd2*	*Lys*

Light blue background shows the same position in gene order as in *M. cartusiana* mitogenome. For gene acronyms (tRNA genes shortened to aminoacid symbol) and references see Table 2.
Colours for the families as in Fig. 2: light blue – Hygromiidae; green – Geomitridae; brown – Polygyridae; red – Helicidae; dark blue – Camaenidae

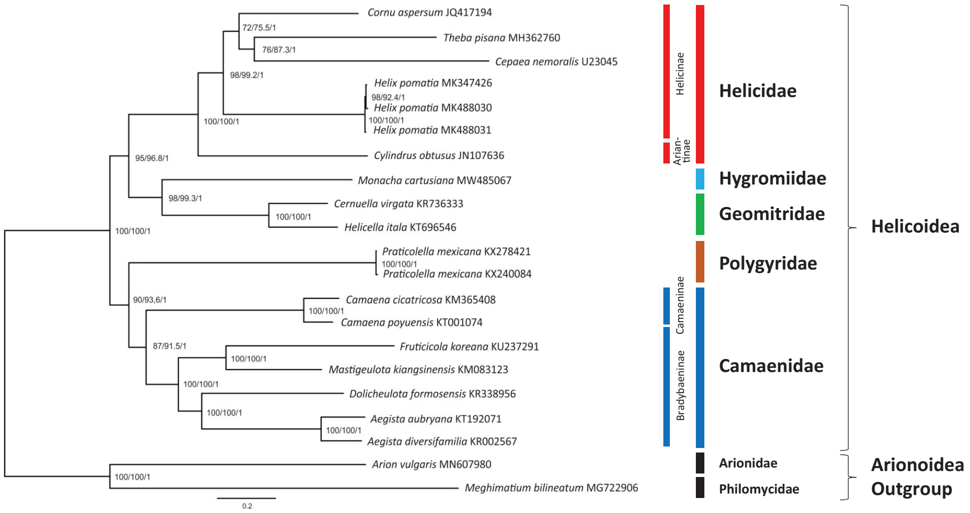

Figure 2. Maximum likelihood (ML) tree of mitochondrial genomes of species representing the superfamily Helicoidea (see Table 1). Mitogenome sequences included all PCGs (except *atp8*) and two rRNA genes were 14,287 positions in length. Ultrafast bootstrap support values (%), SH-aLRT support values (%) and Bayesian posterior probabilities are indicated next to the branches. The tree was rooted with sequences of *Arion vulgaris* (MN607980) and *Meghimatium bilineatum* (MG722906) mitogenomes deposited in GenBank by Doğan et al. (2020) and Yang et al. (2019), respectively.

two clades i.e., Bradybaeninae and Camaeninae, treated frequently as two separate families (Lin et al. 2016; Minton et al. 2016a; Harasewych et al. 2017). Our results agree with the division of Helicidae and Camaenidae into subfamilies (Bouchet at al. 2017). However, the five helicid and seven camaenid species (Table 2, Fig. 2) represent only a tiny fraction of these speciose families. Therefore, more helicoid and stylommatophoran mitogenomes are urgently needed.

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Kelawakaju gen. nov., a new Asian lineage of marpissine jumping spiders (Araneae, Salticidae, Marpissina)

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Abstract

The genus *Kelawakaju* Maddison & Ruiz, **gen. nov.**, is described for a lineage of bark-dwelling Asian marpissine jumping spiders that represent a dispersal to Eurasia separate from that of the *Marpissa-Mendoza* lineage, according to the phylogeny recovered from analysis of four gene regions. All species of *Kelawakaju* are new to science except *Kelawakaju frenata* (Simon, 1901), **comb. nov.**, which is transferred from *Ocrisiona* Simon, 1901. *Kelawakaju frenata* is known from Hong Kong, Guangdong, Guangxi, and likely Taiwan. The five new species are *Kelawakaju mulu* Maddison & Ruiz, **sp. nov.** (type species of *Kelawakaju*, from Sarawak, Malaysia, ♂♀), *K. intexta* Maddison & Ruiz, **sp. nov.** (from Sarawak, ♂), *K. leucomelas* Maddison & Ng, **sp. nov.** (Singapore and Johor Bahru, ♂♀), *K. sahyadri* Vishnudas, Maddison, & Sudhikumar, **sp. nov.** (India, ♂♀), and *K. singapura* Maddison & Ng, **sp. nov.** (Singapore, ♂♀).

Keywords

Classification, Dendryphantini, molecular phylogeny, new genus, new species, Salticinae, Salticoida, taxonomy

Introduction

Jumping spiders of the tribe Dendryphantini diversified into more than 700 known species largely in the Americas (Maddison 2015), but a few lineages reached the Old World: a few genera in the Dendryphantina, one genus in the Synagelina, and two genera in the Marpissina. The two marpissine genera, *Marpissa* C. L. Koch, 1846 and *Mendoza* Peckham & Peckham, 1894, are similar and likely closely related (Logunov 1999), possibly representing a single dispersal into the Palearctic. There is, however, another distinct lineage of the Marpissina in Asia, hidden taxonomically because its one described species has been misplaced to genus and tribe. Simon (1901b) chose the astioid genus *Ocrisiona* Simon, 1901 as the home for his species *O. frenata* Simon, 1901, described from Hong Kong. The type species and others of the primarily Australasian *Ocrisiona* (Astioida: Viciriini) are elongate and flat-bodied, as is *O. frenata*, but the latter species is a marpissine rather than an astioid, as we show here. Field work has revealed that *O. frenata* is not alone but is part of a small radiation of tree trunk dwelling marpissines in tropical Asia. We here describe the new genus *Kelawakaju*, gen. nov., to contain *K. frenata*, comb. nov., and five new species.

Materials and methods

Spider specimens examined for this study are stored in the University of British Columbia Spencer Entomological Collection, Canada (**UBCZ**), the Lee Kong Chian Natural History Museum, Singapore (**LKCNHM**, https://lkcnhm.nus.edu.sg), the Research Collections at National Centre for Biological Sciences, Bengaluru, Karnataka, India (**NCBS**, http://biodiversitycollections.in), and the Centre for Animal Taxonomy and Ecology, Christ College, Thrissur, Kerala, India (**CATE**).

Preserved specimens were examined under both dissecting microscopes and a compound microscope with reflected light. Drawings were made with a drawing tube on a Nikon ME600L compound microscope. Most photographs of living specimens were made with either a Pentax Optio 33WR digital camera with a small lens glued to it for macro capability or an Olympus OM-D E-M10 II camera with 60 mm macro lens.

All measurements are given in millimeters. Descriptions of color pattern are based on the alcohol-preserved specimen. Carapace length was measured from the base of the anterior median eyes not including the lenses to the rear margin of the carapace medially; abdomen length to the end of the anal tubercle. The following abbreviations are used: **PLE**, posterior lateral eyes; **RTA**, retrolateral tibial apophysis.

Molecular data was gathered for four gene regions by traditional Sanger PCR methods and combined with previously published data to compose a dataset of 36 taxa (Table 1) including 32 species of marpissoids (14 Marpissina, 3 Itatina, 8 Dendryphantina, 4 Synagelina, 3 Ballini) and 4 outgroups (1 Plexippini, 1 Baviini, 2 Astioida). Preservation, DNA extraction, PCR, and sequencing of nuclear 28S and Actin 5C and mitrochondrial 16SND1 and COI followed the protocols of Zhang and Maddison (2013) and Maddison et al. (2014). Alignments were done by MAFFT with the L-INS-i option (Katoh and Standley 2013), with edges of coding regions of Actin and ND1 refined by hand using amino acid translation in Mesquite 3.61 (Maddison and Maddison 2021) and comparison to sequences with known boundaries. The Actin intron aligned so poorly that it was excluded entirely from phylogenetic analyses (Maddison et al. 2014).

Maximum-likelihood phylogenetic analyses were performed with IQ-TREE version 1.6.7.1 (Nguyen et al. 2015) using the Zephyr 3.1 package (Maddison and Maddison 2020) in Mesquite 3.7 (Maddison and Maddison 2021). The four genes were concatenated and set into seven partitions expected to have potentially different models of evolution: 28S, 16S (including other non-coding parts of 16SND1), mitochondrial codon positions 1 and 2, mitochondrial codon position 3, Actin codon position 1, Actin 2, and Actin 3. IQ-TREE was run with the options -m TESTMERGE -spp to allow the partitions to be merged and their models chosen according to the Bayesian information criteria. (The best partition scheme united Actin 1 and 2 to yield six partitions, with models 28S: TIM3+F+I+G4, 16S: GTR+F+I+G4, mitochondrial 1, 2: TIM2+F+I+G4, mitochondrial 2: HKY+F+I+G4: Actin 1 + 2: SYM+I, Actin 2: JC, Actin 3: K3Pu+F+G4.) The maximum likelihood tree was sought with 50 search replicates, and repeatability assessed with 1000 standard bootstrap replicates.

Alignments and trees are deposited in the Dryad data repository (http://dx.doi.org/10.5061/dryad.mw6m9060r).

Results

Molecular phylogenety

The reconstructed phylogeny (Fig. 1) gives support for *Kelawakaju* being a monophyletic group within the Marpissina, and distinct from other genera, including the *Marpissa*, another known Eurasian marpissine. As expected, the Dendryphantini and each of its subtribes are monophyletic. The two species of *Kelawakaju* are monophyletic together, distinct from described marpissine genera, and placed as a relatively deep branching lineage in the Marpissina, although the bootstrap support is not high. These results suggest that marpissines dispersed from the Americas (where most marpissoid diversity lies; Maddison 2015) into the Old World at least twice, once for *Marpissa-Mendoza*, and once for *Kelawakaju*.

The phylogenetic results emphasize the difficulties faced in recognizing salticid relationships from general appearances. When one author (WPM) first collected members of the *K. mulu* group, he recorded them as baviines, and assumed that their resemblance to the marpissine *Balmaceda* Peckham & Peckham, 1894 was convergence for trunk-dwelling. It was only with the molecular data that their identity as marpissines became clear. When other authors (EHV, AVS) first collected *K. sahyadri*, they also thought it likely to be a baviine. Simon (1901a, b) considered *K. frenata* congeneric with the viciriine *Ocrisiona*. It is indeed easy to confuse various marpissines, baviines, viciriines, and bredines, for convergence has given them similar body forms.

Table 1. Specimens and GenBank accession numbers of four gene regions analyzed. Accession numbers with * indicate already published (Hedin and Maddison 2001; Maddison and Hedin 2003; Maddison and Needham 2006; Maddison et al. 2007, 2008, 2014; Vink et al. 2008; Bodner and Maddison 2012; Ruiz and Maddison 2015; Maddison 2016; Maddison and Szűts 2019).

Species	Specimen ID	Locality	28S	Actin	16SND1	CO1
Non-marpissoid outgroups						
Evarcha proszynskii Marusik & Logunov, 1998	d096/S232	Canada: British Columbia	DQ665765*	EU522704*	DQ665723*	AY297379*
Bavia cf. *intermedia* (Karsch, 1880)	d079	Malaysia: Sabah	EU815490*	KM032958*	KM032925*	EU815603*
Myrmarachne sp.	d162	Malaysia: Pahang	EU815507*	JX145837*	EU815565*	EU815616*
Simaetha sp.	d027	Australia: Queensland	EU815477*	JX145839*	EU815546*	EU815592*
Ballini						
Afromarengo sp.	MRB262	Gabon: Ngounié: Waka National Park	JX145758*	JX145842*	JX145905*	JX145682*
Mantisatta longicauda Cutler & Wanless, 1973	S209	Philippines: Luzon	AY297270*		AY296689*/AY297333*	AY297399*
Peplometus sp.	d199	Ghana: N. of Cape Coast, Kakum Forest	EU815515*	JX145843*	EU815572*	EU815621*
Dendryphantini: Synagelina						
Admestina sp.	GR057	U.S.A.: Mississippi	OP605970	OP700690	OP700674	
Attidops youngi (Peckham & Peckham, 1888)	S97	U.S.A.: Missouri	AF327933*		AF327961*/AF328020*	AF327990*
Peckhamia sp.	GR137	Dominican Republic: Barahona	OP605980	OP700699	OP700683	
Synageles sp.	GR056	U.S.A.: Mississippi	OP605985	OP700705	OP700689	
Dendryphantini: Dendryphantina						
Dendryphantes hastatus (Clerck, 1757)	d043	Poland: Siedlce	EF201646*	KY200848*	KM032927*	KM033228*
Ghelna canadensis (Banks, 1897)	d005	U.S.A.: North Carolina	EF201651*	EU522708*	OP700675	
	d391	U.S.A.: North Carolina				KT462689
Hentzia grenada (Peckham & Peckham, 1894)	GR064	USA: Florida	OP605971	OP700691	OP700676	
Phanias albeolus (Chamberlin & Ivie, 1941)	GR049	Canada: British Columbia	OP605981	OP700700	OP700684	
Phidippus otiosus (Hentz, 1846)	GR073	USA: Florida	OP605982	OP700701	OP700685	
Rhene sp.	MRB081	China: Guangxi	OP605984	OP700704	OP700688	
Sassacus papenhoei Peckham & Peckham, 1895	S295	U.S.A.: Arizona	AF327953*		AF327982/AF328041*	AF328012*
Zygoballus rufipes Peckham & Peckham, 1885	S142	U.S.A. and Panama	AF327944*		AF327972*/AF328031*	AF328002*
Dendryphantini: Itatina						
Itata sp. A	S181	Ecuador: Manabi	AF327932*		AF327960*/AF328019*	AF327989*
Itata sp. B	GR107	Ecuador: Napo	OP605972	OP700692		
Itata sp. C	ECU11-4724	Ecuador: Orellana:Yasuní	OP605973		OP700677	

Species	Specimen ID	Locality	28S	Actin	16SND1	CO1
Dendryphantini: Marpissina						
Kelawakaju mulu sp. nov.	SWK12-2610	Malaysia: Sarawak: Mulu	OP605974		OP700678	OP606004
Kelawakaju frenata (Simon, 1901)	d224	China: Guangxi	JX145769*		JX145911*	JX145688*
	GR048	China: Guangxi		OP700693		
Maevia inclemens (Walckenaer, 1837)	d465	USA: Tennessee		OP700694		
	GR126	USA: North Carolina	OP605975			
Maevia intermedia Barnes, 1955	S87	USA: Alabama	AY297269*		AY296688*/AY297332*	AY297398*
Marpissa lineata (C. L. Koch, 1846)	GR055	USA: Mississippi	OP605977	OP700696	OP700680	
Marpissa nivoyi (Lucas, 1846)	GR145	Spain: Sitges	OP605978	OP700697	OP700681	
Marpissa pikei (Peckham & Peckham, 1888)	S294/S299	USA: Arizona	AF327936*		AF327964*/AF328032*	AF327993*
Marpissa aff. *pikei* (Peckham & Peckham, 1888)	GR141	Dominican Republic: Pedernales	OP605976	OP700695	OP700679	
Metacyrba pictipes Banks, 1903	GR140	Dominican Republic: Pedernales	OP605979	OP700698	OP700682	
Metacyrba taeniola (Hentz, 1846)	S298	USA: Arizona	AY297271*		AY296690*/AY297334*	
Platycryptus californicus (Pkm & Pkm, 1888)	d316	Canada: British Columbia	KM033194*	KM032960*		KM033229*
	d158	Canada: British Columbia			OP700686	
Platycryptus undatus (De Geer, 1778)	S72	U.S.A.: Florida	AF327935*		AF327963*/AF328022*	AF327992*
	d462	Canada: Ontario: St. Williams		OP700702		
Psecas cf. *viridipurpureus* (Simon, 1901)	S227	Ecuador: Sucumbios	AY297273*		AY297336*	AY297400*
Psecas sp.	GR124	Ecuador: Napo	OP605983	OP700703	OP700687	

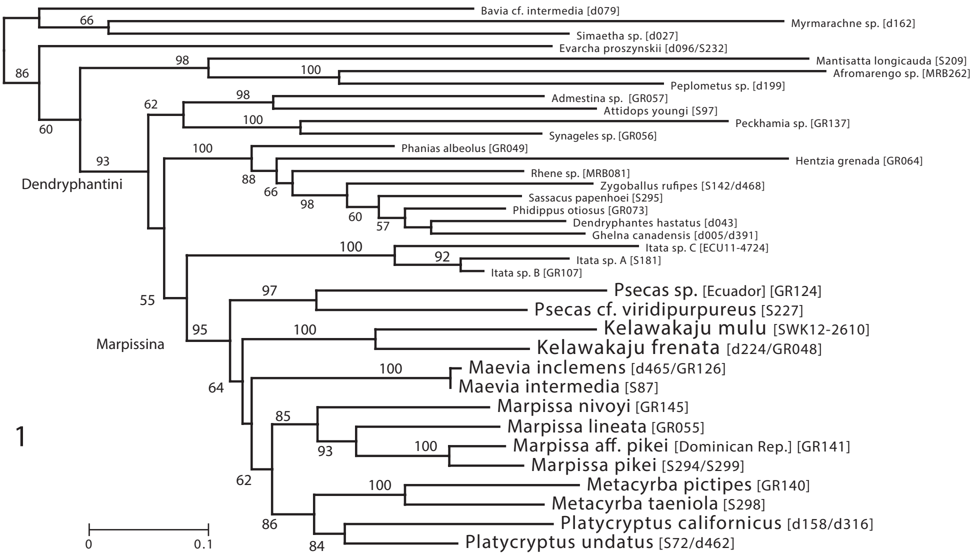


Figure 1. Maximum likelihood phylogeny of Dendryphantini showing placement of *Kelawakaju* species as a distinct lineage in the Marpissina. Based on 28S, Actin 5C, 16SND1, COI gene regions; numbers indicate percentage of 1000 bootstrap replicates showing clade.

Taxonomy

Kelawakaju Maddison & Ruiz, gen. nov.

https://zoobank.org/1A91FAF6-5C6F-4AAB-A770-2395DE6CCAF3

Type species. *K. mulu* Maddison & Ruiz, sp. nov.

Species included.

- *K. mulu* species group:
  - *Kelawakaju mulu* Maddison & Ruiz, sp. nov.
  - *Kelawakaju intexta* Maddison & Ruiz, sp. nov.
- *K. singapura* species group:
  - *Kelawakaju singapura* Maddison & Ng, sp. nov.
- *K. frenata* species group:
  - *Kelawakaju frenata* (Simon, 1901)
  - *Kelawakaju leucomelas* Maddison & Ng, sp. nov.
  - *Kelawakaju sahyadri* Vishnudas, Maddison, & Sudhikumar, sp. nov.

Etymology. The name means tree spider in the Berawan language from the area of Long Terawan, Sarawak (*kelawak* = spider; *kaju* or *kajuh* = tree; Syria Lejau Malang, pers. comm.), where the first specimens of *K. mulu* were found. To be treated grammatically as feminine.

Diagnosis. Elongate and flat-bodied salticids, unusual among marpissines for the elongated or enlarged male chelicerae. Retrolateral tibial apophysis of palp long, blade-like, more or less straight and parallel to axis of palp. Embolus relatively short among marpissines, arising more or less terminally on the bulb (9–12 o'clock in ventral view of left palp). Markings cryptic on tree trunks, either mottled or with low-contrast longitudinal bands.

Description. ***Carapace*** flat, narrower (*K. mulu* group, Figs 10, 11) to broader (*K. leucomelas*, Fig. 14). Lower part of the thorax in some species with 1–3 distinct narrow vertical lines of pale scales (*K. mulu*: Fig. 27; *K. intexta*: Fig. 32; *K. singapura*: Figs 43, 45), resembling similar stripes in the baviine *Piranthus* Thorell, 1895 (Maddison et al. 2020: fig. 263) and the gophoine *Cotinusa* Simon, 1900 (Rubio and Baigorria 2016). ***Chelicerae*** with seta-bearing tubercles on paturon of males and some females (Figs 2–4). Males of all but two species have narrow stripes of white scales on the front face of the chelicerae, forming an inverted V (Figs 3, 4, 74, 79, 83). Two promarginal teeth and one retromarginal tooth (sometimes with a second cusp, Fig. 6). ***Palp's*** RTA a long blade. Embolus appears freely movable, separate from functional tegulum. Cymbium modified at ventral-retrolateral-proximal corner (e.g., Figs 17, 21, 47). ***Abdomen*** long and narrow.

We recognize three species groups in the genus.

Kelawakaju mulu species group

The *mulu* species group includes *K. mulu*, *K. intexta*, and a third as-yet-undescribed species from Singapore. They are smaller-bodied than other *Kelawakaju*, with mottled markings, and narrow chelicerae that project forward in the male. The embolus is narrow and forms a smooth curve bending toward the retrolateral. The lower part of the thorax has three vertical stripes of pale scales on each side. Epigynal openings are delicate and the edges difficult to discern (Fig. 18). Retromarginal tooth of chelicera with small second cusp basally (Figs 5, 6). Members of this group may prefer more shaded habitats than those of the *frenata* group, having been found only inside forests.

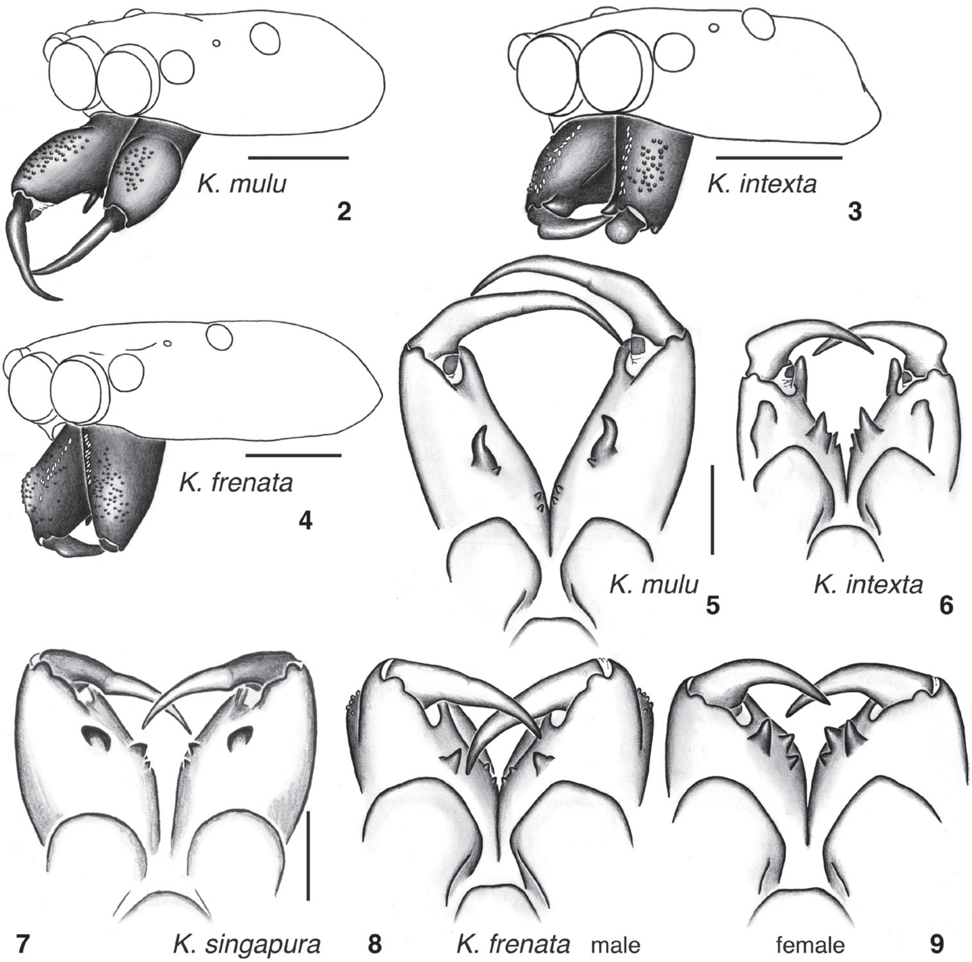
Kelawakaju mulu Maddison & Ruiz, sp. nov.

https://zoobank.org/C1730DAC-227A-4384-B25D-CBDD46B37E76
Figs 2, 5, 10, 16–20, 23–28

Type material. ***Holotype*:** male (SWK12-2610) in UBCZ from Malaysia: Sarawak: Mulu Nat. Pk., Summit Trail near Camp 1, 4.0486°N, 114.8610°E to 4.0483°N, 114.8614°E, 270 m elev., 21 March 2012, Maddison/Piascik/Ang WPM#12-072. ***Paratype*:** female (SWK12-2639) in UBCZ from Malaysia: Sarawak: Mulu Nat. Pk., Summit Trail near Camp 1, 4.0480°N, 114.8626°E to 4.0478°N, 114.8630°E, 290–320 m elev., 22 March 2012, Piascik/Ang/Andyson WPM#12-077.

Etymology. From the name of the type locality (a noun in apposition).

Diagnosis. Dark with only a dusting of golden scales, unlike the similar but more thoroughly scale-covered *K. intexta* (Figs 23–28 vs. 29–34). Embolus shorter than that of *K. intexta*, arising at 11 o'clock (Figs 16 vs. 22).



Figures 2–9. Chelicerae of *Kelawakaju* species **2–4** oblique view with carapace **5–9** ventral view **2** *K. mulu* male holotype **3** *K. intexta* male holotype **4** *K. frenata* male from Guangxi **5** *K. mulu* male holotype **6** *K. intexta* male holotype **7** *K. singapura* male holotype **8** *K. frenata* male from Guangxi **9** *K. frenata* female from Guangxi. Scale bars: 1.0 mm.

Description. Male (based on holotype). Carapace length 2.85; abdomen length 3.05. ***Carapace*** dark brown, with white scales around cephalic region, between AME and sparse on thoracic region. ***Clypeus*** very narrow. ***Chelicera*** dark brown, elongate and projected, with a line of white scales on the prolateral face. Retromarginal tooth with two cusps, the more lateral long and curved (Fig. 5). ***Palp*** with elongate RTA. Embolus narrow and curved, but short, arising distally on the tegulum. Endite subrectangular, with no projection, dark brown. Labium dark brown and sternum light brown, with depressions along coxae I. ***Leg*** I light brown, with mid patella, mid tibia, proximal area of metatarsus and entire tarsus yellow. Legs II–IV yellow. Length of femur I 2.10, II 1.70, III 1.40, IV 1.65; patella + tibia I 3.10, II 2.40, III 1.65, IV 2.35; metatarsus + tarsus I 1.85, II 1.75, III 1.50, IV 1.70. Leg spination reduced: femur I d0, p0-0-1-0 (or p0-0-2-0), II d1-1-0, p0-0-1-0, III 0, IV d1-1-0, r0-0-1-0; patella I–IV 0; tibia I v2-2-2 (asymmetrical), II v1r-1r-1p, III–IV 0; metatarsus I–II v2-2, III 0, IV v0-0-1p. ***Abdomen*** dorsally dark brown, with two transverse wide light stripes, and a third over anal tubercle; ventrally gray.

Female (based on paratype SWK 12-2639). Carapace length 2.7; abdomen length 3.55. Color as in male, except when mentioned. ***Chelicera*** light brown. Retromarginal tooth with two cusps, the distal one almost twice the size of the other, both acute. ***Legs*** II–IV with narrow stripes of white scales. Length of femur I 1.90, II 1.50, III 1.45, IV 1.85; patella + tibia I 2.60, II 1.90, III 1.75, IV 2.60; metatarsus + tarsus I 1.40, II 1.30, III 1.60, IV 1.90. Leg spines as in male, except for femur III, as in II. ***Abdomen*** as in male, except for stripes, medially interrupted; ventrally white, with two longitudinal dark brown stripes extending from booklungs to spinnerets. ***Epigyne*** with a pair of small copulatory openings distant from the posterior border, which has a medial excavation; internally, copulatory ducts fuse with glandular portions, spiral backwards and enter the large spermathecae, from which fertilization ducts emerge.

Natural history. Both specimens were collected on tree trunks on a forested slope.

Kelawakaju intexta Maddison & Ruiz, sp. nov.

https://zoobank.org/58AE0276-1E71-45DA-AAFB-EAD822AE60F3

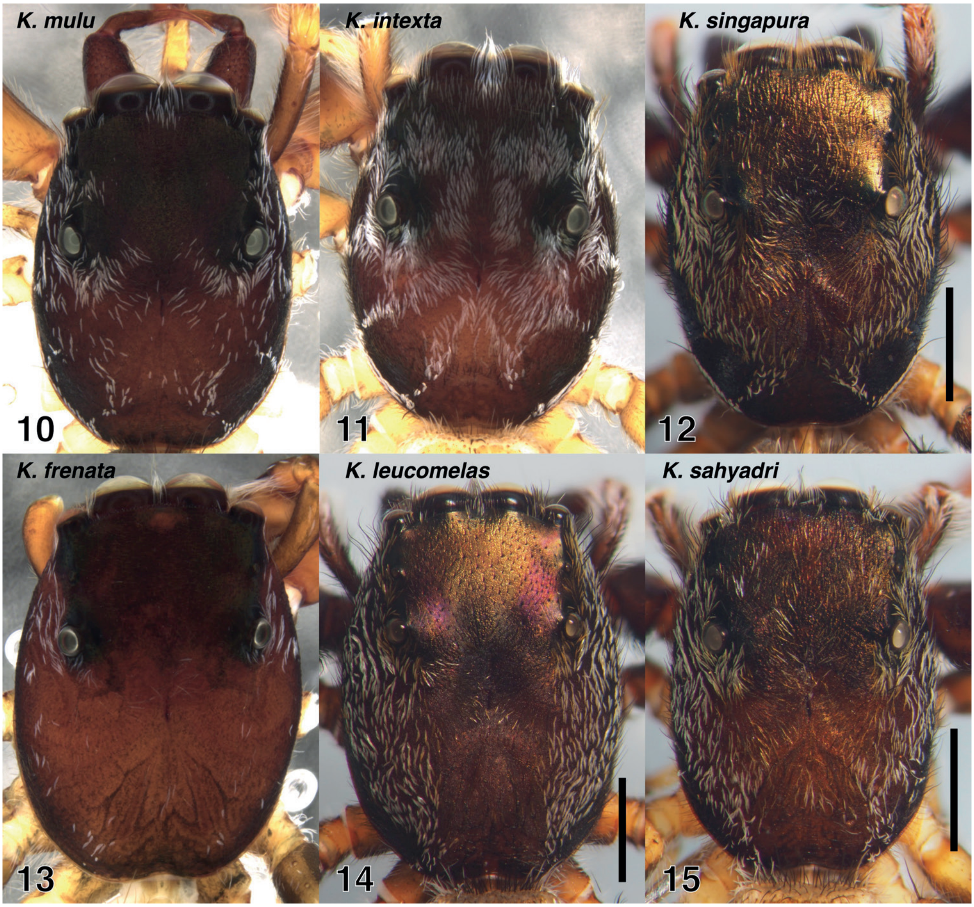
Figs 3, 6, 11, 21, 22, 29–34

Type material. *Holotype*: male (SWK12-3752) in UBCZ from MALAYSIA: Sarawak: Lambir Hills Nat. Pk., headquarters area, 4.197 to 4.198°N 114.0400 to 114.0402°E, 50 m elev., 30 March to 6 April 2012 Maddison/Piascik/Ang WPM#12-104. ***Paratype*:** male (SWK12-0523) in UBCZ from MALAYSIA: Sarawak: Bako Nat. Pk. Ulu Assam Trail, 1.712°N, 110.445°E to 1.713°N, 110.448°E, 30–80, m elev., 8 March 2012, Maddison/Piascik/Ang/Lee WPM#12-005.

Etymology. Latin, interwoven, referring to the textile-like pattern of coloured scales on the body.

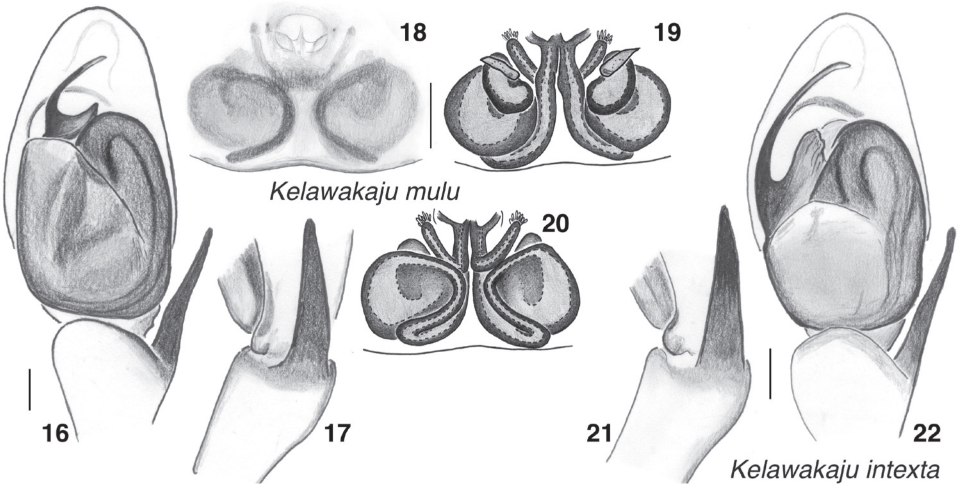
Diagnosis. Body covered with a dense and intricate pattern of pale scales, white on the abdomen and slightly golden on the carapace (Figs 29, 32), and thus paler in appearance than *K. mulu*. Embolus arising at 9 to 10 o'clock, longer than in any other *Kelawakaju* (Fig. 22).

Description. Male (based on holotype). Carapace length 2.45; abdomen length 3.45. ***Carapace*** dark brown, with white scales on cephalic region, sparse on thoracic region and with line of white scales along borders of carapace. ***Clypeus*** very narrow. ***Chelicera*** dark brown, slightly projected, with mastidion. Retromarginal tooth with two cusps, the more lateral larger (Fig. 6). ***Palp*** light brown. RTA elongate. Embolus



Figures 10–15. Carapaces of *Kelawakaju* males **10** *K. mulu* holotype **11** *K. intexta* holotype **12** *K. singapura* holotype **13** *K. frenata* from Guangxi, Dongxing **14** *K. leucomelas* holotype **15** *K. sahyadri* holotype. Scale bars: 1.0 mm.

narrow, gently curving from its base, longer than half the length of the tegulum, arising prolaterally from the tegulum. Endite dark brown. Labium dark brown and sternum light brown. ***Leg*** I dark brown, with proximal portion of femur, mid tibia and metatarsus light brown, and tarsus yellow; II–IV light brown. Length of femur I 2.10, II 1.70, III 1.40, IV 1.65; patella + tibia I 3.10, II 2.40, III 1.65, IV 2.35; metatarsus + tarsus I 1.85, II 1.75, III 1.50, IV 1.70. Leg spination reduced: Femur I–II d1-1-0, p0-0-1, III d1-1-1, p0-0-1, IV d1-1-1, r0-0-1, patella I–IV 0, tibia I v2-2-2, II v1r-1r-1p, III–IV 0, metatarsus I–II v2-2, III 0, IV v0-0-1p. ***Abdomen*** dorsally with three pairs of dark marks with dark scales, among light areas with white scales; entirely covered by scutum; ventrally gray, with dark brown ring around spinnerets. Spinnerets yellow.



Figures 16–22. *Kelawakaju mulu* species group, genitalia **16–20** *K. mulu* **16** holotype male palp, ventral **17** same, retrolateral **18** paratype female SWK12-2639 epigyne, ventral **19** same, vulva, dorsal **20** same, ventral **21, 22** *K. intexta* holotype male palp **21** retrolateral **22** ventral. Scale bars: 0.1 mm.

Figures 23–28. *Kelawakaju mulu* **23–25** holotype male SWK12-2610 **26–28** paratype female SWK12-2639. Scale bars: 1.0 mm.

Figures 29–34. *Kelawakaju intexta* **29–31** holotype male SWK12-3752 **32–34** paratype male SWK12-0523. Scale bars: 1.0 mm.

Female unknown.

Natural history. The paratype from Bako was found along a trail in a forest.

Kelawakaju singapura species group

The *singapura* species group includes only *K. singapura*, distinctive for the robust male chelicerae, short and stout embolus, and the long palp tibia (longer than the tibial apophysis). It is larger-bodied, like the *frenata* group, but has a longer ocular quadrangle, and the abdominal markings are inverted compared to the *frenata* group: dark laterally, paler medially, similar to *K. intexta* of the *mulu* group. There is no clear indication to which of the other two groups *K. singapura* is more closely related, and hence we keep it separate.

Kelawakaju singapura Maddison & Ng, sp. nov.

https://zoobank.org/418101EA-5EED-4C48-87C7-5411F4FDF216
Figs 7, 12, 35–45

Type material. ***Holotype***: male (JK.21.08.02.0001) in LKCNHM from Singapore: Labrador Nature Reserve, 1.2653°N, 103.8019°E, J.K.H. Koh & P.Y.C. Ng, 2 August 2021. ***Paratypes***: One female (JK.21.05.14.0001) in LKCNHM from Singapore:

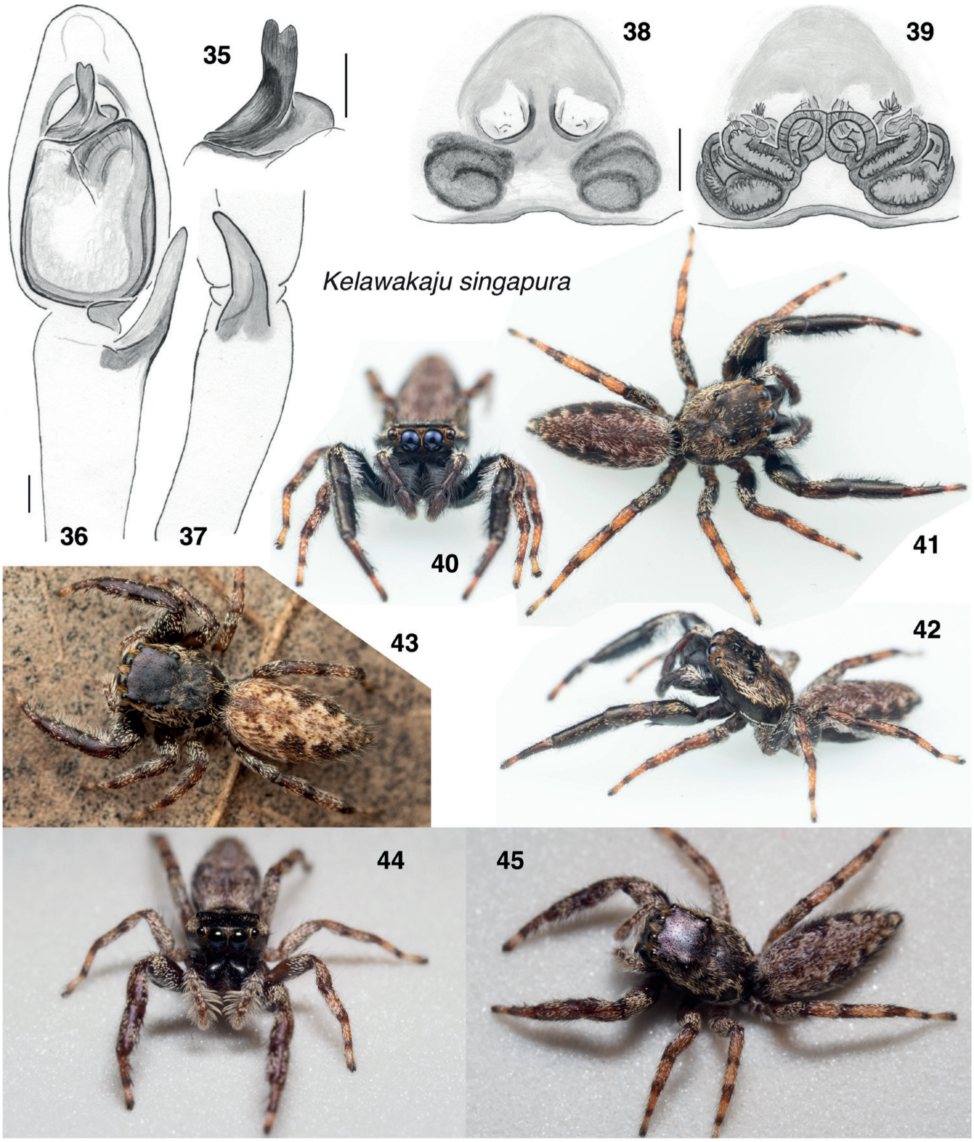
Labrador Nature Reserve, 1.2664°N, 103.8014°E, J.K.H. Koh & P.Y.C. Ng, 14 May 2021. One male (90.10.21.0002) in LKCNHM from Singapore: Simpang, 1.44°N, 103.85°E, J.K.H. Koh, 21 October 1990. One female (AS19.0023) in UBCZ from Singapore: Adam Road, 1.336°N, 103.816°E, 10 m elev., 1–2 June 2019, W. Maddison & P.Y.C. Ng WPM#19-030.

Etymology. From name of the type locality, Singapura in the Malay language, a noun in apposition.

Diagnosis. Distinctive for the abdomen's central pale longitudinal band with wavy edge (Figs 41, 43, 45), short and stout embolus (Figs 35, 36), long tibia on the male palp (Figs 36, 40), and broad rounded retromarginal tooth on the male chelicera (Fig. 7). The male's chelicerae are relatively more robust than in other species, which in contrast have narrower and more projecting or diverging chelicerae.

Description. Male (based on holotype). Carapace length 3.1, width 2.3; abdomen length 3.9. ***Carapace*** (Figs 12, 41, 42): Distinctly wider just behind PLE. Depressed around fovea. Integument black to very dark brown. Thorax with dark setae near lower margin, interrupted by a fine vertical line of pale scales on each side at posterior corner; upper thorax clothed with pale scales; a few scales in ocular quadrangle. Narrow band of white scales along margin posterior to PLE. ***Clypeus*** narrow, dark, with black hairs. ***Chelicerae*** projecting only slightly, robust. Dark brown, with black hairs, many of which arise from tubercles. Retromarginal tooth a broad rounded flange, broadening from base. ***Palp*** tibia long. Embolus erect but short, broad, bifid at tip (Fig. 35). Integument black to brown, with black setae except white setae on last third of femur. Long black setae project laterally along length of tibia (not as a narrow brush). Endite subrectangular, with no projection, dark brown. ***Legs*** medium to dark brown. First leg dark brown except slightly paler at base of patella, which has white setae, and the honey-coloured tarsus. Patella with some white scales above and fringe of white hairs below, which continues onto the distal portion of the femur. Posterior legs with somewhat annulate markings. Length of femur I 2.0, II 1.5, III 1.5, IV 1.6; patella + tibia I 3.0, II 2.1, III 1.7, IV 2.5; metatarsus + tarsus I 1.8, II 1.4, III 1.6, IV 1.8. Leg spination reduced: femur I d0-1-0 (or 0-1-1), p0-2-0, II d1-1-1, p0-0-1, III d1-1-1, p0-0-1, IV d1-1-0, r0-0-1; patella I–IV 0; tibia I v2-2-2 (asymmetrical), II v1r-1r-2, III v0-0-1p, IV v0-0-1p; metatarsus I–II v2-2, III v0-0-3, IV v0-0-1p. ***Abdomen*** narrow. Dorsum with a medial pale band having scalloped edges; darker laterally.

Female (based on specimen AS19.0023). Carapace length 3.2, width 2.2; abdomen length 3.9. ***Carapace*****:** As in male, but not quite so wide, and with two fine vertical lines of pale scales on lower posterior thorax (Figs 43, 45). ***Clypeus*** narrow, dark, with black hairs. ***Chelicerae*** black to brown, with black hairs. Two promarginal and one unident retromarginal tooth, similar to those of *K. frenata* (Fig. 9). ***Legs*** honey-coloured to dark brown, first pair darker, posterior somewhat annulate. Length of femur I 1.7, II 1.5, III 1.4, IV 1.7; patella + tibia I 2.4, II 1.9, III 1.7, IV 2.6; metatarsus + tarsus I 1.5, II 1.4, III 1.5, IV 1.8. Leg spination reduced: femur I d1-1-0, p0-1-0, II d1-1-0, p0-0-1, III d1-1-1, p0-0-1, IV d1-1-0, r0-0-1; patella I–IV 0; tibia I v2-2-2 (asymmetrical), II v1r-1r-2, III v0-0-1p, IV v0-0-1p; metatarsus I–II v2-2, III v0-0-2, IV v0-0-1p. ***Abdomen*** as in male. ***Epigyne*** with openings crescent-shaped, at posterior and medial side of pale desclerotized patch.



Figures 35–45. *Kelawakaju singapura* **35** holotype male JK.21.08.02.001 embolus, ventral **36** paratype male JK.90.10.21.0002 palp, ventral **37** same, retrolateral **38** paratype female AS19.0023 epigyne, ventral **39** same, vulva, dorsal **40–42** holotype male **43** paratype female JK.21.05.14.0001 **44, 45** paratype female AS19.0023. Scale bars: 0.1 mm.

Natural history. The holotype and females from the type locality were found under bark of both small and large trees in open areas at the edge of coastal forest. Female AS19.0023 was found under bark of large tree in roadside clearing.

Kelawakaju frenata species group

The *frenata* species group includes the relatively large-bodied *K. frenata*, *K. leucomelas*, and *K. sahyadri*. They differ from other *Kelawakaju* in having pale longitudinal bands on the sides of the body, a proportionately shorter ocular quadrangle, and longer first legs in the male. The male chelicerae diverge but do not project as forward as in the *mulu* group. A narrow band of white scales descends along the front face of the male chelicerae (Figs 4, 73, 79, 83), also seen in *K. intexta*. As in *K. singapura*, the embolus is terminal on the bulb, and more or less erect, similar to those of many Dendryphantina. Two to three macrosetae on anteriolateral face of first femur are displaced ventrally and basally toward the middle of that face (as in *Padilla* Peckham & Peckham, 1894 and *Padillothorax* Simon, 1901 [Maddison et al. 2020], and more so than in *K. singapura*). *Kelawakaju sahyadri* and *K. leucomelas* have been found on large trees exposed in clearings.

Kelawakaju frenata (Simon, 1901), comb. nov.

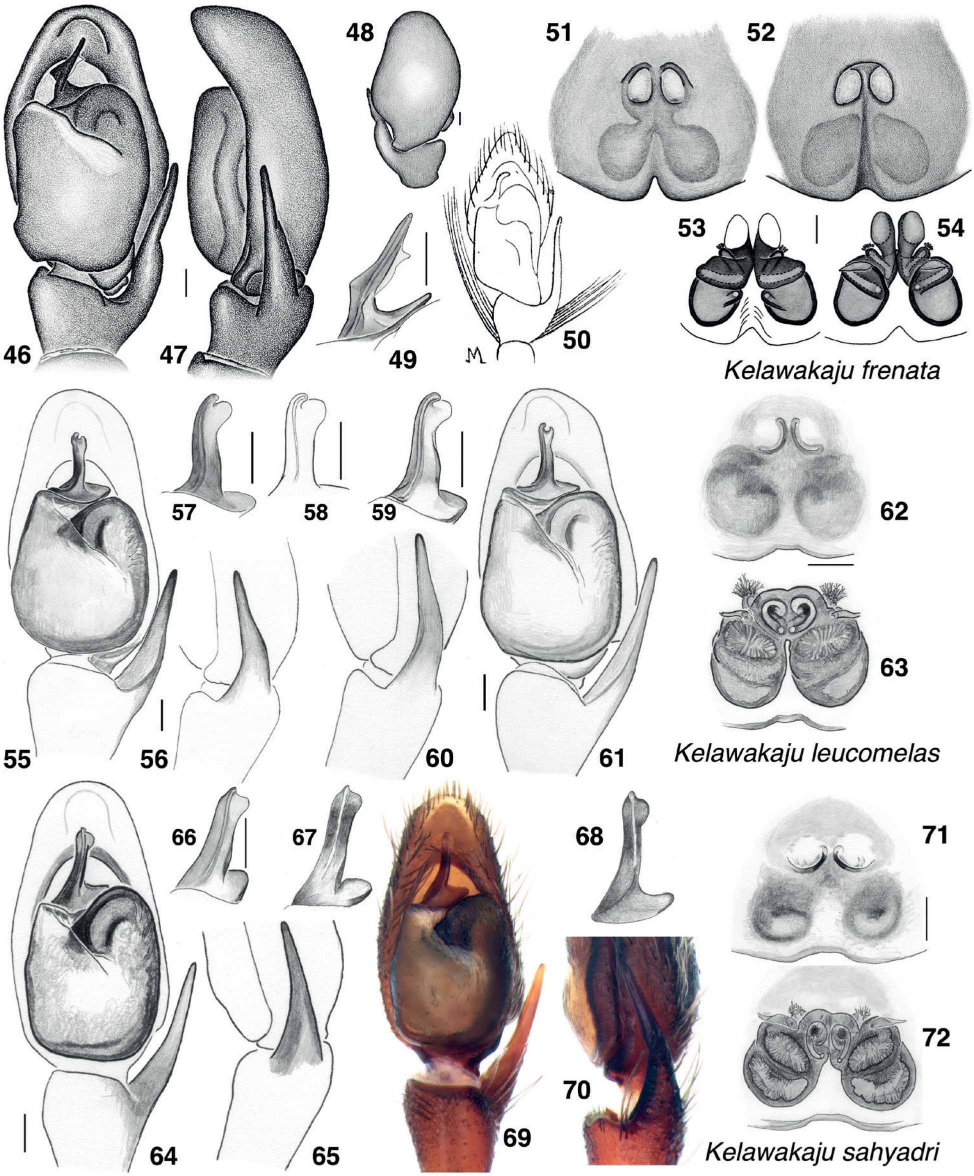
Figs 4, 8, 9, 13, 46–54, 73–78

Ocrisiona frenata Simon, 1901.

Notes. The type specimen of *Ocrisiona frenata* Simon, 1901 has not been found, neither in the Oxford Natural History Museum (O. Pickard Cambridge collection; Simon 1901b) nor in the MNHN (Paris). Nonetheless, the application of the name is reasonably secure, as Simon's figure (1901a: fig. 730, shown here in Fig. 50 reversed so that the right palp appears as the left) and description (1901b) match well specimens from the type locality here illustrated (Hong Kong, Fig. 49) and nearby Guangxi (Figs 46–48). Simon's figure shows clearly the distinctive tibial apophysis of *Kelawakaju*, and the general conformation of this species group. The critical details of the embolus are unclear in Simon's figure, and thus there remains the possibility of two very similar species at the type locality. However, at no locality have we seen two different species sympatric from the same species group, and the many photographs on iNaturalist labeled as "*Ocrisiona frenata*" from Hong Kong are credibly conspecific. Because a good case can be made for the identity of the species, and there is still hope that the type may be found, we will not designate a neotype at this time. This species was labelled "marpissine indet. [China]" in Bodner and Maddison's (2012) molecular phylogeny; that specimen (voucher d224) was lost in the Butantan fire.

Diagnosis. Differs from other *Kelawakaju* in the embolus bending suddenly toward the retrolateral, the epigynal atria with sclerotized edge both anteriorly and posteriorly (not just medially or posteriorly), and posterior notch of epigyne narrow and distinct.

Description. Male (based on specimen from Dongxing City). Carapace length 3.1; abdomen length 4.1. ***Carapace*** dark brown, with sparse white scales. ***Clypeus*** very narrow. ***Chelicera*** dark brown, with a line of white scales on the prolateral face. One



Figures 46–72. *Kelawakaju frenata* species group, genitalia **46–54** *K. frenata* **46** male from Dongxing, palp, ventral **47** same, retrolateral **48** same, dorsal **49** male from Hong Kong, embolus, ventral **50** Simon's (1901a) figure, reversed **51** female d224 from Dongxing, epigyne, ventral **52** second female from Dongxing, epigyne, ventral **53** same, vulva, ventral **54** same, dorsal **55–63** *K. leucomelas* **55** holotype male palp, ventral **56** same, retrolateral **57** same, embolus, oblique **58** paratype male JK13.12.10.0001, embolus, oblique **59** male JK.19.08.18.0010, embolus, oblique **60** same, palp, retrolateral **61** same, ventral **62** female paratype JK.20.11.13.0001, epigyne, ventral **63** same, vulva, dorsal **64–72** *K. sahyadri* **64** holotype male, palp, ventral **65** same, retrolateral **66** same, embolus, oblique **67** paratype male from Kerala, embolus, oblique **68** same, ventral **69** same, palp, ventral **70** same, retrolateral **71** paratype female AS19.4934 epigyne, ventral **72** same vulva, dorsal. Oblique views of embolus are between ventral and prolateral. Scale bars: 0.1 mm.

Figures 73–78. *Kelawakaju frenata* **73, 74** male from Tai Tam County Park, Hong Kong (© 2020 Artur Tomaszek) **75** female from Guangdong, Gaotan Town **76** male from Guangxi, Dongxing, dorsal **77** female from Dongxing, dorsal **78** same, ventral. Specimen in **73, 74** not examined microscopically; inferred as *K. frenata* by appearance and locality.

retromarginal tooth (Fig. 8). ***Palp*** dark brown, with long white scales on tibia. RTA elongate. Embolus short, from base leans slightly toward the prolateral, then twists so that its terminal part leans toward the retrolateral. ***Legs*** dark brown to yellow. First leg reddish dark brown, with sparse short white scales. Tibia with three pairs of ventral macrosetae. Legs II–IV yellow except dark brown femur, brown joints, and sparse short white scales; III and IV additionally have prolateral and retrolateral sides of tibiae and metatarsi dark brown. ***Abdomen*** dorsally cream colored, with a longitudinal, irregular, dark brown stripe, and almost entirely covered by a light brown scutum; laterally dark brown, with a pale stripe on the posterior fourth; ventrally dark brown, with a longitudinal pale stripe. Spinnerets dark brown.

Female (based on specimen from Dongxing City). Carapace length 3.45; abdomen length 5.55. Color as in male, except when mentioned. ***Chelicerae*** dark. One retromarginal tooth. ***Leg*** I light brown, with median third of femur, distal of patella and proximal and distal of tibia dark brown; tarsus yellow; II yellow, with same markings as I; III and IV as II, but with patellae entirely yellow and prolateral side of tibia dark brown. Tibia with three pairs of ventral macrosetae. ***Abdominal*** pattern as in male; no scutum. ***Epigyne*** with a pair of small copulatory openings distant from the posterior border, which has a medial excavation; internally, copulatory ducts fuse with glandular portions, spiral backwards and enter the large spermathecae, from which fertilization ducts emerge.

Material examined. One male and two females in UBCZ from China: Guangxi: Dongxing City, Wanwei Village. 21.5217°N, 108.1383°E, 3 m elev., 23 May 2006, J.X. Zhang, M.S. Zhu, W.G. Lian, H.Q. Ma JXZ06#013. One male (IDWM.20018) in UBCZ from Hong Kong: Mai Po Nature Reserve, 22.2799°N, 113.9296°E, 5 July 2020, Cheuk Lun Alex Ng. One female ZRC_ENT00053870) in LKCNHM from China: Guangdong: Huidong County, Gaotan Town, Y.X. Lim, 1 October 2018. Photographs on iNaturalist suggest the species is also in Taiwan.

Kelawakaju leucomelas Maddison & Ng, sp. nov.

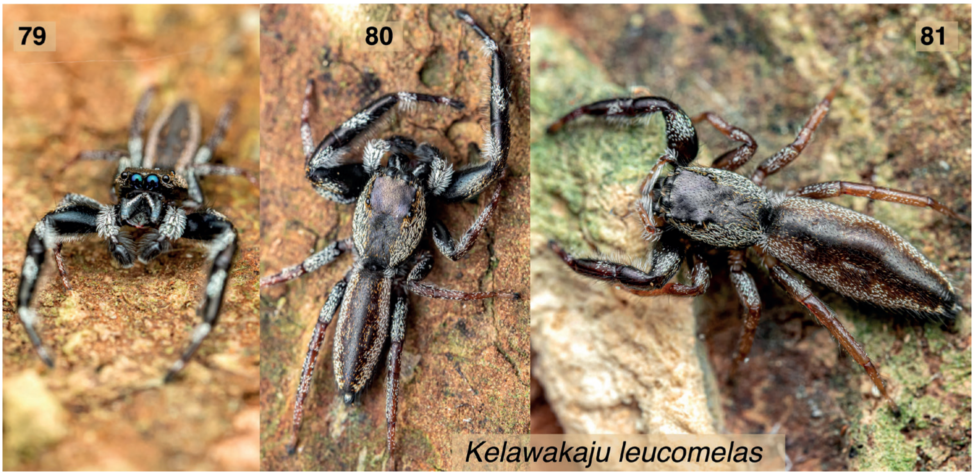
https://zoobank.org/F7326873-F2B9-4DF7-8C0B-C0F6A20522B7
Figs 14, 55–63, 79–81

Type material. ***Holotype*:** male (JK.20.11.13.003) in LKCNHM from Singapore: Lorong Pang Sua 1.3833°N, 103.7567°E, 13 xi 2020, J.K.H. Koh & P. Y. C. Ng. ***Paratypes*:** Two females (JK.20.11.13.0001 and JK.20.11.13.0002) with same data as holotype. One male (JK.13.12.10.0001) from Singapore: Pulau Tekong, 1.4072°N, 104.0283°E, 10 December 2013, J.K.H. Koh.

Etymology. Refers to the longitudinal bands of white scales (*leuco*, Greek for white) on either side of the body contrasting against the black median (*melas*, Greek for black), formed not as an adjective but more simply as the two colours themselves (and thus without an expectation of agreement with the genus name).

Diagnosis. Carapace wider and ocular quadrangle shorter (Fig. 14) than in other species. Embolus differs in shape from that of the similar *K. sahyadri*: embolus tip with retrolateral flange more distinct and larger (Figs 55, 57–59, 61), and prolateral edge of embolus curves abruptly to the distal to make the embolus appear more erect (Figs 55, 61). Long brush of white hairs projecting prolaterally from male palp tibia is lacking (present in *K. frenata* and *K. sahyadri*). In the specimens we have, the body's white side bands are more distinct than in *K. frenata* and *K. sahyadri*, and the posterior legs more uniform coloured, lacking distinct annulate markings.

Description. Male (based on holotype). Carapace length 3.6, width 2.6; abdomen length 4.2. ***Carapace*:** Relatively flat, broad, depressed around fovea. Integument black to dark brown, clothed loosely with white scales in two broad longitudinal bands along sides, below and behind PME. Below these bands, thorax is black, without marginal white scales. ***Clypeus*** very narrow, dark, with some black hairs. ***Chelicerae*** diverging, projecting forward slightly, with a bulge anteriolaterally (as in *K. frenata*, Fig. 4, but more prominent). Bulge covered with hair-bearing tubercles. Dark brown to black, with narrow and dense line of white scales appearing as an inverted V (Fig. 79). Two promarginal and one triangular retromarginal teeth, as in *K. frenata* (Fig. 8). ***Palp*** dark brown. Patella and distal part of femur clothed with long white hairs and a few white scales. Embolus erect, with retrolateral flange separated from the tip by a distinct cleft (Figs 57–59). Endite subrectangular, with no projection, dark brown. ***Legs*:** First pair dark except tarsus, slightly paler, with some patches of white scales and hairs (Fig. 79). Remaining legs medium brown, lightly dusted with white scales, without annulate markings. Length of femur I 2.7, II 1.9, III 1.6, IV 2.0; patella + tibia I 4.1, II 2.4, III 2.0, IV 2.9; metatarsus + tarsus I 2.4, II 1.6, III 1.7, IV 2.0. Leg spination reduced: femur I d1-1-0, p0-2-0, II d1-1-0, p0-0-1, III d1-1-1, p0-0-1, IV d1-1-0, 0; patella I–IV 0; tibia I v2-2-2 (asymmetrical), II v1r-1r-1p, III v0-0-1p, IV 0; metatarsus I–II v2-2, III v0-0-1p, IV v0-0-1p. ***Abdomen*** narrow and long, dark above except for band of white scales on either side, continuing the longitudinal band of the carapace (Fig. 81).



Figures 79–81. *Kelawakaju leucomelas* **79–80** male from the type locality **81** female from same locality. Photographs © Chris Ang 2021. Specimens not examined microscopically; inferred as *K. leucomelas* by appearance and locality.

Female (based on paratype JK.20.11.13.0001). Carapace length 3.2, width 2.4; abdomen length 4.3. ***Carapace*:** As in male, but narrower. ***Clypeus*** as in male. ***Chelicerae*** with bulge and tubercles, but less prominent than in male. Dark, with black setae. Two promarginal and one unident retromarginal tooth, similar to those of *K. frenata* (Fig. 9). ***Legs*:** First pair of legs medium brown; posterior legs honey-brown, without annulate markings. Length of femur I 1.9, II 1.6, III 1.4, IV 1.7; patella + tibia I 2.7, II 1.9, III 1.7, IV 2.5; metatarsus + tarsus I 1.6, II 1.3, III 1.4, IV 1.9. Leg spination reduced: femur I d1-0-0, p0-2-0, II d1-1-0, p0-0-1, III d1-1-0, p0-0-1, r0-0-1, IV d1-1-0, r0-0-1; patella I–IV 0; tibia I v2-2-2 (asymmetrical), II v1r-1r-1p, III 0, IV 0; metatarsus I–II v2-2, III v0-0-1p, IV v0-0-1p. ***Abdomen*** narrow, long, dark medially but with pale longitudinal bands on either side. ***Epigyne*** with two crescent shaped openings posteriomedial to a pale desclerotized area (Fig. 62). (Although this specimen has the openings more medial than shown for *K. sahyadri*, another female of *K. leucomelas*, JK.20.11.13.0002, has them placed much as in *K. sahyadri*.).

Additional material examined. Male (JK.19.08.18.0010) in LKCNHM from MALAYSIA: Johor Bahru, Kota Tinggi, Panti Recreational Forest, 1.7872°N, 103.9425°E, 18 August 2019, P.Y.C. Ng.

Natural history. Approximately ten adult and juvenile specimens were seen on tree bark at the type locality, including the holotype. The male from Kota Tinggi was found on tree bark in a sunny area near the entrance of Panti Recreational Forest.

Kelawakaju sahyadri Vishnudas, Maddison, & Sudhikumar, sp. nov.

https://zoobank.org/34C05BE6-0AC9-4724-808B-1D3CC7E40610

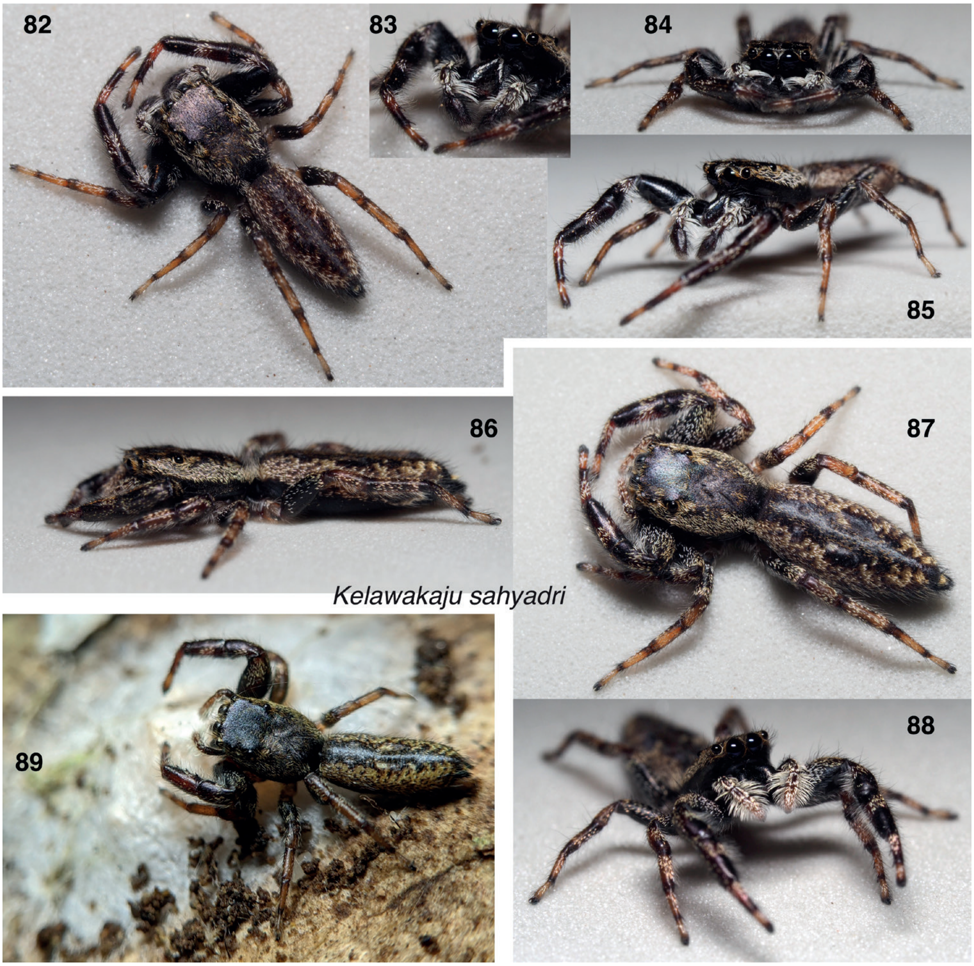
Figs 15, 64–72, 82–88

Type material. ***Holotype*:** male (AS19.4895 = NCBS IBC-BP847) in NCBS from India: Karnataka: Kodagu: Yavakapadi, Honey Valley area, 12.2224°N, 75.6553°E, 1045 m elev., 27 June 2019, W. Maddison WPM#19-083. ***Paratypes*:** Female (AS19.4934 = NCBS IBC-BP848) in NCBS with data as holotype except 12.2214°N, 75.6556°E and 1130 m elev. One male and one female in CATE from India: Kerala: along state highway 21 east of Chalakudy, 10.296°N, 76.685°E, 26 June 2021, Vishnudas & Sudhikumar CATE9826705. One female with same data but 17 July 2021.

Etymology. From the Sanskrit for ’from the Western Ghats mountains’, where this species lives.

Diagnosis. Embolus differs in shape from that of the similar *K. leucomelas*: embolus tip with retrolateral flange less distinct and smaller (Figs 64, 66–69), and prolateral edge of embolus curves gently to the distal to make the embolus appear to be leaning slightly to the retrolateral (Figs 64, 68, 69). Compared to *K. leucomelas*, the longitudinal pale bands on body less distinct, and the carapace is narrower.

Description. Male (based on holotype). Carapace length 3.0, width 2.1; abdomen length 3.9. ***Carapace*:** Relatively flat; area around fovea slightly depressed. Dark brown, loosely clothed with white scales below and behind PLE forming an indistinct



Figures 82–89. *Kelawakaju sahyadri* **82–85** male holotype AS19.4895 **86–88** female paratype AS19.4934 **89** female paratype from Kerala.

longitudinal band on each side. ***Clypeus*** very narrow, dark, with black setae. ***Chelicerae*** diverging slightly, lacking the distinct bulge of *K. frenata* and *K. leucomelas*, but with hair-bearing tubercles. Narrow stripes of white scales form inverted V as in other *frenata* group species (Fig. 83). Two promarginal and one large triangular retromarginal teeth, as in *K. frenata* (Fig. 8). ***Palp*** dark to light brown, with white scales and long white hairs. The prolateral hairs on the tibia appear as a distinct long brush projecting medially (Figs 83, 84). Embolus with prolateral edge gently curved. Retrolateral flange near tip fairly large, but emerges gradually, without strong cleft near tip (Figs 66, 67). Endite subrectangular, with no projection, dark brown. **Legs:** First leg dark to light brown, with loose patches of white setae (Figs 82, 85). Posterior legs paler, darker on femora and near the joints. Length of femur I 2.0, II 1.5, III 1.4, IV 1.7; patella + tibia I 3.1, II 2.0, III 1.7, IV 2.3; metatarsus + tarsus I 2.0, II 1.5, III 1.5, IV 1.7. Leg spination reduced: femur I d1-0-0, p1-1-0, II d1-1-0, p0-0-1, III d1-1-2, 0, IV d1-1-0, 0; patella I–IV 0; tibia I v2-2-2 (asymmetrical), II v1r-1r-1p, III 0, IV 0; metatarsus I–II v2-2, III v0-0-1p, IV v0-0-1p. ***Abdomen*** narrow, dark medially, paler and mottled laterally.

Female (based on specimen NCBS IBC-BP848). Carapace length 4.0, width 2.9; abdomen length 5.0. ***Carapace***, ***Clypeus*** as in male. ***Chelicerae*** dark, with black hairs arising from small tubercles. Two promarginal and one larger triangular retromarginal teeth. ***Legs*****:** First leg darkest, but all legs have dark patches, especially the sides of the femora and near the joints. Length of femur I 2.4, II 1.9, III 1.8, IV 2.1; patella + tibia I 3.3, II 2.5, III 2.3, IV 3.3; metatarsus + tarsus I 2.1, II 1.6, III 2.0, IV 2.3. Leg spination reduced: femur I d0-1-0, p0-3-0 or 2-0, II d1-1-0, p0-0-1, III d1-1-0, p0-0-1, IV d1-1-0, 0; patella I–IV 0; tibia I v2-2-2 (asymmetrical), II v1r-1r-1p, III 0, IV 0; metatarsus I–II v2-2, III v0-0-1p, IV v0-0-1p. ***Abdomen*** long, narrow, dark medially and pale laterally. ***Epigyne*** with two crescent-shaped openings behind a pale desclerotized area (Fig. 71).

Natural history. The holotype and female paratype from Kodagu were found under loose bark of large trees standing in a field, beside a small road. The specimens from Kerala were found in crevices in the bark of *Swietenia* mahogany trees.

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A review of the *Augochloropsis* (Hymenoptera, Halictidae) and keys to the shiny green Halictinae of the midwestern United States

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Abstract

Augochloropsis and other shiny green Halictinae have had various taxonomic issues and are often misidentified. One prevailing taxonomic issue is that *Augochloropsis metallica* (Fabricius) has two subspecies, that have long been recognized as morphologically distinct (*Augochloropsis metallica metallica* and *Augochloropsis metallica fulgida* (Smith), but the subspecies are inconsistently applied in the literature. Here, we review the *Augochloropsis* of the Midwest and further address the *Augochloropsis* species in the broader United States to resolve the outstanding taxonomic issues with the midwestern species. We provide identification keys and diagnoses for the genera and species of the shiny green Halictinae of the midwestern United States, which includes the genera *Agapostemon*, *Augochlora*, *Augochlorella*, and *Augochloropsis*. This work results in taxonomic changes to *Augochloropsis*. *Augochloropsis sumptuosa* (Smith) is split into two species, with the name *Augochloropsis sumptuosa* retained for the eastern form, and *Augochloropsis humeralis* (Patton), **stat. nov.**, reinstated for the western form. *Augochloropsis metallica* is split into five species, with two of those species occurring in the midwestern United States: *Augochloropsis metallica* and *Augochloropsis viridula* (Smith), **stat. nov.** Examination of the holotype of *Augochloropsis fulgida* (Smith) revealed that it does not agree with the prevailing concept of *Augochloropsis metallica fulgida*; it is reinstated as *Augochloropsis fulgida*, **stat. nov.**, but is currently known only from the holotype female from Florida. *Augochloropsis cuprea* (Smith), long considered to be a synonym of *Augochloropsis metallica*, is also distinct, and we are reinstating *Augochloropsis cuprea*, **stat. nov.**, though the range of this species is unclear. We further recognize *Augochloropsis fulvofimbriata* (Friese), **stat. nov.**, from South and Central America, as distinct. These changes result in a total of three *Augochloropsis* species in the Midwest and seven named species in the United States. We are aware of additional species from the southern and southwestern United States that are undescribed, and we highlight additional taxonomic work that remains to be done.

Keywords
Agapostemon, *Augochlora*, *Augochlorella*, identification, *Paraugochloropsis*, species complex

Introduction

The genus *Augochloropsis* Cockerell contains approximately 140 species, recognizable by their metallic coloration and distinctly-shaped tegula (Hurd 1979; Engel 2000; Michener 2007; Ascher and Pickering 2022) and occurs throughout most of the Western Hemisphere (Moure and Hurd 1987). *Augochloropsis* was originally erected as a subgenus of *Augochlora* Say by Cockerell (1897) and later elevated to genus by Schrottky (1906). This classification was later confirmed by the in-depth generic revision of augochlorine bees by Eickwort (1969). The number of *Augochloropsis* species that occur in the United States has been a matter of some debate, with different authors variously claiming that there are anywhere from two to five species (Sandhouse 1937 claimed two, Dreisbach 1945 claimed five, though did not list them all). In the most recent treatment, covering the Eastern United States, Mitchell (1960) recognized three species and one additional subspecies.

The species of *Augochloropsis* in the United States and Canada have undergone many taxonomic changes. In the first revisionary work, Sandhouse (1937) recognized two species: *Augochloropsis caerulea* (Ashmead) and *Augochloropsis cuprea* (Smith). Dreisbach (1945) recognized that what Sandhouse regarded as *Augochloropsis cuprea* was in fact two species in his region and split it into *Augochloropsis cuprea* and *Augochloropsis viridula* (Smith). Dreisbach (1945) also replaced the name *Augochloropsis caerulea* with the earlier name of *Augochloropsis humeralis* (Patton). After examination of the Fabricius types, and apparently unaware of the work by Dreisbach, Moure (1960) synonymized *Augochloropsis cuprea* with the older name *Augochloropsis metallica* (Fabricius). Moure (1960) also split *Augochloropsis metallica* into subspecies, suggesting *Augochloropsis metallica fulgida* (Smith) for the "southern variety." Moure's classification was followed by the most recent treatment performed by Mitchell (1960), who recognized two subspecies of *Augochloropsis metallica*, replaced the name *Augochloropsis humeralis* with *Augochloropsis sumptuosa* (Smith) based on correspondence with Moure, and recognized a third species, *Augochloropsis anonyma* Cockerell.

There has been inconsistent use of the names and species concepts of the *Augochloropsis* in the United States in recent bee diversity studies, primarily with the usage of the subspecies of *Augochloropsis metallica*, with some researchers recognizing them and others not. As a result, when papers refer to "*Augochloropsis metallica*" it is often impossible to know whether they were referring to "*Augochloropsis metallica metallica*" or "*Augochloropsis metallica fulgida*," especially given that many publications fail to cite the identification resources or taxon concepts they used (see Packer et al. 2018). More recently, several authors have recognized four species of *Augochloropsis* in the United States, informally elevating the subspecies *Augochloropsis metallica fulgida* (Smith) to full species (e.g., Camilo et al. 2018; Stephenson et al. 2018; Decker et al. 2020), but this has not been widely adopted. Overall, this has made it difficult to compare different publications and has hindered our ability to build even a basic understanding of the ranges and patterns of occurrence of these two taxa.

More broadly, the green Halictinae in general are plagued by misidentifications, particularly of males. This is in part due to the lack of up-to-date or high-quality identification resources. Indeed, some widely used identification resources contain characters that are too variable to be useful or are outright incorrect (e.g., the keys on discoverlife.org; Ascher and Pickering 2022). To help alleviate this issue, we continue the tradition of regional keys of shiny green Halictinae (e.g., Lovell 1942; Dreisbach 1945). Our keys cover the midwestern United States, defined as containing the states Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, Ohio, and Wisconsin. We do not include the Dakotas, Nebraska, and Kansas due to the shift from eastern to western fauna that occurs within these states, though the keys will still work in the easternmost parts of these states.

Here, we review the *Augochloropsis* species of the Midwest, recognizing three species from the region: *Augochloropsis humeralis*, *Augochloropsis metallica* sensu stricto, and *Augochloropsis viridula*. While we originally aimed to simply clarify the subspecies of *Augochloropsis metallica*, it necessarily expanded into a larger project after examination of the type specimens revealed numerous issues that necessitated a geographic expansion and a more in-depth update of the taxonomy. As a result of the updated taxonomy, we are making the following changes: *Augochloropsis humeralis* is resurrected from synonymy with *Augochloropsis sumptuosa*, we define *Augochloropsis fulgida* in a different sense than it has traditionally been used, and *Augochloropsis viridula* is resurrected from synonymy and recognized as a valid species. We further recognize as valid species two former synonyms of *Augochloropsis metallica: Augochloropsis cuprea* and *Augochloropsis fulvofimbriata* Friese. We also point to more work that remains to be done, as we recognize seven species in the United States, but there appear to be at least four more undescribed or unrecognized species. Lastly, we provide an illustrated key to the *Augochloropsis* and the other shiny green Halictinae of the midwestern United States, which covers the genera *Agapostemon* Guérin-Méneville, *Augochlora*, *Augochlorella* Sandhouse, and *Augochloropsis*.

Materials and methods

The keys used here are variously adapted and modified from existing sources, primarily from Arduser (2015) and Mitchell (1960), but also incorporate pieces and characters from Sandhouse (1937), Lovell (1942), Dreisbach (1945), Ordway (1966), and Michener et al. (1994). Various novel characters are also included. Higher-level classification and morphological terminology follow Michener (2007), with “metasoma” used for what is colloquially called the abdomen, and metasomal tergum and sternum are abbreviated to **T** and **S**, respectively. Antennal flagellomeres are abbreviated to **F**.

The keys and diagnoses follow the species concepts from the most recent revisions of those groups:

- *Agapostemon*: Roberts (1972).
- *Augochlorella*: Coelho (2004).
- *Augochlora*: Mitchell (1960).
- *Augochloropsis*: taxon concepts revised here.

The following museum and collection acronyms are used in the paper:

ANSP	The Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA (J. Weintraub).
NHMUK	The Natural History Museum, London, United Kingdom (J. Monks).
CNBL	The collection of the Cariveau Native Bee Lab, St. Paul Minnesota, USA (Z. Portman).
CRC	Catherine Reed Collection. Currently resides in the Cariveau Native Bee Lab and will be accessioned into the UMSP.
EERC	Elaine Evans Research Collection (E. Evans). Housed at the Cariveau Native Bee Lab (CNBL) and will be accessioned into the UMSP.
IDNP	Indiana Dunes National Park. Examined specimens deposited at the UMSP.
iNat	Selected high-quality records from the community science portal iNaturalist.com were examined for *Augochloropsis humeralis*. All record information is included in the material examined section.
MASR	Mike Arduser specimen record. Includes a combination of specimens in Mike Arduser's personal collection, as well as specimens Mike Arduser has personally identified but no longer has in hand.
MNDNR	The Minnesota Department of Natural Resources, St. Paul, MN, USA (J. Petersen and N. Gerjets). These are primarily deposited in the UMSP except for a small synoptic collection.
NHMD	Natural History Museum of Denmark, Copenhagen, Denmark (L. Vilhelmsen).
USNM	Smithsonian National Museum of Natural History, Washington D.C., USA.
OSUC	C.A. Triplehorn Insect Collection, Ohio State University Columbus, Ohio, USA (L. Musetti).
OUMNH	University Museum of Natural History, Oxford, United Kingdom (J. Hogan).
UMSP	University of Minnesota Insect Collection, St. Paul, Minnesota, USA (R. Thomson).

This study represents material from multiple sources, often examined over the course of many years. As a result, in the reports of material examined we are reporting a combination of specimen-level and county-level data. Historic specimens were manually georeferenced using Google Earth Pro software (v. 7.3.4.8248). For county level records, points were mapped to the county centroids. Specimen images were taken using an Olympus DP27 camera mounted on an Olympus SZX16 stereo microscope, with the images stacked using CombineZP software (Hadley 2010). Images of type specimens were provided by the type depositories. Figures were made with Adobe Photoshop software. Maps were created using the R statistical environment (R Core Team 2022), using both the *'ggplot2'* package (Wickham 2016) and the '*sf*' package (Pebesma 2018). State and province borders were imported from the '*rnaturalearth*' package (South 2017).

Results and systematics

Identification of the shiny green Halictinae of the midwestern United States.

Key to genera

1 Tegula enlarged and asymmetric, with the inner posterior margin hooked or angled (Fig. 1A) .... ***Augochloropsis* Cockerell**

– Tegula normal and ovoid (Fig. 1B).. **2**

2 Propodeum with posterior surface encircled by a raised rim or carina (Fig. 2A, B); males with black and yellow striped metasoma.. ***Agapostemon* Guérin-Méneville**

– Propodeum with posterior surface not encircled by a carina (Fig. 2C, D), though lateral carinae may be present; males with metasoma metallic green. **3**

3 Female S1 with central keel (Fig. 3A); both sexes with paraocular lobe prominent, forming a rounded acute angle (Fig. 3C, E); female with apex of mandible with two large and equal-sized teeth; male with posterior and lateral faces of propodeum closely, distinctly punctate (Fig. 3B) and S4 apical margin entire .... ***Augochlora pura* (Say)**

– Female S1 without keel; both sexes with paraocular lobe not prominent, forming an obtuse or right angle (Fig. 3D, F); mandible with a small preapical tooth; male with posterior and lateral faces of propodeum rugose to rugosopunctate, punctures obscure (Fig. 2D), and S4 apical margin weakly to strongly concave (compare to S3, which is entire) .... ***Augochlorella* Sandhouse**

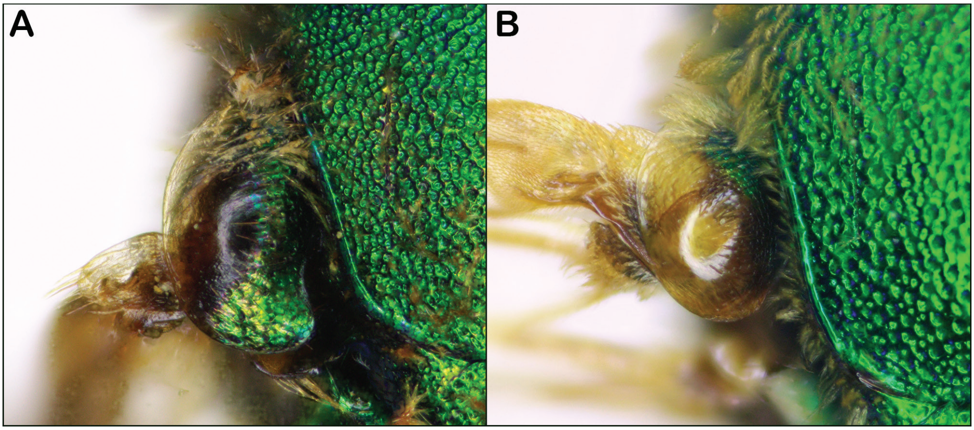

Figure 1. A tegula of *Augochloropsis*, enlarged and asymmetric, with the inner posterior margin angled (*Augochloropsis metallica* female pictured) **B** normal oval tegula (*Agapostemon splendens* female pictured).

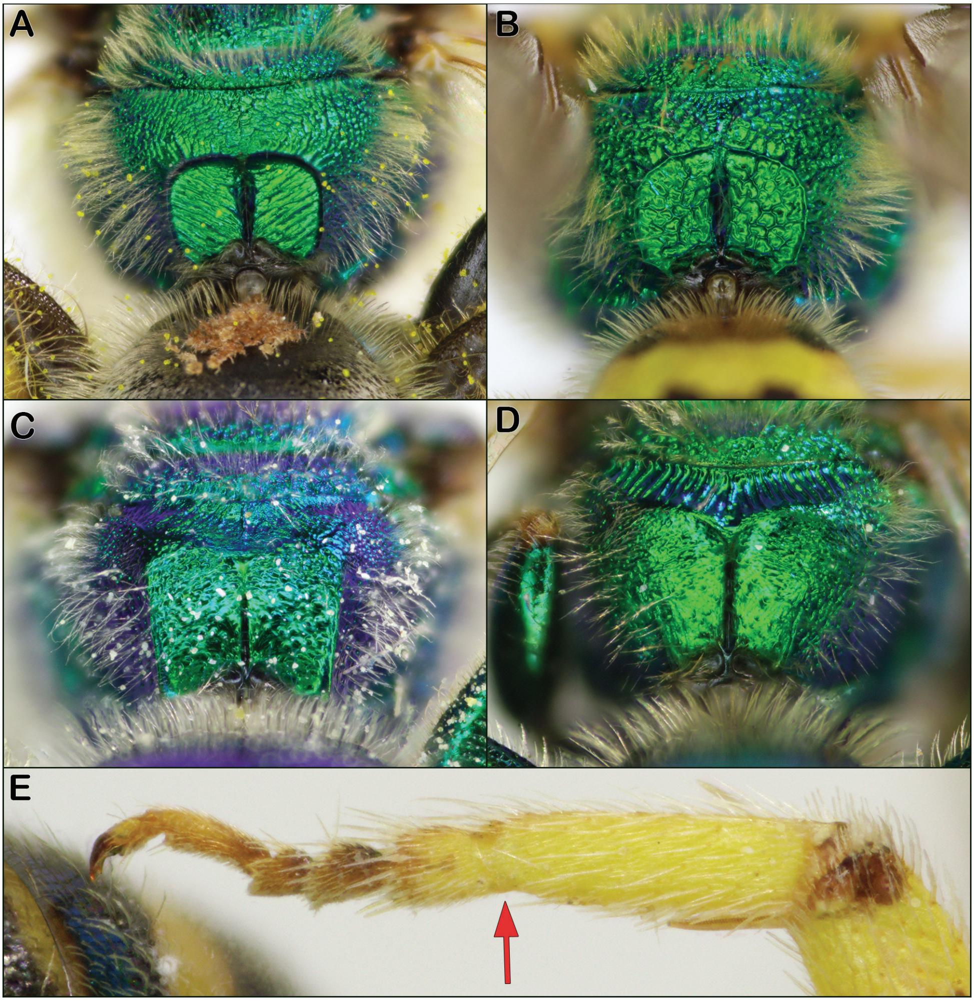

Figure 2. Characters to separate *Agapostemon* from Augochlorini: Complete raised carina on the rear face of the propodeum in *Agapostemon* **A** female and **B** male. Incomplete carina in **C** *Augochloropsis* female and **D** *Augochlorella* male **E** *Agapostemon* male hind leg with first two tarsomeres fused (red arrow pointing to point of fusion).

Genus *Agapostemon* Guérin-Méneville

Diagnosis. Both sexes of *Agapostemon* are diagnosed by the complete carina on the rear face of the propodeum (Fig. 2A, B). Other metallic green Halictinae genera, such as *Augochloropsis*, can have a pair of lateral carinae (e.g., Fig. 2C), but these are well-separated dorsally and never forming a complete carina as in *Agapostemon*. Females can be further recognized by having the hind tibial spurs with broad teeth. Males can be further recognized by having the metasoma black and yellow striped rather than metallic green and by having the basitarsus fused with the next tarsal segment (Fig. 2E).

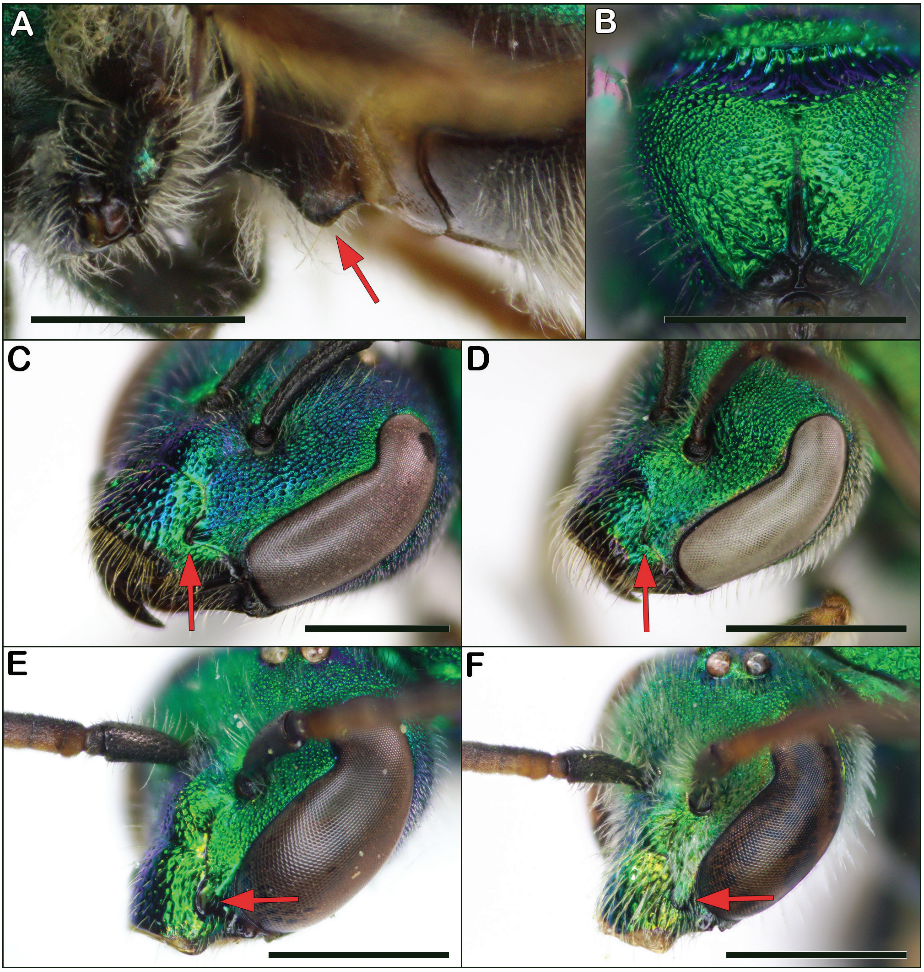

Figure 3. Characters to separate *Augochlora* and *Augochlorella* **A** S1 of *Augochlora pura* female with a median keel indicated by red arrow **B** *Augochlora pura* male rear propodeum showing distinct punctures **C** *Augochlora pura* female face with protruding paraocular lobe indicated by red arrow **D** *Augochlorella aurata* female face with undeveloped paraocular lobe indicated by red arrow **E** *Augochlora pura* male face with protruding paraocular lobe indicated by red arrow **F** *Augochlorella aurata* male with undeveloped paraocular lobe indicated by red arrow. Scale bars: 1 mm.

Keys to the midwestern species of *Agapostemon*

Note: We include two principally western species, *Agapostemon angelicus* Cockerell and *Agapostemon melliventris* Cresson, that may potentially occur in the midwestern states.

Key to females

1 Metasoma black or amber-colored (Fig. 4A, B) **2**
– Metasoma metallic green like thorax (Fig. 4C) **3**

2 Metasomal terga blackish (Fig. 4A), and clypeus blackish apically; common and widespread species .... ***virescens*** **(Fabricius)**

– Metasomal terga amber-colored, at least in part (Fig. 4B); clypeus yellow apically; Great Plains species in part, furthest eastern occurrence in eastern Kansas .... ***melliventris*** **Cresson**

3 Scutum and scutellum "doubly punctate", i.e., with uniformly scattered large punctures among the more numerous small ones (Fig. 5A, note that this is a variable character with quite a bit of variation in the size and density of the punctures) .... ***texanus*** **Cresson or** ***angelicus*** **Cockerell**

– Scutum densely punctate, rugosopunctate or weakly reticulate (Fig. 5B, C), but not "doubly punctate" **4**

4 Pronotum with dorsolateral angle pointed and produced at a distinct right angle; dorsolateral ridge sharply edged (Fig. 5B, red outline); scutum more reticulate (Fig. 6A); ventral pleural tubercle flush with rest of plate (Fig. 6C) .... ***sericeus*** **(Forster)**

– Pronotum with dorsolateral angle and dorso-lateral ridge blunted (Fig. 5C, red outline), not pointed or sharply edged; scutum with more distinct punctures (Fig. 6B); ventral pleural tubercle upraised, not flush with rest of plate (Fig. 6D) .... ***splendens*** **(Lepeletier)**

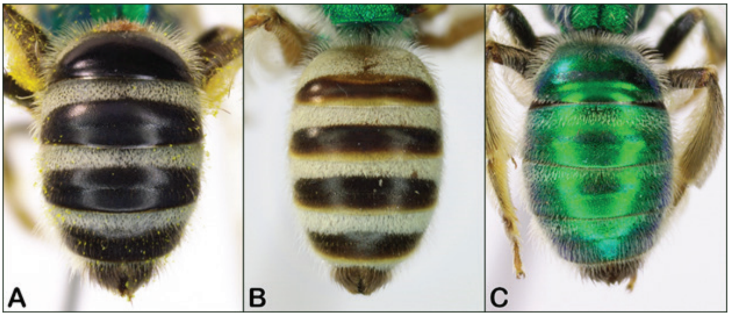

Figure 4. *Agapostemon* female metasomas **A** entirely black (*Agapostemon virescens* pictured) **B** dark brown with amber (*Agapostemon melliventris* pictured), note this is a darker specimen **C** metallic green (*Agapostemon texanus* pictured).

Figure 5. *Agapostemon* female pronotal collar and scutum **A** *Agapostemon texanus* doubly punctate **B** *Agapostemon sericeus* rugosopunctate with sharp pronotal angle outlined in red **C** *Agapostemon splendens* densely punctate with obtuse pronotal angle outlined in red.

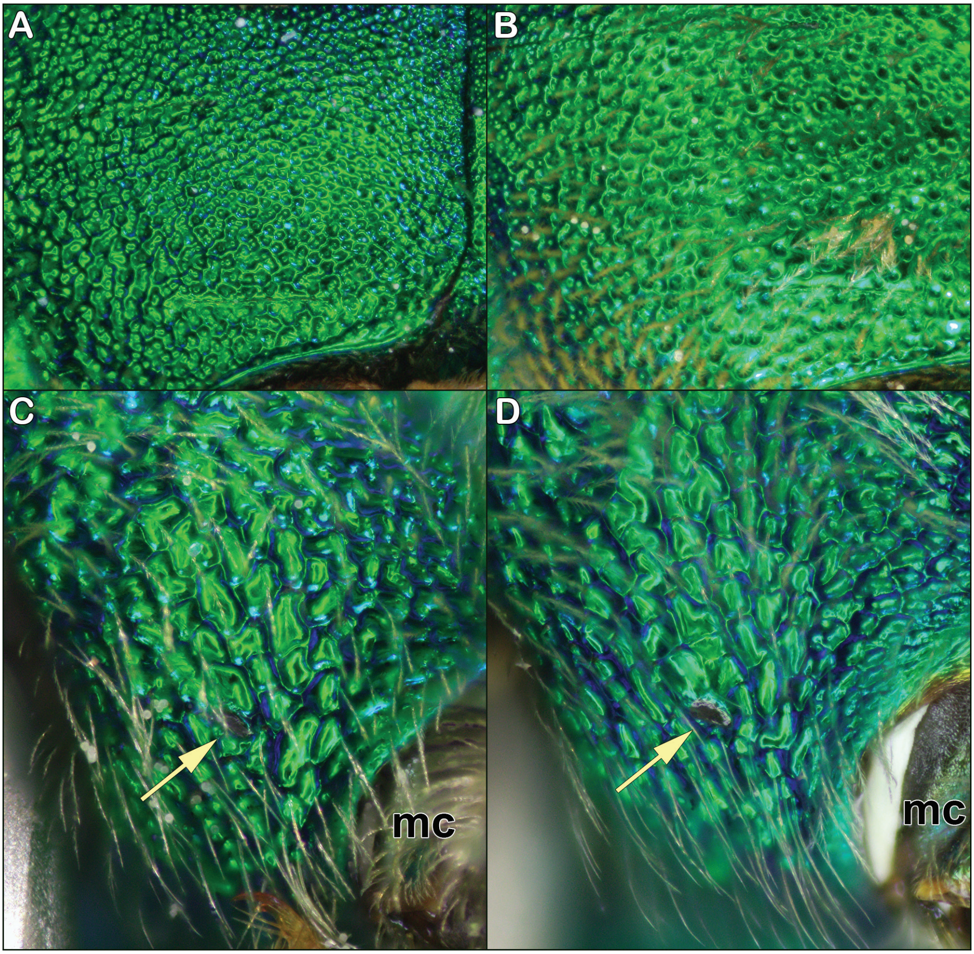

Figure 6. *Agapostemon* thorax characters (anterior of bee to left, "mc" refers to the base of the middle coxa) **A** *Agapostemon sericeus* close-up of rugosopunctate scutum **B** *Agapostemon splendens* close-up of densely punctate scutum **C** *Agapostemon sericeus* with ventral pleural tubercle flush with rest of plate **D** *Agapostemon splendens* with ventral pleural tubercle slightly upraised. Yellow arrows indicate the ventral pleural tubercle.

Key to males

1	S4 entirely flat, without a low, transverse swelling along the apical or preapical margin (Fig. 7A); S5 and S6 usually all dark brown to black, without any yellow maculations .... ***virescens* (Fabricius)**
–	S4 (and S3 to a lesser extent) with a low, transverse swelling along the apical or preapical margin (Fig. 7B–D; best seen in oblique lateral view); S5 and S6 usually (but not always) yellow in part (e.g., Fig. 7B) **2**

2 Hind femur skinny, not swollen at all (Fig. 8A); metasoma mostly yellow (Fig. 9A); Great Plains species in part, furthest eastern occurrence in eastern Kansas .... ***melliventris* Cresson**

– Hind femur moderately to grossly swollen (Fig. 6B–D); metasoma with large black bands (e.g., Fig. 9B) **3**

3 Hind legs quite swollen, width of hind femur about half the length (Fig. 8C) .... ***splendens* (Lepeletier)**

– Hind legs only moderately swollen (Fig. 8B, D) **4**

4 F1 slightly more than half length of F2 (Fig. 10A, antennae should be viewed on the lighter portion where it meets the brown portion); wings slightly brownish .... ***sericeus* (Forster)**

– F1 at least three-fourths length of F2 (Fig. 10B); wings clear **5**

5 Hind tibia with brown to black stripe present anteriorly (and posteriorly) (e.g., Fig. 8D for anterior view), or, if lacking anterior stripe, then also without black stripe on posterior surface; genitalia with relatively large medial plate, base of apical stylus of gonostylus not inflated (Fig. 12); widespread across North America .... ***texanus* Cresson**

– Lacking brown to black stripe on anterior surface of hind tibia (Fig. 11A), but stripe present on posterior surface (Fig. 11B); genitalia with small medial plate, basal stylus slightly inflated (Fig. 12); primarily western species .... ***angelicus* Cockerell**

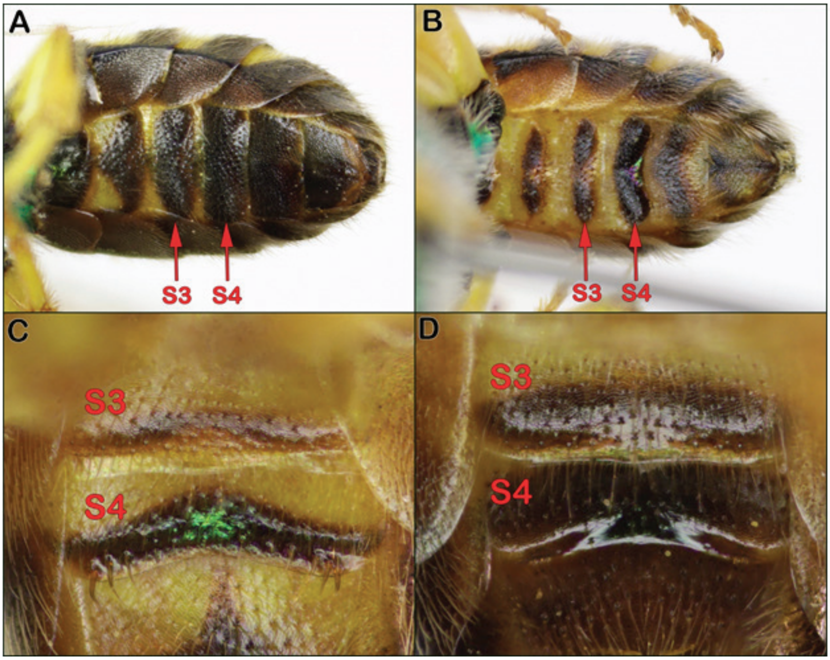

Figure 7. A *Agapostemon virescens* metasomal sterna with unmodified S3 and S4 **B** *Agapostemon texanus* metasomal sterna with swelling on S4 (and S3 to a lesser extent) **C** *Agapostemon sericeus* modified S3 and S4 **D** *Agapostemon texanus* modified S3 and S4.

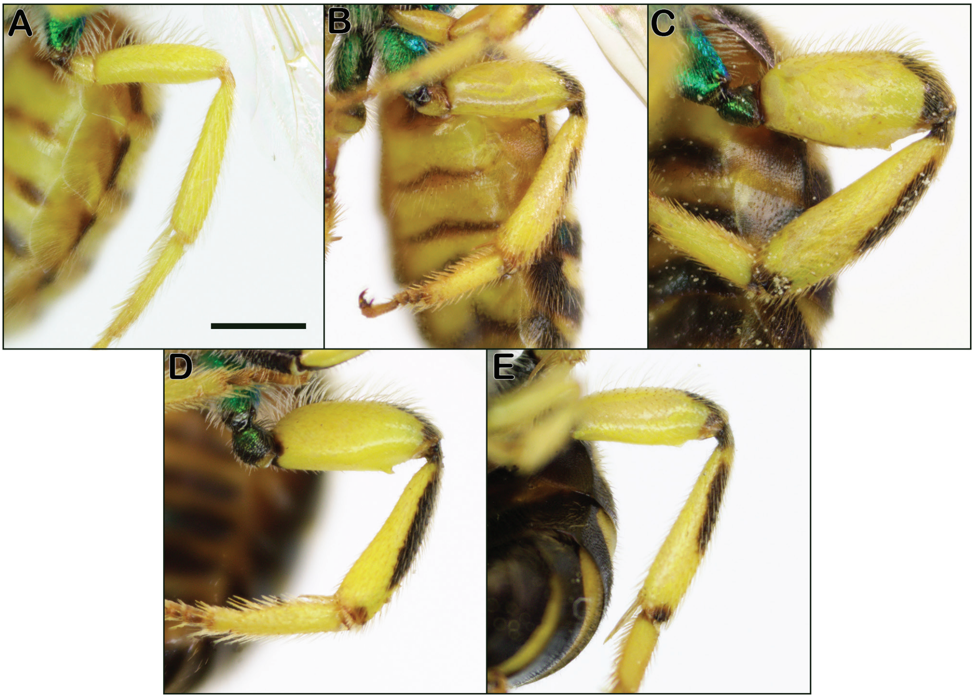

Figure 8. Male *Agapostemon* hind legs **A** *Agapostemon melliventris* **B** *Agapostemon sericeus* **C** *Agapostemon splendens* **D** *Agapostemon texanus* **E** *Agapostemon virescens*. Scale bar 1 mm, all images at the same scale.

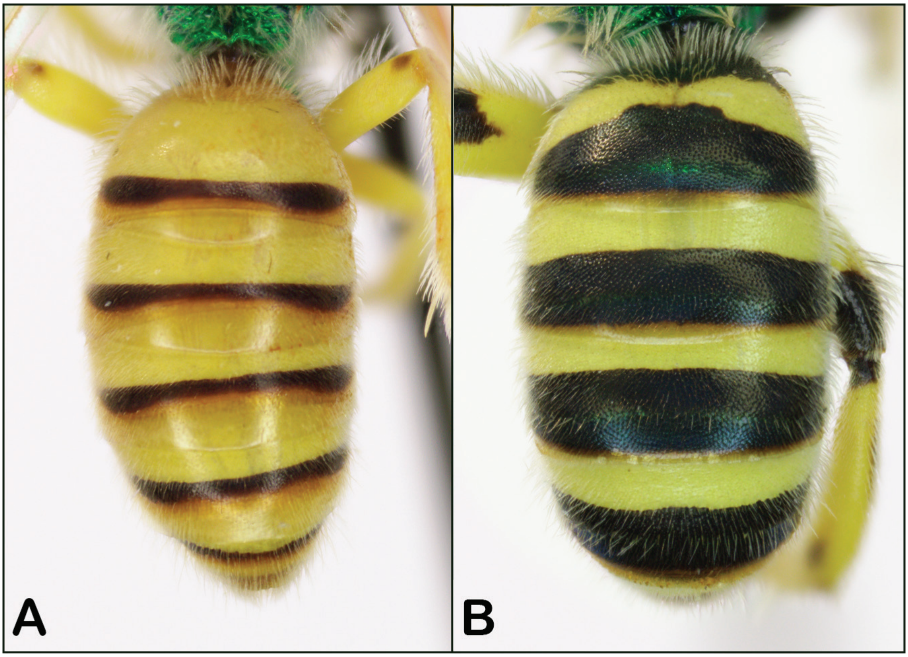

Figure 9. Male metasomal coloration **A** *Agapostemon melliventris* with mostly yellow metasoma **B** *Agapostemon texanus* with mostly dark metasoma.

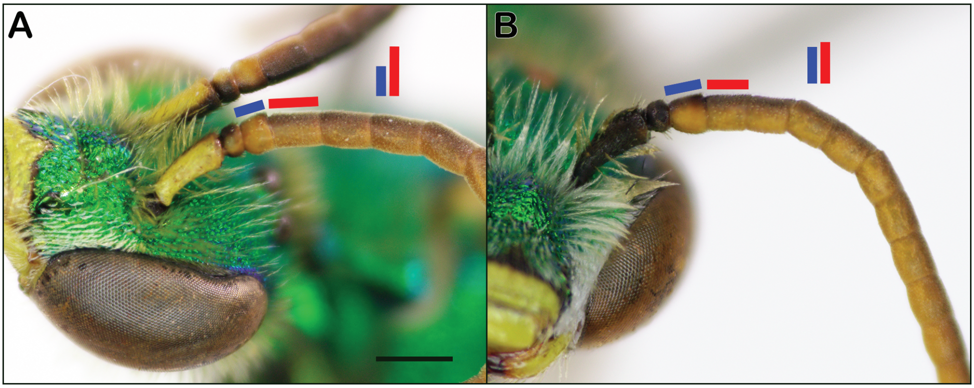

Figure 10. Male antennae with segments highlighted with bars to help illustrate their relative lengths **A** *Agapostemon sericeus* **B** *Agapostemon texanus*. Scale bars: 500 µm, both images at same scale.

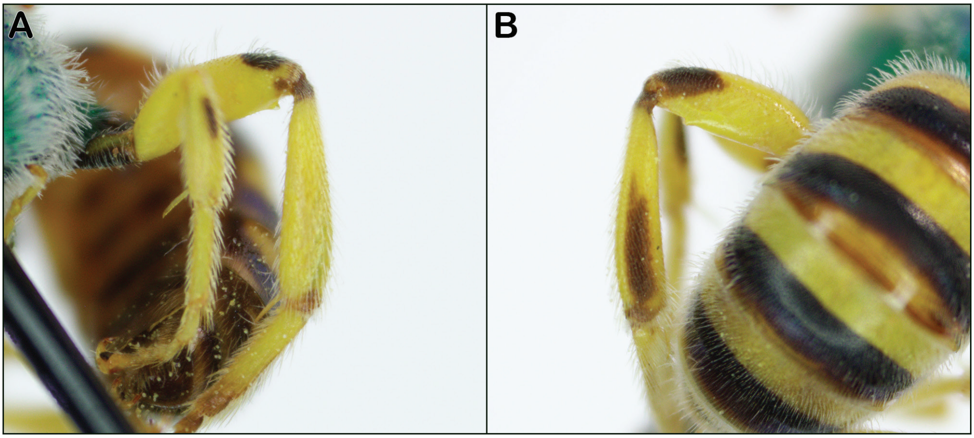

Figure 11. *Agapostemon angelicus* hind tibia **A** anterior view of tibia lacking a dark mark **B** posterior view of tibia with dark mark present.

Agapostemon (*Agapostemon*) *angelicus* Cockerell

Diagnosis. Females of *Agapostemon angelicus* can be recognized by the unique double-punctate scutum (as in Fig. 5A), a character they share with *Agapostemon texanus*. Our efforts to find characters to separate the females of these two species for the most part have been fruitless, and like workers before us (Roberts 1972), we consider females of *Agapostemon angelicus* and *Agapostemon texanus* to be morphologically indistinguishable. Males of *Agapostemon angelicus* can be separated from males of *Agapostemon texanus* using the leg and genitalia characters given in the key.

Remarks. *Agapostemon angelicus* is primarily a western species, though Roberts (1972) records it from central Iowa and extreme eastern Kansas. As far as we have been able to determine, there are no recent records of *Agapostemon angelicus* east of the 98th Meridian. A 2018–2019 statewide survey of Kansas bees by Morphew (2017) did not find any *Agapostemon angelicus* males (verified by MSA) east of the central part of the state, with

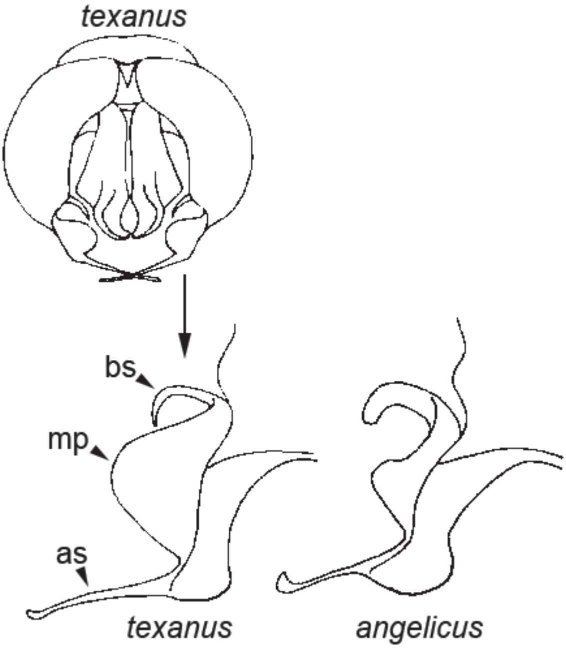

Figure 12. *Agapostemon texanus* and *Agapostemon angelicus* genitalia. Abbreviations: bs = basal stylus, mp = medial plate, as = apical stylus. Figure modified from Roberts (1972).

the easternmost records from Ellsworth and Rice counties. Recent survey efforts in eastern Nebraska have not found any *Agapostemon angelicus* east of the Grand Island area (Hall Co.). No confirmed recent records are known from Minnesota, Missouri, or Iowa, despite extensive collection efforts in those states. However, care should be taken to look for it and more work needs to be done to confirm the eastern extent of the range of *Agapostemon angelicus*. In areas where the two species may overlap, it is recommended that females identified morphologically as *Agapostemon angelicus* or *Agapostemon texanus* be treated as a single morphospecies. The two species can also be separated by DNA barcodes.*

***Agapostemon* (*Agapostemon*) *melliventris* Cresson**

Diagnosis. Female *Agapostemon melliventris* can be recognized by having the apex of the clypeus yellow as well as their non-metallic, light-colored metasoma. The terga are generally amber-colored but can be dark enough (e.g., Fig 4B) to resemble *Agapostemon virescens*.

Male *Agapostemon melliventris* can be recognized by having the metasoma primarily yellow (Fig. 9A), with just thin dark bands, and they also have the hind femur much skinnier (Fig. 8A) than any of the other species treated here.

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* **Addendum** - While this article was in press, a male *Agapostemon angelicus* was identified by ZP from southwestern Minnesota. It was collected in 2021 in Jackson County. This represents the first record of *Agapostemon angelicus* from Minnesota.

Remarks. *Agapostemon melliventris* is not known from the midwestern US, though Roberts (1972) records if from eastern Nebraska and Kansas, so there is the potential for it to be found in Missouri and Iowa. We are not aware of any recent collections east of the 98th Meridian.

Agapostemon (*Agapostemon*) *sericeus* (Forster)

Diagnosis. The female of *Agapostemon sericeus* can be recognized by the combination of the metallic green metasoma (as in Fig. 4C) and the reticulate sculpturing of the scutum (Figs 5B, 6A). It is most similar to *Agapostemon splendens*, but *Agapostemon splendens* has the scutum more punctured (Fig. 6B) rather than reticulate, and *Agapostemon sericeus* can be further distinguished by its sharply angled dorsolateral ridge of the pronotum (Fig. 5B) and by having the ventral pleural tubercle flush with the plate (Fig. 6C).

Male *Agapostemon sericeus* have S3 and S4 with a low transverse swelling and generally have distinct yellow marks on the apical sterna (Fig. 7C). They are most similar to males of *Agapostemon texanus* but can be distinguished by the relative lengths of F1 and F2: in *Agapostemon sericeus* F1 is slightly more than half the length of F2, whereas in *Agapostemon texanus* F1 is about three-fourths the length of F2 (Fig. 10). They can also be separated by the genitalia (see Roberts 1972).

Remarks. *Agapostemon seriecеus* was previously known as *Agapostemon radiatus* (Say) (e.g., Mitchell 1960; Roberts 1972) but was synonymized by Day and Fitton (1977).

Females of *Agapostemon femoratus* Crawford, primarily a western species not recorded east of New Mexico, Colorado and Wyoming by Roberts (1972), are essentially identical to females of *Agapostemon sericeus*, though the males are quite distinct, possessing a grossly enlarged hind femur, its width and length equal or nearly so. The key in Roberts (1972) indicates the scutum of female *Agapostemon sericeus* is more distinctly punctate than *Agapostemon femoratus*, but we do not consider this a reliable separating character. Curiously, there are several Missouri records of *Agapostemon femoratus* from the 1960s identified by Roberts in separate online databases, (discoverlife.org, Ascher and Pickering 2022), but these were not included in his 1972 revision. We have not seen these specimens, but assume they represent mis-determined females of *Agapostemon sericeus*, not *Agapostemon femoratus*.

Agapostemon (*Agapostemon*) *splendens* (Lepeletier)

Diagnosis. The female of *Agapostemon splendens* can be recognized by the combination of the metallic green metasoma (as in Fig. 4C) and the coarsely punctured sculpturing of the scutum (Figs 5C, 6B). It is similar to *Agapostemon sericeus*, but that species has the sculpturing of the scutum more reticulate (Figs 4B, 6A). *Agapostemon splendens* can be further distinguished by the obtuse dorsolateral ridge (Fig. 5C), the upraised ventral pleural tubercle (Fig. 6D), and it is generally larger than *Agapostemon sericeus* (though their sizes can intergrade).

Male *Agapostemon splendens* can be recognized from all other midwestern *Agapostemon* by their very enlarged hind femur, with the length twice the width (Fig. 8C). They also tend to be larger than related species and have darker wings, but this character is subtle.

Remarks. Some previous works (e.g., Mitchell (1960) and the keys on discoverlife.org) have used the shape of the ridges of the propodeal triangle (which often form a depressed medial triangle) to separate female *Agapostemon splendens* from *Agapostemon sericeus* (which have parallel striae throughout the propodeal triangle), but we have found the character variable and it can be quite subtle, particularly in smaller *Agapostemon splendens*. *Agapostemon splendens* is largely restricted to areas of deep sands. We have examined material from throughout the range of *Agapostemon splendens*, and there are many individuals, especially in the southern US, that have the scutal sculpturing more reticulate, similar to *Agapostemon sericeus*. More work is needed to determine whether this represents normal variation or is potentially due to a cryptic species complex.

Agapostemon (*Agapostemon*) *texanus* Cresson

Diagnosis. The females of *Agapostemon texanus* have the metasoma metallic green (Fig. 4C) and can be recognized by the "double-punctured" scutum, which has a combination of intermixed large and small punctures (Fig. 5A). Females cannot be reliably distinguished from *Agapostemon angelicus*, so they should be separated based on range or DNA barcodes (see remarks for *Agapostemon angelicus* above).

Male *Agapostemon texanus* have S3 and S4 with a low transverse swelling and generally have distinct yellow marks on the apical sterna (Fig. 7B, D). They are extremely similar to *Agapostemon angelicus*, but *Agapostemon texanus* have the hind tibia with black stripes on the front and back (Fig. 8D), whereas *Agapostemon angelicus* has the hind tibia yellow anteriorly (Fig. 11). In addition, the two species can be separated based on the genitalia characters given in the key (Fig. 12), and at least in the midwestern US, the range of the two species largely does not overlap.

Male *Agapostemon texanus* are also similar to (and frequently misidentified as) *Agapostemon sericeus* but can be distinguished based on the relative lengths of F1 and F2: *Agapostemon texanus* has F1 about three-fourths the length of F2 (Fig. 10A), whereas *Agapostemon sericeus* has F1 slightly more than half the length of F2 (Fig. 10B).

Remarks. *Agapostemon texanus* and *Agapostemon angelicus* largely do not overlap in range in the midwestern region, though Roberts (1972) reports *Agapostemon angelicus* from Iowa and eastern Kansas (see remarks under *Agapostemon angelicus*, above).

Agapostemon (*Agapostemon*) *virescens* (Fabricius)

Diagnosis. Females of *Agapostemon virescens* are the only midwestern species that has the metasoma dark (Fig. 4A), rather than metallic green (but see comments on dark *Agapostemon melliventris*).

Males of *Agapostemon virescens* can be recognized by the lack of a transverse swelling on S4 (Fig. 7A). In addition, S5 and S6 are usually all dark (Fig. 7A), whereas those sterna usually (though not always) have at least some yellow in other *Agapostemon* species. Finally, *Agapostemon virescens* males have a relatively slender hind femur compared to most other midwestern *Agapostemon* species (see Fig. 8E).

Remarks. Two western species with females with non-metallic metasomas have been recorded from nearby states though they have not been recorded from Iowa, Minnesota, or Missouri. *Agapostemon melliventris* has been found as far east as eastern Kansas and Nebraska, but they have the metasoma lighter and the apex of the clypeus yellow, compared to black in *Agapostemon virescens* females. In addition, *Agapostemon coloradinus* (Vachal) is a Great Plains species which occurs as far east as eastern Kansas, though *Agapostemon coloradinus* is usually noticeably larger than *Agapostemon virescens* with finer, closer striations on the hypostomal area on the underside of the head (see Roberts 1972). Males of *Agapostemon coloradinus* are similar to males of *Agapostemon virescens*, but *Agapostemon coloradinus* males have a dark stripe on the posterior surface of the hind femur and the inner gonostylar flap of *Agapostemon coloradinus* lacks a pronounced, medially-directed process basally, which is present in *Agapostemon virescens*.

Genus *Augochlorella* Sandhouse

Diagnosis. The genus *Augochlorella* can be recognized by the combination of a normal oval-shaped tegula (as in Fig. 1B), the incomplete carina on the rear face of the propodeum (Fig. 2D), and the lack of a protruding paraocular lobe (Fig. 3D, F). Females lack the keel on S1 seen in *Augochlora* and they have simple hind tibial spurs. Males are quite similar to *Augochlora*, but *Augochlorella* males have the S4 apical margin weakly to strongly concave, versus straight in *Augochlora.* In addition, *Augochlorella* males lack distinct punctures on the rear of the propodeum (Fig. 2D) compared to *Augochlora* males which do have distinct punctures (Fig. 3B). Some *Augochlorella* are more of a greenish-bronze color.

Keys to the midwestern species of *Augochlorella*

Key to females

1 Propodeal triangle with striae continuing to posterior margin, or very nearly so (Fig. 13C–E); head round, only slightly broader than long (Fig. 13A); clypeus with apical fourth dark (Fig. 13A) .... ***aurata* (Smith)**

– Propodeal triangle with striae not reaching posterior margin, leaving a distinct smooth portion (Fig. 13F–H); head slightly broader than long (Fig. 13B); clypeus with apical third dark (Fig. 13B) .... ***persimilis* (Viereck)**

Key to males

1 Inner edge of hind basitarsus with hairs on apical two-thirds only slightly elongate, their length about equal to width of basitarsus (Fig. 13I); propodeal triangle with striae reaching posterior margin or nearly so (as in Fig. 13C–E) .... ***aurata* (Smith)**

– Inner edge of hind basitarsus with hairs on apical two-thirds distinctly elongate, their length distinctly longer than width of basitarsus (Fig. 13J); propodeal triangle with striae not reaching posterior margin, leaving a smooth portion (as in Fig. 13F–H, though this character is subtle and less pronounced than in females) .... ***persimilis* (Viereck)**

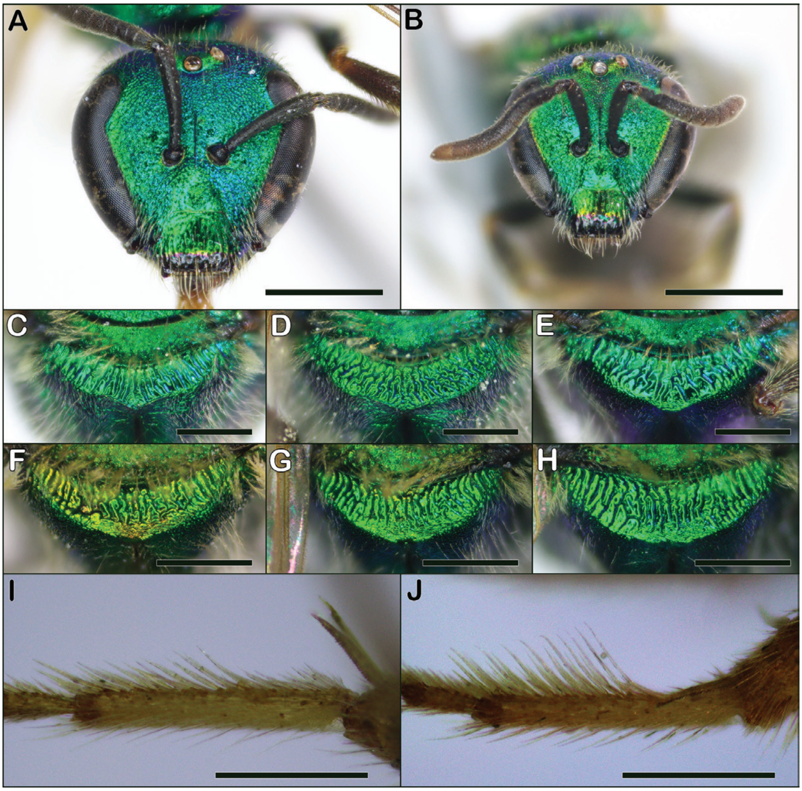

Figure 13. *Augochlorella* characters **A** *Augochlorella aurata* female face **B** *Augochlorella persimilis* female face **C–E** *Augochlorella aurata* female propodeal triangles demonstrating the range of variation **C** apical margin carinate **D** apical margin largely lacking a carina **E** apical margin completely lacking a carina and striae partially removed from margin **F–H** *Augochlorella persimilis* female propodeal triangles demonstrating the range of variation **F** propodeum with narrow smooth margin **G** propodeum with broad smooth margin **H** propodeum with narrow and irregular smooth margin **I** *Augochlorella aurata* male hind basitarsus **J** *Augochlorella persimilis* male hind basitarsus. Scale bars: 1 mm (**A, B**); 500 µm (**C–H, I, J**).

Augochlorella aurata (Smith)

Diagnosis. *Augochlorella aurata* is very similar to *Augochlorella persimilis*. Female *Augochlorella aurata* can be recognized by having the striations of the propodeum continuing to the posterior margin (Fig. 13C–E), which often, but not always, is bordered by a carina (e.g., Fig. 13C). In contrast, females of *Augochlorella persimilis* always have a distinct smooth portion before the margin of the propodeum (Fig. 13F–H). In addition, female *Augochlorella aurata* are generally larger, have the head slightly longer and the apex of the clypeus is black only on the apical fourth (Fig. 13A). In contrast, *Augochlorella persimilis* females are generally quite small, have the head slightly broader, and the apex of the clypeus is black on the apical third (Fig. 13B).

Female *Augochlorella aurata* are also often confused with *Augochlora pura*, but *Augochlorella aurata* have the paraocular lobes less protuberant (Fig. 3D, F) than *Augochlora pura*, and *Augochlorella aurata* also lack a keel on S1.

Male *Augochlorella aurata* can be separated from *Augochlorella persimilis* by the hair on the apical two-thirds of the inner edge of the hind basitarsus, which is short in *Augochlorella aurata*, with the length of the hairs about equal to the width of the basitarsus (Fig.13I), whereas *Augochlorella persimilis* has the hairs distinctly longer than the width of the basitarsus (Fig. 13J). In addition, the striae on the propodeal triangle of *Augochlorella aurata* reach the posterior margin (as in Fig. 13C–E) whereas male *Augochlorella persimilis* generally have a smooth portion before the margin.

Male *Augochlorella aurata* are often confused with *Augochlora pura* males, but *Augochlorella aurata* have the margin of S4 concave rather than straight, and they lack distinct punctures on the rear of the propodeum (Fig. 2D), compared to distinctly punctured in *Augochlora pura* (Fig. 3B).

Comments. *Augochlorella aurata* and *Augochlorella persimilis* are often confused in collections and some females can intergrade to the degree where they are impossible to differentiate. Males are also frequently confused because the hind basitarsus character is often misinterpreted since both species have the basal third of the basitarsus with distinctly shorter hairs, which can cause confusion in keys that focus on the length of the basal hairs rather than the apical hairs, such as Coelho (2004), or the keys on discoverlife.org that incorrectly state that *Augochlorella aurata* males have the "hair on rear basitarsus all about the same length".

Given the high level of variation in *Augochlorella aurata*, it seems likely that it is a species complex. Supporting this hypothesis are the various forms that Ordway (1966) recognized, one of which was elevated to species rank by Coelho (2004), as well as the high barcode diversity found in the species (Sheffield et al. 2009).

Augochlorella persimilis (Viereck)

Diagnosis. *Augochlorella persimilis* is very similar to *Augochlorella aurata*. Females can be distinguished by the lack of rugae at the rear of the propodeal triangle, though this character can often be subtle (Fig. 13F–H). In addition, *Augochlorella persimilis* tend to be smaller than *Augochlorella aurata*, and they have a more extensive apical black mark on the clypeus, with the black part taking up approximately one-third of the length of the clypeus (Fig. 13B), compared to approximately one-fourth the length of the clypeus in *Augochlorella aurata* (Fig. 13A). Note that there are often females of *Augochlorella persimilis* and *Augochlorella aurata* that cannot be reliably separated.

Male *Augochlorella persimilis* can be separated from *Augochlorella aurata* by the length of the hairs on the inner side of the hind basitarsus: *Augochlorella persimilis* have the hairs very short for the basal third, then the hairs flare out to about twice the width of the basitarsus (Fig. 13J). In contrast, the hairs on *Augochlorella aurata* are short for the basal third, and only get slightly longer, about equal in length to the width of the basitarsus (Fig. 13I). Like females, the males of *Augochlorella persimilis* also have a lack of rugae at the rear of the propodeal triangle but it is less distinct (see Fig. 13F–H).

Comments. This species has a more southern distribution than *Augochlorella aurata*, though the species commonly overlap and co-occur. The northern extent of the range of *Augochlorella persimilis* reaches the southern part of Michigan, Minnesota, and Wisconsin (Wolf and Ascher 2008; Gibbs et al. 2017).

Genus *Augochlora* Smith

Comments. *Augochlora pura* is the only species of *Augochlora* that occurs in the midwestern United States.

Augochlora (*Augochlora*) *pura* (Say)

Diagnosis. *Augochlora pura* is most similar to *Augochlorella aurata* and *Augochlorella persimilis*. Both sexes of *Augochlora pura* can be recognized by the distinct and prominent facial lobes (Fig. 3C, E), which extend below the level of the base of the mandible and are stronger than those found in *Augochlorella*, but the difference is subtle and easy to confuse. Female *Augochlora pura* are unique in having a keel on S1 (Fig. 3A) and the hind tibial spur is simple. In addition, the mandibles of *Augochlora pura* females are more robust, with 2 distinct and nearly equally-sized apical teeth, whereas *Augochlorella* have 1 main tooth and a smaller subapical tooth.

Males of *Augochlora pura* can be further recognized from *Augochlorella* by their straight apical margin on S4 (compared to concave in *Augochlorella*) and they have distinct punctures on the rear of the propodeum (Fig. 3B), compared to impunctate or obscure punctures in *Augochlorella* males (Fig 2D).

Comments. *Augochlora* and *Augochlorella* are frequently confused in collections, especially males. Midwestern specimens of *Augochlora pura* fall under subspecies *Augochlora pura pura*. More work is needed to determine whether *Augochlora pura pura* and *Augochlora pura mosieri* Cockerell are distinct taxa.

Genus *Augochloropsis* Cockerell

Diagnosis. Both sexes of *Augochloropsis* are diagnosed by the unique shape of the tegula, which has the inner posterior margin hooked (Fig. 1A). Females have the inner hind tibial spur with multiple straight teeth compared to broad teeth in *Agapostemon* or untoothed spurs in *Augochlorella* and *Augochlora*. *Augochloropsis* males have a uniquely-shaped S4 (see Fig. 20C, H, M), with a median point and lateral arms, though the sternum is typically hidden. Though typically strongly metallic green, many individuals are metallic bluish or even purplish.

Keys to the midwestern species of *Augochloropsis*

Key to females

1 Vertex (in frontal view) rising above ocelli by at least one ocellar diameter (Fig. 14A); dorsolateral angle of pronotum strongly lamellate, lamella produced as a strong right angle or nearly so (Fig. 14D); terga dull, strongly tessellate, with surfaces appearing granular, even on apical rims of terga (Fig. 14G); sand obligate species .... ***humeralis* (Patton)**

– Vertex (in frontal view) **not** rising above ocelli (Fig. 14B, C); dorsolateral angle of pronotum more weakly lamellate, lamella forming a very broad obtuse angle (Fig. 14E, F); tergal surfaces not strongly dull, at least somewhat shining (Fig. 14H, I); found in various habitats.. **2**

2 T2 hair fringe on apical margin with thickened flattened hairs unlike the hairs elsewhere on T2, and arranged closely together and appearing like the teeth of a comb along the apical margin of T2 (Fig. 15A); T2 with small, close punctures (typically about 1–2 puncture widths apart), surface between punctures generally appearing weakly tessellate (Fig. 14H)..................... ***metallica* (Fabricius)**

– T2 hair fringe on apical margin with hairs identical to the hairs elsewhere on T2 (Fig. 15B); T1 and T2 punctures more widely separated, typically 2–4 puncture widths apart on T2, space between punctures strongly shining, without tessellation or other microsculpture (Fig. 14I) .... ***viridula* (Smith)**

Key to males

1 Vertex (in frontal view) rising above ocelli by at least one ocellar diameter (Fig. 16A); dorsolateral angle of pronotum produced as a strong right angle or nearly so (Fig. 16D); terga dull, strongly tessellate, with surfaces appearing granular (Fig. 16G); sand obligate species .... ***humeralis* (Patton)**

– Vertex (in frontal view) flattened, **not** rising above ocelli (Fig. 16B, C); dorsolateral angle of pronotum less pronounced and forming a very broad obtuse angle (Fig. 16E, F); tergal surfaces not strongly dull, at least somewhat shining (Fig. 16H, I); found in various habitats.. **2**

2 T2 with apical fringe of distinctly thickened hairs (Fig. 16H); terga densely punctate, with punctures on T2 typically 1–2 puncture widths apart (Fig. 16H); propodeal triangle not as shiny, and more sculptured, than in *viridula*; genitalia with lateral margins of gonostyli parallel (Fig. 20F) ....***metallica* (Fabricius)**

– T2 with apical fringe composed of unthickened hairs (Fig. 16I); T2 surface shining (Fig. 16H), and T2 punctures more widely separated, typically 2–4 puncture widths apart; propodeal triangle shiny and less sculptured than in *metallica*; genitalia with lateral margins of gonostyli diverging apically (Fig. 20K) ....***viridula* (Smith)**

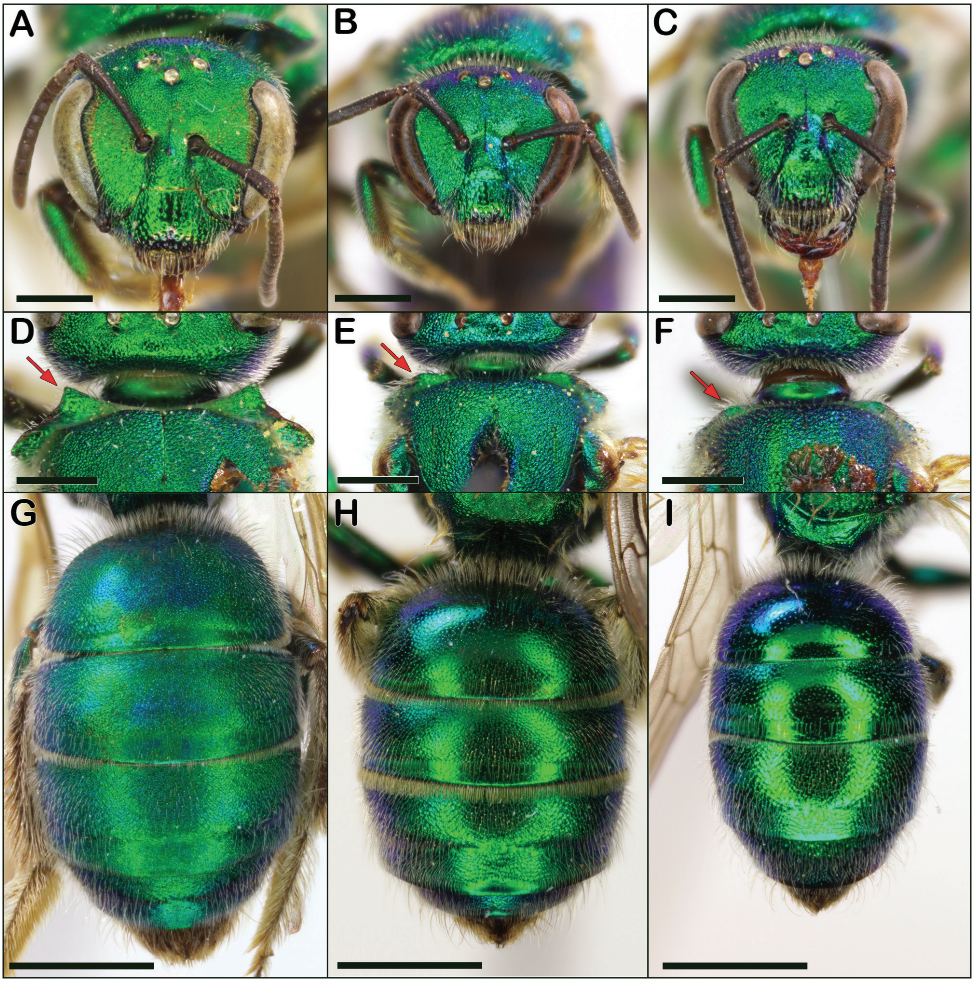

Figure 14. *Augochloropsis* female characters **A** *Augochloropsis humeralis* face **B** *Augochloropsis metallica* face **C** *Augochloropsis viridula* face **D** *Augochloropsis humeralis* well-developed, 90-degree pronotal flange indicated by red arrow **E** *Augochloropsis metallica* obtuse pronotal flange indicated by red arrow **F** *Augochloropsis viridula* obtuse pronotal flange indicated by red arrow **G** *Augochloropsis humeralis* metasoma **H** *Augochloropsis metallica* metasoma **I** *Augochloropsis viridula* metasoma. Scale bars: 1 mm (**A–F**); 2 mm (**G–I**).

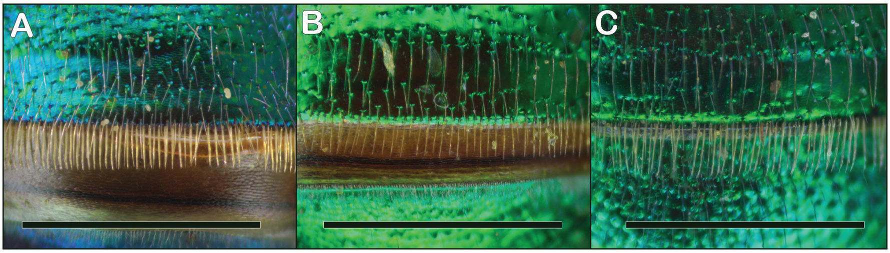

Figure 15. *Augochloropsis* female T2 hair fringes **A** *Augochloropsis metallica* with thickened hairs **B** *Augochloropsis viridula* with unthickened, slender hairs **C** *Augochloropsis* sp. (likely undescribed species from Eastland, Texas) with intermediate hairs. Note the specimens in **A** and **B** have their metasomas stretched out, revealing the brown basal part of the tergum that is normally hidden under the preceding tergum; this was done to increase contrast of the hairs and make the differences clearer. Scale bars: 1 mm, all images at the same scale.

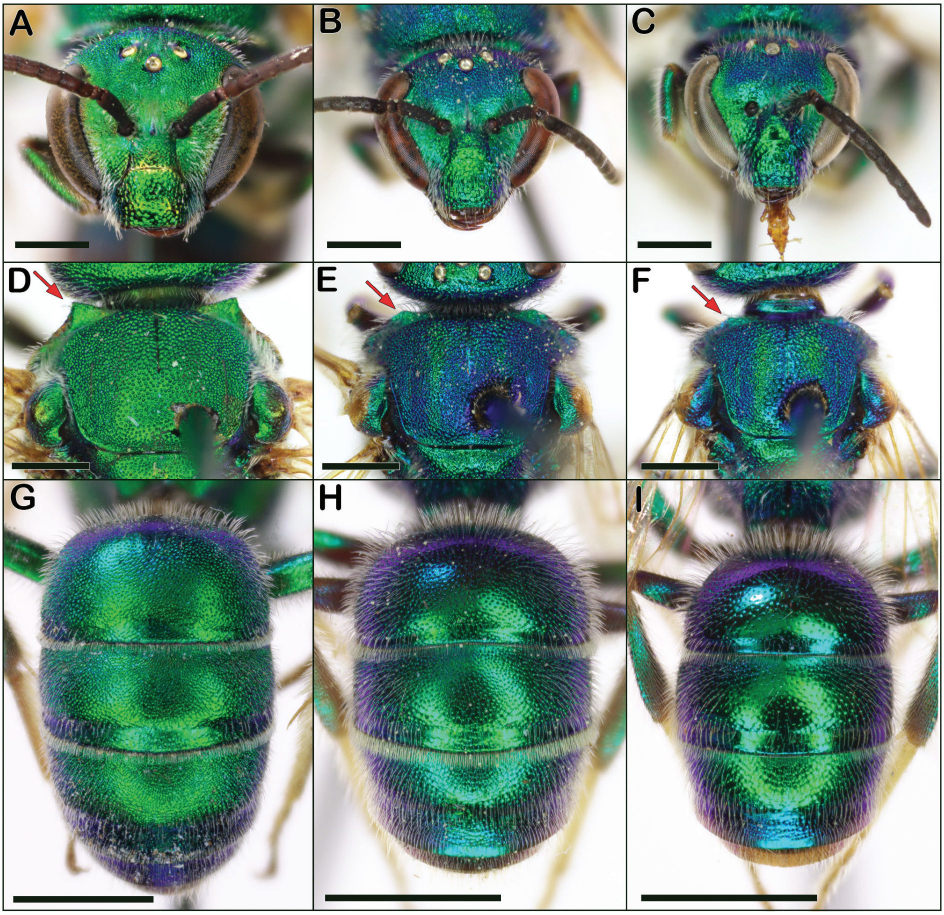

Figure 16. *Augochloropsis* male characters **A** *Augochloropsis humeralis* face **B** *Augochloropsis metallica* face **C** *Augochloropsis viridula* face **D** *Augochloropsis humeralis* well-developed, 90-degree pronotal flange indicated by red arrow **E** *Augochloropsis metallica* obtuse pronotal flange indicated by red arrow **F** *Augochloropsis viridula* obtuse pronotal flange indicated by red arrow **G** *Augochloropsis humeralis* metasoma **H** *Augochloropsis metallica* metasoma **I** *Augochloropsis viridula* metasoma. Scale bars: 1 mm (**A–F**); 2 mm (**G–I**).

Midwestern *Augochloropsis* species

***Augochloropsis* (*Paraugochloropsis*) *humeralis* (Patton), stat. nov.**

Augochlora humeralis Patton, 1879: 365 ♀♂. **Lectotype**: ♀ USA, North-western Kansas, 8 Sep 1877 leg. S.W. Williston, on goldenrod [ANSP]. Images examined by ZP and MA. **New lectotype designation.** (Labels read: "N.W. Kans. / Williston // Augochlora ♀ / humeralis n.s.").

Agapostemon caeruleus Ashmead, 1890: 7 ♂ (not ♀) (syn. Sandhouse 1937). **Holotype**: ♂ USA, Colorado, Denver [USNM ENT 00536769]. Images examined by ZP and MA. Online record: http://n2t.net/ark:/65665/320b8ee01-69e8-40bd-ab90-fcb717151953. (Labels read: "Col. // [illegible symbol] Type / No 5516 / U.S.N.M. [red label] // Ashmead / Collection // Collection / Ashmead // Augochlora (Agapostemon) / ♀ coerulea Ash // USNM ENT / 00536769 [yellow label with barcode]").

Augochlora sumptuosa bolliana Cockerell, 1909: 31 ♀ (syn. Under *Augochloropsis caerulea* by Sandhouse 1937). Images cursorily examined by ZP and MA. **New synonym. Syntype(s?)**: USA, Texas, Lee Co. [USNM Type No. 23306 barcode #: 00536763]. Online record: http://n2t.net/ark:/65665/32fdc8c3b-b5b4-4cec-968e-4040825fa92d (Labels read: "Lee Co. / TX. ~~06~~ / VI. 0 [illegible symbol] // [red label] Type No. / 23306 / U.S.N.M. // A. sumptuosa / bolliana Ckll / TYPE // USNM ENT / 00536763 [yellow label with barcode]").

Halictus (*Augochlora*) *pattoni* Vachal, 1903: 132 (proposed replacement name for *humeralis* Patton; syn. by Sandhouse 1937).

Augochlora (*Augochloropsis*) *humeralis* (in Titus 1901: taxonomy).

Augochloropsis caerulea (in Sandhouse 1937 [in part]: key; Lovell 1942: key).

Augochloropsis humeralis (in Dreisbach 1945: key).

Augochloropsis (*Paraugochloropsis*) *sumptuosa* (in Mitchell 1960 [in part]: key, redescription; Hurd 1979 [in part]: catalog; Moure and Hurd 1987 [in part]: catalog).

Diagnosis. Both sexes of *Augochloropsis humeralis* can be distinguished from *Augochloropsis metallica* and *Augochloropsis viridula* by multiple characters. The pronotal flange of *Augochloropsis humeralis* has the lateral edges approaching 90 degrees (Figs 14D, 16D) whereas, the lateral edges of the pronotal flange in *Augochloropsis metallica* and *Augochloropsis viridula* are obtuse (Figs 14E, F, 16E, F, note they do still have a distinct pronotal flange as well). In addition, the vertex of *Augochloropsis humeralis* rises distinctly above the ocelli (Figs 14A, 16A) whereas it does not rise above the ocelli in *metallica* and *viridula* (Figs 14B, C, 16B, C). Finally, the strongly tessellate and "silky" texture of *Augochloropsis humeralis* (Figs 14G, 16G) is distinct in comparison to *Augochloropsis metallica* and *Augochloropsis viridula* (Figs 14H, I, 16H, I).

Augochloropsis humeralis is similar in most respects to *Augochloropsis sumptuosa*. The females can be separated by the more densely punctate metasomal terga: *Augochloropsis humeralis* has the punctures on T1 and T2 close together and separated by about one puncture width (at least over most of the terga), whereas *Augochloropsis sumptuosa* has the punctures always well-separated (about 3–5 puncture widths apart). In addition, females of *Augochloropsis sumptuosa* have a weak but distinct semicircular carina around the propodeal triangle (Fig. 17D), which *Augochloropsis humeralis* lacks (Fig. 17A). More work is needed on how to separate the males of *Augochloropsis sumptuosa*, but the male of *Augochloropsis humeralis* appears to have the median emargination of S4 more acute (Fig. 20C), compared to more rounded truncate in *Augochloropsis sumptuosa* (see Mitchell 1960: fig 111 (mislabeled as S5)), though this character is variable and it's not clear how reliable it is.

Comments. What has previously been called *Augochloropsis sumptuosa* by Mitchell (1960) is not a single species but rather a species complex. Therefore, we have reinstated the name *Augochloropsis humeralis* Patton for the species occurring in the midwestern United States and retained the name *Augochloropsis sumptuosa* Smith for the species occurring in the southeastern United States. The exact extent of the range of *Augochloropsis sumptuosa* is unclear, and it is not clear to what extent the ranges of *Augochloropsis humeralis* and *Augochloropsis sumptuosa* may overlap. However, we have so far found no evidence that the two species overlap in range, with *Augochloropsis sumptuosa* appearing to be limited to the east coast of the United States and *Augochloropsis humeralis* appearing to be limited to the prairie region (Fig. 18). Historic records of *Augochloropsis sumptuosa* from Ohio were found to be misidentified *Augochloropsis metallica*. Since the identity of the midwestern species is clear, we have decided to proceed with a formal split; further delineation of the range of *Augochloropsis sumptuosa* must be accomplished in future research.

Two syntypes of *Augochloropsis humeralis* (1 male and 1 female) were located in the ANSP collection, where Sandhouse (1937) reported examining them. Though the specimens are undated and not clearly labeled as type specimens, the labels indicate that they are from the type locality. In addition, the specimens bear labels stating "Augochlora humeralis n.s." and "Augochlora humeralis n.sp.". The combination of the little-used name, the "n. sp.", the type locality, and the fact that Sandhouse (1937) considered these types, makes us confident that these are indeed Patton's syntypes. As a result, we have designated the female as the lectotype, making the male a paralectotype. Additional paralectotypes may potentially be present at the Smithsonian, as Titus (1901) states "Mr. Ashmead very kindly examined specimens in the U.S.N.M. of *A. humeralis* Patt., marked 'N. W. Kans., Williston'". However, our inquiries to the Smithsonian have received no answer.

Sandhouse (1937) considered the name *Augochloropsis caerulea* (Ashmead) to have priority because the name *humeralis* is a secondary homonym in the genus *Halictus*. However, *humeralis* is not a secondary homonym in the genus *Augochloropsis* and the substitute name is no longer in use, so following IZCN Article 59.3, the name *humeralis* is available and has priority.

Augochlora sumptuosa bolliana Cockerell is from Texas and was synonymized with *Augochloropsis sumptuosa* by Sandhouse (1937). Based on the online images of one of the syntypes, we are tentatively assigning it as a synonym of *Augochloropsis humeralis*, but a more critical evaluation of the specimen, with additional Texas material, should be performed.

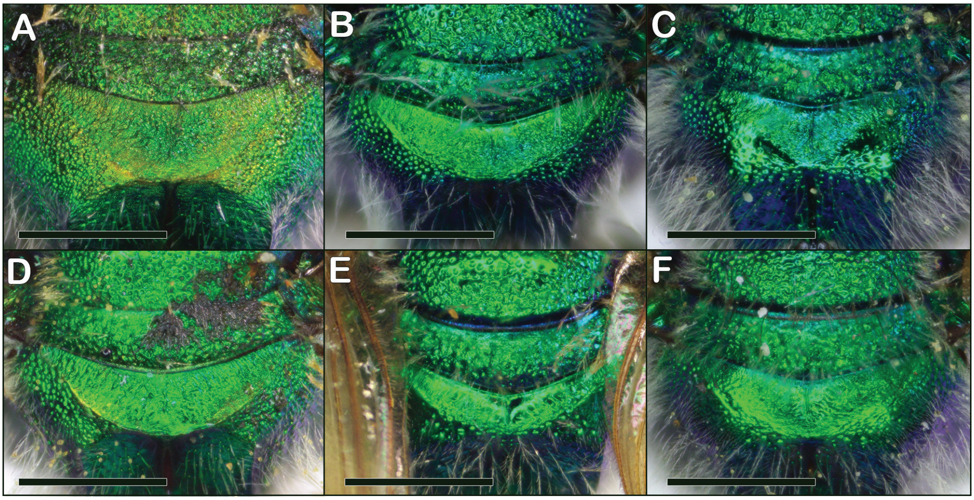

Figure 17. *Augochloropsis* female propodea **A** *Augochloropsis humeralis* **B** *Augochloropsis metallica* **C** *Augochloropsis viridula* **D** *Augochloropsis sumptuosa* **E** *Augochloropsis anonyma* **F** *Augochloropsis* sp. (likely undescribed species from Eastland, Texas). Scale bars: 1 mm, all images at the same scale.

Range. *Augochloropsis humeralis* occurs throughout the prairie region, ranging from North Dakota and Minnesota south to New Mexico and Texas, extending to Colorado in the west and Indiana in the east (Fig. 18). Specimens from Indiana Dunes National Park represent the easternmost records.

Biology. *Augochloropsis humeralis* is polylectic and nests are associated with deep sand (MA, pers. obs.). The sociality and the specifics of the nesting biology are unknown.

Material examined. **Colorado: Adams Co.:** Denver (39.8207, -104.8613): 1 ♂ [iNat], 29 Aug 2019, @francesco167 leg.; **Douglas Co.:** (39.3467, -104.7511): 1 ♀ [iNat], Jul 2020, @calebcam leg.; **Logan Co.:** (40.7752, -103.2721): 1 ♂ [iNat], 22 Aug 2014, R. Webster leg. **Illinois: Hancock Co.:** Warsaw (40.3427, -91.4493): 1 ♂ [iNat], 14 Aug 2016, A. Moorehouse leg., *Monarda punctata*; **Madison Co.:** [MASR]; **Mason Co.:** (40.3921, -89.9104): 1 ♀ [iNat], 18 Jun 2019, A. Moorehouse leg., *Asclepias* sp. **Indiana: Lake Co.:** Indiana Dunes NP, Marquette Trail (41.6111, -87.2365): 1 ♀ [IDNP], 19 Jun 2019, McGill leg., blue pan; Indiana Dunes NP, Miller woods (41.6057, -87.2644): 1 ♂ [IDNP], 12 Sep 2018, McGill leg., white pan; 1 ♀ [IDNP], 4 Jun 2019, McGill leg., yellow pan; 1 ♀ [IDNP], 23 Jul 2019, McGill leg., yellow pan; Indiana Dunes NP, Miller woods (41.6071, -87.2644): 1 ♀ [IDNP], 23 Jul 2019, McGill leg., yellow pan; **Newton Co.:** Kankakee Sands (41.0848, -87.402): 1 ♀ [iNat], 24 May 2018, D. Lucas leg.; **Porter Co.:** Indiana Dunes National Lakeshore, Mnoke Prairie (41.6185, -87.1012): 1 ♀ [IDNP], 29 Jun 2017, J. Villalpando leg., bee bowl. **Minnesota: Faribault Co.:** (43.7, -93.96): 1 ♀ [UMSP], 18 Sep 1911; **Fillmore Co.:** Pin Oak SNA (43.79261, -92.21915): 1 ♀ [MNDNR], 24 Jul 2017, bowl; **Hennepin Co.:** (44.9, -93.4): 1 ♂ [UMSP], date unknown; **Norman Co.:** Agassiz Dunes SNA (47.51154, -96.28976): 1 ♂ [MNDNR], 24 Aug 2015, bowl; **Sherburne**

Co.: Sherburne National Wildlife Refuge (45.46477, -93.67435): 2 ♀ [EERC], 15 Aug 2016, E. Evans leg., bowl; **Wabasha Co.:** Weaver Dunes (44.27746, -91.93892): 1 ♀ [UMSP], 28 May 2015, M.J. Hatfield leg., *Ceanothus herbaceus*; Weaver Dunes TNC/SNA (44.25096, -91.93795): 21 ♀ [MNDNR], 6 May 2017, bowl; 15 ♀ [MNDNR], 26 Jun 2017, bowl; 8 ♂ [MNDNR], 24 Jul 2017, bowl; 3 ♂ [MNDNR], 19 Aug 2017, bowl; 1 ♀ [MNDNR], 21 Sep 2017, bowl; **Washington Co.:** Belwin Conservancy (44.9241, -92.7931): 1 ♀ [EERC], 4 Sep 2015, J. Gardner leg., net, *Solidago nemoralis*; Belwin Conservancy (44.92569, -92.80001): 1 ♀ [CRC], 12 Jun 1995, C.C. Reed leg., net, *Penstemon grandifloris*; 1 ♀ [UMSP], 12 Jun 1995, C.C. Reed leg., net, *P. grandiflorus*; 9 ♀ [CRC], 15 Jun 1995, C.C. Reed leg., net, *P. grandifloris*; 6 ♀ [CRC], 16 Jun 1995, C.C. Reed leg., net, *P. grandifloris*; 1 ♀ 3 ♂ [CRC, UMSP], 15 Aug 1995, C.C. Reed leg., net, *Dalea purpurea*; 3 ♀ [CRC], 13 Jun 1997, C.C. Reed leg., net, *P. grandifloris*; Gray Cloud Dunes (44.79, -92.957): 1 ♀ 4 ♂ [UMSP], 9 Jul 1988; Grey Cloud Dunes (44.79, -92.957): 1 ♂ [CNBL], 23 Jul 2018, J. Petersen leg., net; Grey Cloud Dunes (44.7912, -92.9601): 1 ♂ [iNat], 14 Sep 2018, A. Birkey leg.; Grey Cloud Dunes SNA (44.79004, -92.95536): 1 ♂ [MNDNR], 9 Oct 2018, net, *S. nemoralis*; Grey Cloud Dunes SNA (44.790046, -92.955076): 1 ♂ [MNDNR], 31 Jul 2018, net, *D. villosa*; **Winona Co.:** Whitewater WMA (44.15033, -92.00066): 1 ♀ [MNDNR], 6 May 2017, bowl; 1 ♀ [MNDNR], 26 Jun 2017, bowl. **Missouri: Clark Co.:** [MASR]; **Scott Co.:** [MASR]. **Nebraska: Hooker Co.:**

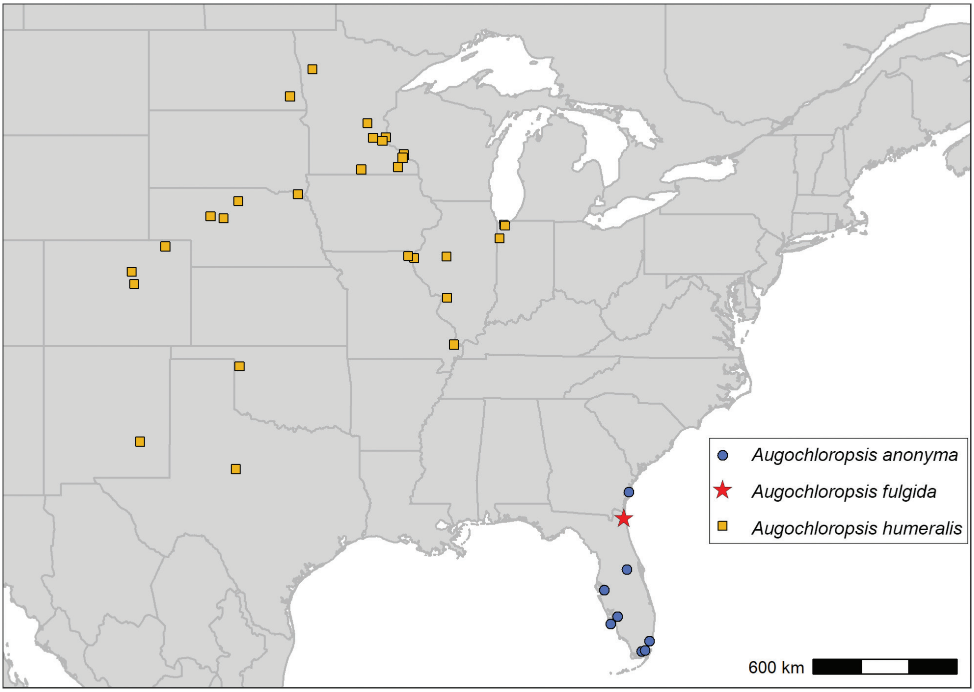

Figure 18. Map of specimens or observations examined for this study from the species *Augochlorpsis humeralis*, *Augochloropsis anonyma*, and *Augochloropsis fulgida*.

[MASR]; **Rock Co.:** (42.5, -99.8): 1 ♂ [iNat], Sep 2018, @allysond leg.; **Thomas Co.:** Neb Ntl For, near Halsey, 1 ♂ [WRME], 9 Aug 1991, Arduser leg.; Neb. Ntl For. Nr Whitetail campground: 1 ♀ [WRME], 10 Aug 1991, Arduser leg., *Helianthus petiolarus*. **New Mexico: Chaves Co.:** [MASR]. **North Dakota: Ransom Co.:** (46.474534, -97.342645): 1 ♂ [iNat], 9 Aug 2021, E. Wood leg.. **Oklahoma: Ellis Co.:** [MASR]. **South Dakota: Clay Co.:** Missouri National Recreation River (42.76215, -96.9743): 1 ♂ [iNat], 7 Jul 2021, @stenthesnake leg. **Texas: Taylor Co.:** (32.32, -99.92): 1 ♀ [OSUC], 18 Jun 1952, J.N. Knull, D.J. Knull leg.

Augochloropsis (*Paraugochloropsis*) *metallica* (Fabricius)

Andrena metallica Fabricius, 1793: 309 ♀. **Holotype**: ♀ "America" [NHMD 308680]. Images examined by ZP and MA (Fig. 19) (Labels read: "metalli. / ??[line illegible] // NHMD / 308680 [label with QR code] // Megilla metallica F. / Syst. Piez. 1804: 332. 19 // TYPE [red label]").

Augochlora fervida Smith, 1853: 81 ♂ (syn. [under *cuprea*] by Sandhouse 1937, syn. by Mitchell 1960 and Moure 1960). **Holotype**: ♂ North America [NHMUK014024969] Images examined by ZP and MA. Online record: https://data.nhm.ac.uk/object/3429259d-5af9-4c5f-9062-96a4a2770077 (Labels read: "Type / H.T. [label is circular with red border] // B.M. TYPE / HYM / 14.a.1230 // B.M. TYPE / HYM. / augochlora / fervida / smith 1853 // fervida / Type Sm. // Ent. Club. / 44-12. // NHMUK 014024969 [label with QR code]").

Augochlora (*Augochloropsis*) *cleomis* Titus, 1901: 135 ♀♂ (syn. by Moure 1960). **Syntypes**: ♀♂ USA, Colorado, Horsetooth Gulch, near Ft. Collins. Not examined.

Halictus chorisis Vachal, 1903: 136 ♀ (syn. by Sandhouse 1937 [under *cuprea*], syn. by Mitchell 1960 [under *metallica metallica*]). **Lectotype:** ♀ USA, Georgia (designated by Moure and Hurd 1987). Not examined.

Megilla metallica (in Fabricius 1804: taxonomy).

Augochlora fervida (in Robertson 1895: taxonomy; Robertson 1902: key; Cockerell 1906: notes).

Augochloropsis cuprea (in Sandhouse 1937 [in part]: key; Lovell 1942: key; Dreisbach 1945: key).

Augochloropsis (*Paraugochloropsis*) *metallica metallica* (in Mitchell 1960: key, redescription; Hurd 1979: catalog; Moure and Hurd 1987: catalog).

Augochloropsis (*Paraugochloropsis*) *metallica* (in Stephenson et al. 2018: checklist; Camilo et al. 2018: checklist; Decker et al. 2020: checklist).

Diagnosis. Both sexes of *Augochloropsis metallica* are most similar to *Augochloropsis viridula*, but *Augochloropsis metallica* can be separated from *Augochloropsis viridula* by the thicker hair fringe on the apical edge of T1 and T2; *Augochloropsis metallica* has the hairs noticeably thicker than the other hairs of the metasoma (Figs 14H, 15A, 16H), whereas the fringe hairs of *Augochloropsis viridula* are not noticeably thicker than the other metasomal hairs (Figs 14I, 15B, 16I). In addition, the terga of *Augochloropsis metallica* are more closely punctured, separated by about one puncture width on T2 (Fig. 14H, 16H), whereas the terga of *Augochloropsis viridula* are more sparsely punctured and separated by at least 2–4 puncture widths on T2 (Figs 14I, 16I).

Both sexes of *Augochloropsis metallica* can be separated from *Augochloropsis humeralis* by the shape of the pronotal flange and angle, which is smaller and has an obtuse lateral angle in *Augochloropsis metallica* (Figs 14E, 16E), compared to the larger flange and 90-degree lateral angle in *Augochloropsis humeralis* (Figs 14D, 16D). In addition, *Augochloropsis metallica* has the metasomal terga shining, with at most weak tessellation (Figs 14H, 16H), whereas *Augochloropsis humeralis* has the metasomal terga strongly and densely tessellate, resulting in dull, silky coloration (Figs 14G, 16G).

Comments. The holotype of *Augochloropsis metallica* (Fig. 19) is missing its head, but the punctures and hair bands on the metasoma, combined with the locality of "America" (Moure (1960) states "probably middle eastern U.S.A.") are sufficient to confirm its identity.

We define *Augochloropsis metallica* in a much more restricted sense than previous authors, who lumped multiple taxa under *Augochloropsis metallica* (e.g., Sandhouse 1937; Mitchell 1960). We are here splitting *Augochloropsis metallica* (as defined by Mitchell 1960) into five taxa: *A. metallica*, *A. cuprea*, *A. fulgida*, *A. fulvofimbriata*, and *A. viridula*. In the original revision of the *Augochloropsis* of the United States, Sandhouse (1937) lumped at least six distinct taxa under the name *Augochloropsis cuprea* (Table 1). One reason for this over-lumping appears to be that Sandhouse (1937) did not actually examine any of the type specimens, and synonymized many species based on the description alone or through correspondence. Examination of Sandhouse-determined material in the UMSP shows that she consistently lumped specimens of *Augochloropsis metallica*, *Augochloropsis viridula*, and a third unknown species together. Mitchell (1960) clearly recognized that *Augochloropsis metallica* and *Augochloropsis viridula* [as *Augochloropsis metallica fulgida*] were distinct, and it is unclear why he only split them into subspecies.

The traditional view that *Augochloropsis metallica* extends down through Mexico and Central America is almost certainly incorrect and merely an artifact of the erroneously broad definition of the species adopted by previous workers. Though we have examined relatively little material from south of the United States, the material we have examined has not matched any of the US *Augochloropsis* treated here. The synonymy of *Augochloropsis fulvofimbriata* Friese, described from Costa Rica, is almost certainly incorrect. The source of the synonymy of *Augochloropsis fulvofimbriata* was originally made by Sandhouse (1937), who synonymized the male of *Augochloropsis fulvofimbriata* under *Augochloropsis ignita* and the female of *Augochloropsis fulvofimbriata* under *Augochloropsis cuprea*. However, Michener (1954), in his revision of the bees of Panama, treated *Augochloropsis fulvofimbriata* as valid, and though he did not mention the synonymy of *A. fulvofimbriata* under *Augochloropsis cuprea*, he did state about *A. fulvofimbriata*: "Sandhouse incorrectly placed this species in the synonymy if [sic] *ignita*." Based on that, Michener (1954)

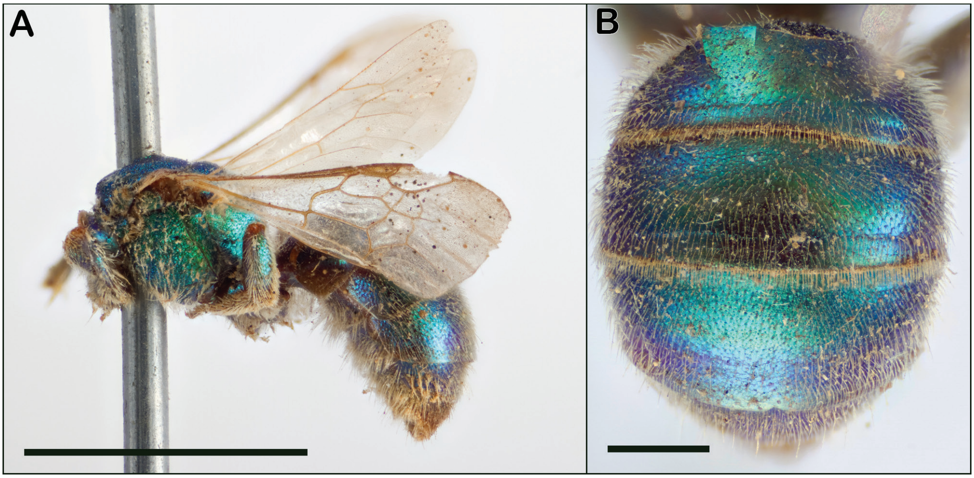

Figure 19. *Augochloropsis metallica* holotype female **A** lateral view **B** metasoma. Images provided by Lars Vilhelmsen, Sree Selvantharan, and Anders Illum of the Natural History Museum of Denmark, and used with permission. Scale bars: 5 mm (**A**); 1 mm (**B**).

clearly considered *Augochloropsis fulvofimbriata* a valid species (and he certainly would have been familiar with *Augochloropsis metallica*, which was then called *A. cuprea*). Moure (1960) did not list *Augochloropsis fulvofimbriata* as a synonym of *Augochloropsis metallica metallica*. However, following that, the works of Mitchell (1960), Hurd (1979), Moure and Hurd (1987), and Moure et al. (2007) all treat *Augochloropsis fulvofimbriata* as a synonym of *Augochloropsis metallica metallica*, but none of them indicate it is a new synonym, which suggests they were just carrying over the synonymy by Sandhouse (1937). Here, though we have not examined any material of *Augochloropsis fulvofimbriata*, we follow the classification of Michener (1954) who was the last worker to treat the species, and we formally treat *Augochloropsis fulvofimbriata* Friese (**stat. nov.**), as valid. This is supported by the findings of Celis and Cure (2017), who recognized *Augochloropsis fulvofimbriata* and even classified it in a separate subgenus than *Augochloropsis metallica* (*Augochloropsis s.s.* rather than *Paraugochloropsis*).

Another synonym with issues is *Augochloropsis chorisis* Vachal, which was originally synonymized under *Augochloropsis cuprea* by Sandhouse (1937) and listed as a synonym of *Augochloropsis metallica metallica* by Michell (1960). The type series of *Augochloropsis chorisis* contains specimens ranging from Georgia and Texas to Brazil (Rasmussen 2012), making it undoubtedly a composite series (Cockerell 1949). The specimen from Georgia was designated as a lectotype by Moure and Hurd (1987), who considered it a synonym of *Augochloropsis metallica metallica*. We have not been able to examine the lectotype which cannot be located at the National Museum of Natural History in Paris, France (A. Touret-Alby, pers. comm.) and we are nominally accepting the synonymy.

Augochlora (*Augochloropsis*) *cleomis* was described from a male and female specimen from near Fort Collins, Colorado (Titus 1901). The types were not examined and it is not entirely clear from the description whether it is a synonym of *Augochloropsis metallica* or *Augochloropsis humeralis*. It was originally synonymized with *Augochloropsis cuprea* by Sandhouse (1937) and was later synonymized with *Augochloropsis metallica metallica* by Moure (1960). Sandhouse (1937) did not examine any specimens and it is unclear whether Moure (1960) did. Regardless, it is likely a synonym of *Augochloropsis metallica*, so we are nominally accepting the synonym.

Biology. *Augochloropsis metallica* is polylectic and nests in the ground. However, the specifics of the nesting biology and sociality are unknown. *Augochloropsis metallica* is often associated with sandy areas, and it has been found in natural habitats (e.g., native prairies, wetlands), as well as disturbed sites and urban areas.

Range. *Augochloropsis metallica* occurs in the eastern states and across the Great Plains (Fig. 21A). Recent surveys (2009 to present) by MSA and co-workers in Oklahoma, Kansas and Nebraska have found *Augochloropsis metallica* throughout these states and further to the west (whereas *Augochloropsis viridula* is absent from those western areas).

Material Examined. Arkansas: Arkansas Co.: [MASR]; **Faulkner Co.:** [MASR]; **Franklin Co.:** [MASR]; **Jackson Co.:** [MASR]; **Monroe Co.:** [MASR]; **White Co.:** [MASR]; **Woodruff Co.:** [MASR]. **Illinois: Calhoun Co.:** [MASR]; **Carroll Co.:** [MASR]; **Jasper Co.:** [MASR]; **Madison Co.:** [MASR]; **Marion Co.:** [MASR]; **Randolph Co.:** [MASR]; **Williamson Co.:** [MASR]. **Iowa: Jasper Co.:** [MASR]. **Kansas: Barton Co.:** [MASR]; **Bourbon Co.:** [MASR]; **Butler Co.:** [MASR]; **Chase Co.:** [MASR]; **Coffey Co.:** [MASR]; **Dickinson Co.:** [MASR]; **Douglas Co.:** (38.88, -95.29): 1 ♀ [UMSP], 11 Jun 1919, W.F. Hoffman leg.; 1 ♀ [UMSP], 2 Jul 1919, W.F. Hoffman leg.; **Geary Co.:** [MASR]; **Gove Co.:** [MASR]; **Greenwood Co.:** [MASR]; **Hodgeman Co.:** [MASR]; **Lane Co.:** [MASR]; **Lyon Co.:** [MASR]; **Morris Co.:** [MASR]; **Osage Co.:** [MASR]; **Pawnee Co.:** [MASR]; **Pottawatomie Co.:** [MASR]; **Reno Co.:** [MASR]; **Rice Co.:** [MASR]; **Riley Co.:** [MASR]; **Sheridan Co.:** [MASR]; **Thomas Co.:** [MASR]; **Trego Co.:** [MASR]. **Minnesota: Anoka Co.:** Bunker Hills Reg. Pk. (45.2176, -93.2898): 1 ♀ [EERC], 8 Jun 2015, J. Gardner leg., net, *Tradescantia occidentalis*; Bunker Hills Regional Park (45.2176, -93.2899): 1 ♀ [EERC], 13 Jul 2016, E. Evans leg., bowl; Bunker Pr. Dunes (45.21, -93.27): 1 ♀ [UMSP], 20 Jun 1947; Cedar Creek Ecosystem Science Reserve (45.4323, -93.1894): 2 ♀ [EERC], 22 May 2015, J. Gardner leg., bowl trap; Cedar Creek Nat. Hist. (45.402673, -93.202601): 1 ♂ [CRC], 1 Aug 1991, C.C. Reed leg., net, *Dalea purpurea*; 1 ♂ [UMSP], 20 Aug 1991, C.C. Reed leg.; Cedar Creek Natural History Area (45.402673, -93.202601): 1 ♀ [UMSP], 23 Jul 1986; 1 ♂ [UMSP], 30 Jul 1990; 1 ♀ [UMSP], 21 Sep 1992; 1 ♀ [UMSP], 15 Aug 1995; Cedar Creek Ecosystem Science Reserve (45.4037, -93.1834): 1 ♂ [EERC], 12 Aug 2015, J. Gardner leg., net, *D. villosa*; Helen Allison Savanna SNA (45.38454, -93.16319): 1 ♀ [MNDNR], 6 May 2017, bowl; Rum River Cent. Reg. Pk. (45.2907, -93.3811):

1 ♀ [EERC], 12 Jun 2015, E. Evans leg., net, *Amorpha fruticosa*; **Anoka/Isanti Co.:** Cedar Creek Natural History Area (45.402673, -93.202601): 1 ♀ [UMSP], 15 Aug 2000; **Hennepin Co.:** Crow Hassan Park Reserve (45.2, -93.63): 2 ♀ [UMSP], 13 Jul 1995, C.C. Reed leg., net, *Aster sericeus*; **Isanti Co.:** Cedar Creek Natural History Area (45.402673, -93.202601): 1 ♀ [UMSP], 29 Aug 1981; 1 ♀ [UMSP], 13 Jul 1991; 1 ♀ [UMSP], 14 Jul 1992; 1 ♀ [UMSP], 30 Sep 1992; 1 ♀ [UMSP], 11 Aug 1993; Irving & John Anderson County Park (45.4602, -93.0594): 1 ♂ [EERC], 20 Jul 2015, E. Evans leg., net, *Asclepias tuberosa*; **Lincoln Co.:** Hole in the Mountain (44.25680554, -96.29248338): 1 ♀ [UMSP], 15 Jun 2016, N. Pennarolla, J. Leone leg., bowl; 1 ♀ [UMSP], 27 Jun 2017, N. Pennarolla, J. Leone leg., bowl; Hole-in-the-Mountain TNC (44.2412, -96.29963): 2 ♀ [MNDNR], 6 Jun 2016, bowl; 1 ♀ [MNDNR], 27 Jun 2016, bowl; **Murray Co.:** (44.0709, -95.5718): 1 ♀ [CNBL], 29 Jun 2019, Bee Bowls; **Pipestone Co.:** Prairie Coteau SNA (44.1241, -96.15275): 1 ♀ [MNDNR], 6 Jun 2016, bowl; **Stearns Co.:** St. Cloud (45.44, -94.16): 1 ♀ [UMSP], 22 Jun 1967; **Yellow Medicine Co.:** Mound Spring Prairie SNA (44.74521, -96.42999): 6 ♀ [MNDNR], 6 Jun 2016, bowl. **Missouri: Barry Co.:** [MASR]; **Barton Co.:** [MASR]; **Benton Co.:** [MASR]; **Boone Co.:** Columbia (38.943, -92.333): 1 ♀ [OSUC], 19 Oct 1955, W.A. Dimmitt leg.; **Camden Co.:** [MASR]; **Douglas Co.:** [MASR]; **Franklin Co.:** [MASR]; **Harrison Co.:** [MASR]; **Howard Co.:** Fayette (39.141, -92.686): 9 ♂ [UMSP], 25 Sep 1966, D.B. Crockett leg.; **Jackson Co.:** [MASR]; **Jasper Co.:** [MASR]; **Jefferson Co.:** [MASR]; **Laclede Co.:** [MASR]; **Lafayette Co.:** [MASR]; **Linn Co.:** [MASR]; **Macon Co.:** [MASR]; **Mercer Co.:** [MASR]; **Miller Co.:** [MASR]; **Monroe Co.:** [MASR]; **Newton Co.:** [MASR]; **Pettis Co.:** [MASR]; **Ray Co.:** [MASR]; **Reynolds Co.:** [MASR]; **Saline Co.:** [MASR]; **Scott Co.:** [MASR]; **St. Clair Co.:** [MASR]; **St. Louis Co.:** [MASR]; **Ste. Genevieve Co.:** [MASR]; **Stoddard Co.:** [MASR]; **Sullivan Co.:** [MASR]; **Taney Co.:** [MASR]. **Nebraska: Co.:** Halsey (41.904, -100.27): 1 ♀ [UMSP], 3 Sep 1924, R.W. Dawson leg.; **Lancaster Co.:** [MASR]; **Richardson Co.:** [MASR]. **North Carolina: Wake Co.:** Raleigh (35.799, -78.617): 1 ♀ [UMSP], 26 May 1940; 1 ♂ [UMSP], 17 Nov 1940. **Ohio: Gallia Co.:** (38.82, -82.3): 1 ♀ [OSUC], 23 Aug 1942, C.H. Kennedy leg.; **Jackson Co.:** (39.01, -82.61): 1 ♂ [OSUC], 9 Aug 1942, J.E. Gillaspy leg.; 1 ♀ [OSUC], 9 Aug 1942, R.W. Strandtmann leg.; **Lawrence Co.:** (38.6, -82.52): 1 ♂ [OSUC], 8 Aug 1942, R.W. Strandtmann leg.; 4 ♀ 1 ♂ [OSUC], 9 Aug 1942, R.W. Strandtmann leg.; 6 ♀ 1 ♂ [OSUC], 23 Aug 1942, C.H. Kennedy leg.; **Muskingum Co.:** New Concord (39.995, -81.741): 1 ♀ [OSUC], 22 May 1975, C. Dasch leg. **Oklahoma: Ellis Co.:** [MASR]. **South Dakota: Co.:** Black Hills (43.96, -103.77): 1 ♀ [UMSP], 15–30 Jun 1931, F. Miller leg. **Texas: Dallas Co.:** (32.73, -96.8): 1 ♀ [UMSP], 14 May 1937, H.C. Knutson leg., *Marshallia caespitosa*; **Smith Co.:** (32.39, -95.26): 1 ♀ [UMSP], May 1947, Barr leg. **Virginia: Arlington Co.:** (38.87, -77.09): 2 ♂ [UMSP], 20 Jul 1929, C.E. Michel leg.; **Fauquier Co.:** Warrentown (38.721, -77.799): 1 ♂ [UMSP], 28 Jul 1929, C.E. Michel leg.

Augochloropsis (*Paraugochloropsis*) *viridula* (Smith), stat. nov.

Augochlora viridula Smith, 1853: 81 ♂. **Holotype**: ♂ USA, New York, Trenton Falls [NHMUK 014024971]. Images examined by ZP and MA. Online record: https://data.nhm.ac.uk/object/10fb10b0-58d6-448c-b1b8-d3807ca35e0e (Labels read “Type / H.T. [label is circular with red border] // B.M. TYPE / HYM / 14.a.1232 // B.M. TYPE / HYM. / augochlora / viridula / smith 1853 // viridula / Type Sm // Ent. Club. / 44-12. // NHMUK 014024971 [label with QR code]”).

Augochlora lucidula Smith, 1853: 81 ♀ (syn. Patton 1879). **Holotype**: ♀ North America. Images examined by ZP and MA. Online record: https://data.nhm.ac.uk/

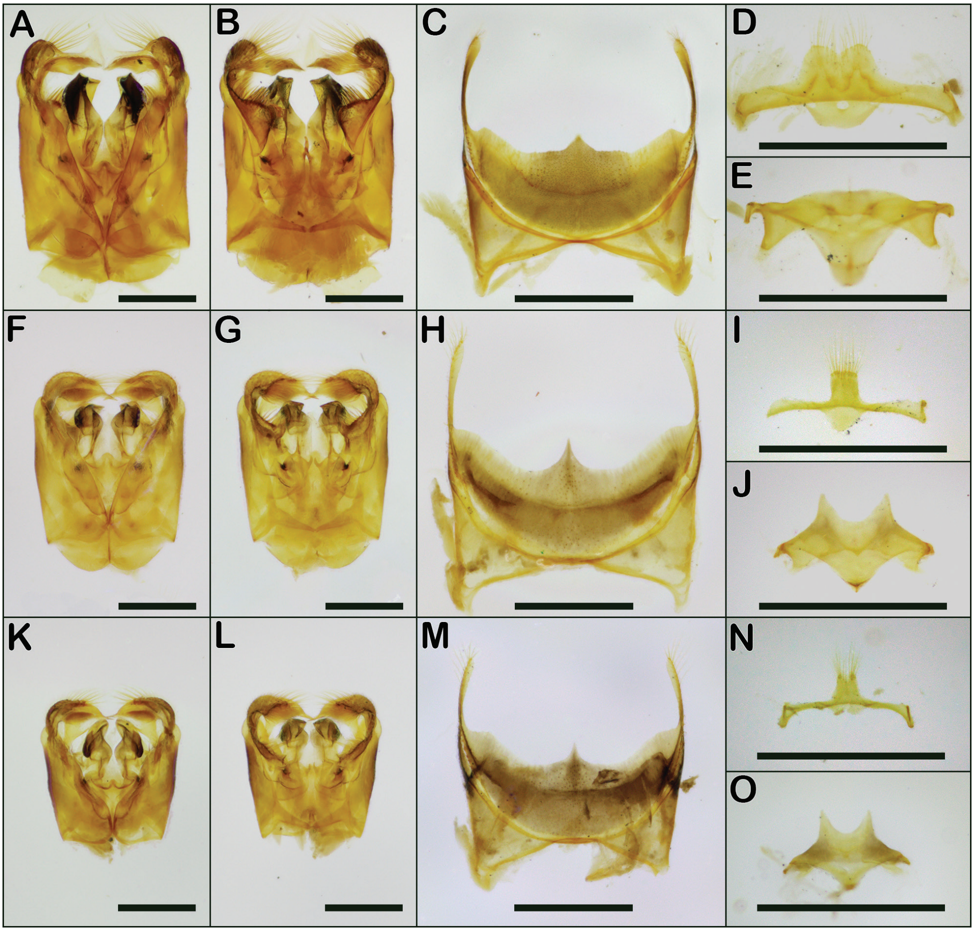

Figure 20. *Augochloropsis* male terminalia **A** *Augochloropsis humeralis* dorsal genitalia **B** *Augochloropsis humeralis* ventral genitalia **C** *Augochloropsis humeralis* S4 **D** *Augochloropsis humeralis* S8 **E** *Augochloropsis humeralis* S7 **F** *Augochloropsis metallica* dorsal genitalia **G** *Augochloropsis metallica* ventral genitalia **H** *Augochloropsis metallica* S4 **I** *Augochloropsis metallica* S8 **J** *Augochloropsis metallica* S7 **K** *Augochloropsis viridula* dorsal genitalia (note the gonobase was torn off) **L** *Augochloropsis viridula* ventral genitalia **M** *Augochloropsis viridula* S4 **N** *Augochloropsis viridula* S8 **O** *Augochloropsis viridula* S7. Scale bars: 1 mm.

object/9195d66b-dde0-4554-a11e-8352601fa232 (Labels read "Type / H.T. [label is circular with red border] // B.M. TYPE / HYM / 14.a.1233 // B.M. TYPE / HYM / augochlora / lucidula / Smith 1853 // lucidula / Type Sm. // Ent. Club. / 44-12 // NHMUK 014024972 [label with QR code]").

Halictus (*Augochlora*) *viridissimus* Viereck, 1910: 688 (proposed replacement name for *viridula* Smith, preoccupied in *Halictus*).

Augochlora viridula (in Robertson 1895: taxonomy; Robertson 1902: key; Cockerell 1905: taxonomy).

Augochloropsis cuprea (in Sandhouse 1937 [in part]: key; Lovell 1942: key).

Augochloropsis viridula (in Dreisbach 1945: key).

Augochloropsis metallica (Fabricius) (in Eickwort 1969: generic revision, description of genitalia and other features).

Augochloropsis (*Paraugochloropsis*) *metallica fulgida* (in Mitchell 1960: key, redescription; Hurd 1979: catalog; Moure and Hurd 1987: catalog; Gibbs 2017: biology).

Augochloropsis (*Paraugochloropsis*) *fulgida* (in Stephenson et al. 2018: checklist; Camilo et al. 2018: checklist; Decker et al. 2020: checklist).

Diagnosis. Both sexes of *Augochloropsis viridula* can be recognized primarily by the lack of a thickened hair fringe on T1 and T2; the hairs that are present along the margin are slender and the same size and width as the rest of the hairs on the terga (Fig. 15B). This is in contrast to the females of *Augochloropsis metallica* which have the fringe hairs noticeably thickened (Fig. 15A). In addition, the terga of *Augochloropsis viridula* are more shining and sparsely punctured, and this is most apparent on T1 and T2, with punctures on T2 separated by at least 2–4 puncture widths on T2 (Figs 14I, 16I). In contrast, *Augochloropsis metallica* has the punctures on T1 and T2 closer together (punctures typically separated by 1–2 puncture widths on T2) and the interspaces between the punctures have slight tessellation, though they are still somewhat shining (Figs 14H, 16H).

Augochloropsis viridula can be separated from *Augochloropsis humeralis* by its less developed pronotal flange, which is weak and forms an obtuse angle in *Augochloropsis viridula* (Figs 14F, 16F) compared to extensive and forming a right angle in *Augochloropsis humeralis* (Figs 14D, 16D), and *Augochloropsis viridula has* the terga smooth and shining (Figs 14I, 16I), compared to heavily tessellate and dull in *Augochloropsis humeralis* (Figs 14G, 16G).

Augochloropsis viridula can be separated from *Augochloropsis anonyma* and *Augochloropsis fulgida* by the relative lack of black hairs on the metasoma, having at most a few scattered black hairs on the apical terga (Fig.14I), compared to copious black hairs over most of the terga in *Augochloropsis anonyma* and *Augochloropsis fulgida* (Fig. 23C, D).

Biology. *Augochloropsis viridula* is a polylectic ground-nester. Nesting and sociality were documented by Gibbs (2017) [as *Augochloropsis metallica fulgida*]. Gibbs (2017) found a nest with two females, one of which had undeveloped ovaries and could have been a worker, suggesting that this bee may be primitively eusocial, however more work is needed to understand the degree of sociality of this species.

Range. *Augochloropsis viridula* occurs throughout the eastern United States (Fig. 21B). It does not spread as far west as *Augochloropsis metallica* (see Fig. 21A), and recent surveys (2009 to present) by MSA and co-workers in Oklahoma, Kansas and Nebraska have found *viridula* only on the extreme eastern margins of these states, while *metallica* has been found throughout these states and further to the west. Mitchell records it [as *metallica fulgida*] extending south to Florida, though we have not evaluated material from the purported southernmost portion of the range.

Comments. This species has historically been referred to as *Augochloropsis metallica fulgida* sensu Mitchell (1960). However, after examination of the holotype of *Augochloropsis fulgida* (Fig. 23), we found that it does not match the species concept used by Mitchell (1960) for *Augochloropsis metallica fulgida*. As a result, we resurrect the name *Augochloropsis viridula* (Smith), which was previously used by Robertson (1902) and Dreisbach (1945). *Augochloropsis fulgida* is reinstated as a separate species (see remarks for that species).

The species-level (rather than subspecies-level) recognition of *Augochloropsis metallica* and *Augochloropsis viridula* (previously classified as *Augochloropsis metallica metallica* and *Augochloropsis metallica fulgida*, respectively, by Mitchell (1960)) is supported by multiple characters, including the hair fringe on T2 (see Fig. 15A, B), difference in the degree of punctures and tessellation, the male terminalia, and differences in the extent of range. In particular, the male terminalia are distinct, with *Augochloropsis metallica* having the gonostyli more expanded (Fig. 20F, G), the gonocoxites more parallel-sided (Fig. 20F, G), the lateral arms of S4 more straight (Fig. 20H), and the lateral apodemes of S7 wider (Fig. 20J), in comparison, *Augochloropsis viridula* have the gonostyli narrower (Fig. 20K, L), the gonocoxites diverging apically (Fig. 20K, L), the lateral arms of S4 more curved (Fig. 20M), and the lateral apodemes of S7 narrower (Fig. 20O). The shape of S8 (Fig. 20I, N) appears to be too variable to be useful as a splitting character.

That *Augochloropsis viridula* (Smith) and *Augochloropsis lucidula* (Smith) were different sexes of the same species was recognized by Patton (1879), Robertson (1895), and Cockerell (1905). However, both names were synonymized under *Augochloropsis cuprea* (along with *Augochloropsis anonyma*) by Sandhouse (1937). The name *Augochloropsis viridula* was then correctly applied by Dreisbach (1945). Mitchell (1960) clearly did not consider *viridula* and *lucidula* conspecific as he considered *Augochloropsis viridula* a junior synonym of *Augochloropsis metallica metallica* and *Augochloropsis lucidula* a junior synonym of *Augochloropsis metallica fulgida*. Moure (1960) considered both *viridula* and *lucidula* junior synonyms of *Augochloropsis metallica*. Here, after examination of the primary types, we agree with the interpretation of Patton (1879) and Robertson (1895) in considering *Augochloropsis viridula* and *Augochloropsis lucidula* as both conspecific and a true species.

In the generic revision of augochlorine bees by Eickwort (1969), the subspecies of *Augochloropsis metallica* were not recognized. However, the illustrations of the genitalia and other characters are clearly of *Augochloropsis viridula* (rather than *Augochloropsis metallica*) based on the apically diverging lateral margins of the gonostyli.

Material examined. USA: Alabama: Hale Co.: [MASR]. **Arkansas: Lawrence Co.:** [MASR]; **Monroe Co.:** [MASR]; **White Co.:** [MASR]; **Woodruff Co.:** [MASR]. **Georgia: Catoosa Co.:** [MASR]. **Illinois: Carroll Co.:** [MASR]; **Jasper Co.:** [MASR]; **Madison Co.:** [MASR]; **Marion Co.:** [MASR]; **Ogle Co.:** (41.8751, -89.3474): 1 ♀ [NACH], 1 Jul 2017, B. Bruninga-Socolar leg., net, *Parthenium integrifolium*; (41.896, -89.3461): 1 ♀ [NACH], 13 Jun 2017, B. Bruninga-Socolar leg., net, *Trifolium pratense*; **Randolph Co.:** [MASR]; **Williamson Co.:** [MASR]. **Indiana: Lake Co.:** Indiana Dunes NP, Miller woods (41.6057, -87.2644): 1 ♀ [IDNP], 23 Aug 2019, McGill leg., blue pan. **Iowa: Clayton Co.:** [MASR]; **Jasper Co.:** [MASR]; **Pottawattamie Co.:** [MASR]; **Story Co.:** Ames (42.016, -93.624): 2 ♀ [UMSP], 16 Jun 1930, B.A. Haws leg., Swept from sweet clover. **Kansas: Johnson Co.:** [MASR]; **Linn Co.:** [MASR]. **Maine: Knox Co.:** (44.04, -69.04): 1 ♀ [OSUC], 15 Jul 1956, D.J. Borror leg. **Michigan: Cheboygan Co.:** (45.48, -84.49): 1 ♀ [OSUC], date unknown, C.H. Kennedy leg.; **Gladwin Co.:** [MASR]. **Minnesota: Anoka Co.:** Bunker Hills Regional Park (45.2143, -93.2797): 1 ♀ [EERC], 24 Jun 2016, J. Gardner leg., net, *Crepis tectorum*; Cedar Creek Nat. Hist. (45.402673, -93.202601): 1 ♂ [UMSP], 1 Aug 1991, C.C. Reed leg.; Cedar Creek Natural History Area (45.402673, -93.202601): 1 ♀ [UMSP], 10 May 1993; Rum River Cent. Reg. Pk. (45.28686656, -93.37669731): 1 ♀ [EERC], 12 Jun 2015, E. Evans leg., net, *Rosa arkansana*; Rum River Cent. Reg. Pk. (45.2883, -93.38): 2 ♀ [EERC], 12 Jun 2015, E. Evans leg., net, *Zizia aurea*; Rum River Cent. Reg. Pk. (45.2907, -93.3811): 7 ♀ [EERC], 12 Jun 2015, E. Evans leg., net, *Amorpha fruticosa*; **Anoka/Isanti Co.:** Cedar Creek Natural History Area (45.402673, -93.202601): 1 ♀ [UMSP], 17 Sep 2004; **Blue Earth Co.:** Gilfillan Lake WMA (44.21091, -93.8494): 1 ♀ [MNDNR], 3 Oct 2016, net, *Symphyotrichum lanceolatum*; Maple River WMA (43.979867, -94.042629): 1 ♂ [MNDNR], 14 Aug 2015, net, *Solidago altissima*; **Carver Co.:** Schneewind WMA (44.80941, -93.82892): 1 ♀ [MNDNR], 8 Aug 2018, net, *Melilotus alba*; Schneewind WMA (44.80952, -93.82793): 1 ♀ [MNDNR], 16 Jul 2018, bowl; **Chisago Co.:** Wild River SP (45.5215, -92.7309): 1 ♀ [MNDNR], 22 Jun 2020, N. Gerjets leg., pantrap; **Douglas Co.:** StaffansonTNC (45.81606, -95.74604): 1 ♀ [CNBL], 5 Jun 2018, G. Pardee leg., net, *Z. aptera*; 1 ♀ [CNBL], 5 Jun 2018, I. Lane leg., net, *Z. aptera*; **Fillmore Co.:** (43.7, -92.2): 1 ♀ [UMSP], 24 May 1937, G. Kohls leg.; **Goodhue Co.:** Frontenac (44.53, -92.351): 1 ♀ [UMSP], 29 May 1930, C.E. Michel leg.; Spring Creek Prairie SNA (44.55522, -92.59502): 1 ♂ [MNDNR], 11 Aug 2017, net, *Asclepias verticillata*; **Goodhue/Wabasha Co.:** E Frontenac, Lake Pepin (44.53, -92.351): 1 ♀ [UMSP], 29 May 1941, M.W. Wing leg.; Frontenac, Lake Pepin (44.53, -92.351): 1 ♀ [UMSP], 29 May 1941, M.W. Wing leg., net; **Hennepin Co.:** (44.9, -93.4): 1 ♀ [UMSP], 27 May 1922, A.A. Nichol leg.; Crow-Hassan Park Reserve (45.2018, -93.6311): 1 ♀ [MNDNR], 25 Aug 2015, bowl; Minnesota Valley National Wildlife Refuge (44.79892, -93.38589): 1 ♀ [MNDNR], 17 Jul 2017, net, *Solanum dulcamara*; St Bonifacius: 6 Mile Marsh (44.9113, -93.71958): 1 ♀ [CNBL], 28 Jul 2018, Z. Portman leg., net, *M. alba*; St Bonifacius: 6 Mile Marsh (44.9121, -93.7217): 1 ♀ [CNBL], 5 Jun 2020, Z. Portman leg., net, *Z. aurea*; **Houston Co.:** (43.67, -91.5): 3 ♀ [UMSP], 21 May 1938, H.E. Milliron leg.;

(43.68, -91.47): 2 ♀ [UMSP], 23 May 1936, C.E. Michel leg.; 4 ♀ [UMSP], 23 May 1936, D. Murray leg.; 1 ♀ [UMSP], 23 May 1936, O. Elster leg.; 3 ♀ [UMSP], 23 May 1936, R. Cottrell leg.; 1 ♀ [UMSP], 22 May 1937, H.S. Telford leg.; 2 ♀ [UMSP], 24 May 1937, C.E. Michel leg.; 1 ♀ [UMSP], 20 May 1938, P. Nicholson leg.; 3 ♀ [UMSP], 21 May 1938, C.E. Michel leg.; 2 ♀ [UMSP], 21 May 1938, H.E. Milliron leg.; 1 ♀ [UMSP], 21 May 1938, R. Anderson leg.; 1 ♀ [UMSP], 22 May 1938, R. Anderson leg.; 1 ♀ [UMSP], 21 Jun 1938, C.E. Michel leg.; 1 ♀ [UMSP], 26 May 1940, I. Tarshie leg.; Beaver Crk. Valley St. Park (43.642, -91.581): 2 ♀ [UMSP], 4 Jul 1973, Malaise trap; Eitzen (43.51, -91.46): 1 ♀ [UMSP], 23 May 1936; Mississippi Bluff, 1–2 m N State Line (43.524, -91.28): 1 ♀ [UMSP], 30 May 1941, J.H. Hughes leg.; 1 ♀ [UMSP], 27 May 1950; 1 ♀ [UMSP], May 1957; Mississippi Bluffs 1 mi N. New Albin, Ia. (43.514, -91.279): 1 ♀ [UMSP], 29 May 1960; Mound Prairie SNA (43.76248, -91.42277): 1 ♀ [MNDNR], 26 Jun 2017, bowl; S.E. tip of county (43.52, -91.29): 1 ♀ [UMSP], 24 May 1935, H. Dodge leg.; Winnebago Cr. Vy., 2–4 m NE Eitzen (43.541, -91.415): 1 ♀ [UMSP], 27 Jun 1956; **Isanti Co.:** Cedar Creek Natural History Area (45.402673, -93.202601): 1 ♀ [UMSP], 1 Aug 1985; 2 ♀ [UMSP], 21 May 1987, *Rubus sp*; 1 ♂ [UMSP], 30 Sep 1992; 1 ♀ [UMSP], 1 Sep 1993; 2 ♀ [UMSP], 27 Jul 1994; 1 ♂ [UMSP], 17 Sep 1994; 1 ♀ [UMSP], 19 Aug 2000; 1 ♀ [UMSP], 19 Aug 2001; **Jackson Co.:** Des Moines River SNA (43.79222, -95.09111): 6 ♀ [MNDNR], 6 Jun 2016, bowl; **Kanabec Co.:** Rice Creek WMA (45.7389, -93.2044): 1 ♀ [MNDNR], 30 Jun 2020, D. Drons leg., net, *Rhus glabra*; **Kandiyohi Co.:** Brenner (45.4006, -95.2462): 1 ♀ [CNBL], 7 Jun 2018, G. Pardee leg., net, *Z. aptera*; Brenner Lake WPA (45.39926, -95.24568): 2 ♀ [MNDNR], 6 Jul 2016, bowl; Nelson (45.35289989, -95.11923718): 1 ♀ [CNBL], 26 Jun 2017, R. Tucker leg., net, *Cirsium arvense*; 1 ♀ [CNBL], 4 Jun 2018, I. Lane leg., net, *Z. aurea*; 3 ♀ [CNBL], 4 Jun 2018, S. Marconie leg., net, *Z. aurea*; 1 ♀ [CNBL], 4 Jun 2018, T. Eicholz leg., net, *Z. aurea*; Rudningen (45.32725, -95.17902): 1 ♀ [CNBL], 26 Jun 2017, C. Herron-Sweet leg., net, *Achillea millefolium*; **Le Sueur Co.:** Dove Lake WMA (44.22547, -93.7065): 1 ♀ [MNDNR], 1 Sep 2017, net, *So. Sp*; Kasota Prairie SNA (44.26502, -94.00384): 1 ♀ [MNDNR], 6 May 2017, bowl; **Lyon Co.:** Glynn Prairie SNA (44.2637757, -95.69623097): 1 ♀ [UMSP], 20 Jul 2017, N. Pennarolla, J. Leone leg., bowl; **Mille Lacs Co.:** Kunkel WMA (45.5741, -93.6623): 1 ♀ [MNDNR], 24 Jun 2020, D. Drons leg., pantrap; Princeton (45.571, -93.578): 1 ♀ [UMSP], 3 Oct 1994, A. Johnson leg.; **Murray Co.:** (44.0709, -95.5718): 1 ♀ [CNBL], 29 Jun 2019, Bee Bowls; **Olmsted Co.:** Oronoco Prairie SNA (44.14002349, -92.48913144): 1 ♀ [MN-DNR], 13 Sep 2013, bowl; **Pine Co.:** Chengwatana State Forest (45.819, -92.7864): 1 ♂ [MNDNR], 16 Jul 2020, N. Gerjets leg., net, *Veranicastrum virginicum*; St. Croix SP (45.9543, -92.5799): 1 ♀ [MNDNR], 25 Aug 2020, N. Gerjets leg., net, *So.* Sp.; **Pope Co.:** Glacial Lakes State Park (45.541, -95.531): 1 ♂ [UMSP], 25 Jul 1973, Malaise trap; **Ramsey Co.:** Bald Eagle Otter Lk. Reg. Pk. (45.09588474, -93.0494575): 1 ♀ [EERC], 5 Sep 2015, E. Evans leg., bowl trap; Battle Creek Reg. Pk. (44.9346, -93.0141): 1 ♀ [EERC], 10 Jun 2015, J. Gardner leg., net, *Cornus sericea*; Battle Creek Reg. Pk. (44.93505, -93.015467): 2 ♀ [EERC], 27 May 2015, J. Gardner leg., net, *Geranium* *maculatum*; Battle Creek Regional Park (44.9345, -93.013): 1 ♀ [EERC], 17 May 2016, E. Evans leg., bowl trap; Battle Creek Regional Park (44.94, -93.001): 2 ♀ [EERC], 8 Jun 2016, J. Gardner leg., net, *Ru. Allegheniensis*; Roseville, 3035 Fairview Avenue N (45.03262, -93.17757): 1 ♀ [UMSP], 5–7 Sep 2014, R.W. Holzenthal leg.; St Anthony Park (44.98, -93.2): 1 ♀ [UMSP], Jun year unknown; **Redwood Co.:** Cedar Mountain SNA (44.50489, -94.89886): 12 ♀ [MNDNR], 6 Jul 2016, bowl; **Renville Co.:** Morton Outcrops SNA (44.5501, -94.9902): 1 ♀ [MNDNR], 6 Jul 2016, bowl; 1 ♀ [MNDNR], 18 Jul 2016, bowl; **Sherburne Co.:** Sherburne National Wildlife Refuge (45.4973, -93.6851): 1 ♀ [EERC], 10 Jun 2016, E. Evans leg., net, *R. arkansana*; Uncas Dunes SNA (45.42750645, -93.69554017): 1 ♀ [MNDNR], 11 Jun 2013, net; **Stearns Co.:** Avon Hills Forest SNA (45.63589, -94.50259): 1 ♂ [MNDNR], 13 Sep 2018, net, *So. Altissima*; St. Cloud (45.44, -94.16): 2 ♀ [UMSP], 25 May 1968; 1 ♂ [UMSP], 30 Jul 1968; **Stevens Co.:** Freeman WMA (45.46042, -95.97334): 1 ♀ [MNDNR], 21 Jun 2015, net, *R. sp*; Verlyn Marth Memorial Prairie SNA (45.7451, -96.00017): 3 ♀ [MNDNR], 6 Jul 2016, bowl; **Swift Co.:** Rice WPA (45.34486541, -95.32010344): 1 ♀ [UMSP], 26 Jun 2016, N. Pennarolla, J. Leone leg., bowl; **Wabasha Co.:** Reads Landing (44.402, -92.08): 1 ♀ [UMSP], 22 Jun 1934, C.E. Michel leg.; **Washington Co.:** (45.04, -92.89): 1 ♀ [UMSP], 9 May 1959; Afton State Park (44.846, -92.789): 1 ♀ [CRC], 11 Sep 1992, C.C. Reed leg., net; Arcola Bluffs SAC (45.1209, -92.7509): 1 ♀ [CNBL], 31 May 2018, K. Friedrich leg., vac, *G. maculatum*; 1 ♀ [CNBL], 14 Jun 2018, K. Friedrich leg., vac, *Erigeron philadelphicus*; Big Marine Park Res. (44.2014, -92.8796): 6 ♀ [EERC], 7 Jun 2016, J. Gardner leg., net, *R. woodsii*; Lost Valley Prairie SNA (44.80086892, -92.81775955): 1 ♀ [MNDNR], 13 Sep 2013, bowl; Lost Valley SNA (44.802885, -92.823067): 1 ♀ [UMSP], 19 Sep 1990, C.C. Reed leg.; 1 ♀ [CRC], 19 Sep 1990, C.C. Reed leg., net; 1 ♀ [UMSP], 28 Jul 1992, C.C. Reed leg.; St. Croix Savanna SNA (45.00322082, -92.78344361): 1 ♀ [MNDNR], 16 Sep 2013, bowl; St. Croix Savanna SNA (45.00540834, -92.78347343): 1 ♀ [MNDNR], 13 Sep 2013, bowl; St. Croix Savanna SNA (45.006475, -92.785823): 1 ♀ [UMSP], 5 Aug 1994, C.C. Reed leg., *Monarda fistulosa*; **Winona Co.:** Great River Bluffs SP (43.93895, -91.4113): 1 ♀ [MNDNR], 19 Aug 2017, bowl; **Wright Co.:** Lake Maria SP (45.31787, -93.93487): 1 ♀ [MNDNR], 6 May 2017, bowl. **Mississippi: Bolivar Co.:** Cleveland (33.741, -90.742): 1 ♀ [UMSP], 21 Apr 1937, R.W. Dawson leg. **Missouri: Atchison Co.:** [MASR]; **Barry Co.:** [MASR]; **Barton Co.:** [MASR]; **Benton Co.:** [MASR]; **Bollinger Co.:** [MASR]; **Callaway Co.:** [MASR]; **Camden Co.:** [MASR]; **Crawford Co.:** [MASR]; **Dallas Co.:** [MASR]; **Dent Co.:** [MASR]; **Douglas Co.:** [MASR]; **Franklin Co.:** [MASR]; **Greene Co.:** [MASR]; **Grundy Co.:** [MASR]; **Harrison Co.:** [MASR]; **Jackson Co.:** [MASR]; **Jasper Co.:** [MASR]; **Jefferson Co.:** [MASR]; **Johnson Co.:** [MASR]; **Laclede Co.:** [MASR]; **Lafayette Co.:** [MASR]; **Lewis Co.:** [MASR]; **Lincoln Co.:** [MASR]; **Macon Co.:** [MASR]; **Madison Co.:** [MASR]; **Mercer Co.:** [MASR]; **Monroe Co.:** [MASR]; **Montgomery Co.:** [MASR]; **Pemiscot Co.:** [MASR]; **Pettis Co.:** [MASR]; **Putnam Co.:** [MASR]; **Randolph Co.:** [MASR]; **Ray Co.:** [MASR]; **Reynolds Co.:** [MASR]; **Saline Co.:** [MASR]; **Shannon Co.:** [MASR]; **St. Francis Co.:** [MASR]; **St. Louis Co.:** [MASR]; **Ste. Genevieve Co.:** [MASR]; **Stoddard**

Co.: [MASR]; **Taney Co.:** [MASR]; **Warren Co.:** [MASR]. **New York: Tompkins Co.:** Ithaca (42.442, -76.501): 1 ♀ [OSUC], 27 Aug 1950, J. Cillie leg. **North Carolina: Sampson Co.:** Ivanhoe (34.58, -78.25): 1 ♀ [UMSP], 3 May 1945, T.B. Mitchell leg. **Ohio: Champaign Co.:** (40.13, -83.77): 1 ♂ [OSUC], 24 Jul 1954; 1 ♀ [OSUC], 8 Jun 1994, N.F. Johnson leg., Malaise trap; **Delaware Co.:** (40.27, -83.01): 1 ♀ [OSUC], 2 Aug 1942, R.W. Strandtmann leg.; **Fairfield Co.:** (39.75, -82.63): 1 ♀ [OSUC], 16 Jun 1994, A. Sharkov leg.; **Franklin Co.:** (39.97, -83.01): 1 ♂ [OSUC], 21 Aug 1942; 1 ♀ [OSUC], 18 Jun 1952; **Greene Co.:** [MASR]; (39.69, -83.89): 1 ♀ [OSUC], 6 Jun 1956, J.N. Knull leg.; 1 ♀ [OSUC], 20 Jun 1957, J.N. Knull, D.J. Knull leg.; **Hocking Co.:** (39.49, -82.48): 1 ♀ [OSUC], 10 May 1935, R.C. Osburn leg.; 1 ♀ [OSUC], 14 Jun 1943, R.C. Osburn leg.; 1 ♀ [OSUC], 23 May year unknown, J.N. Knull, D.J. Knull leg.; 1 ♀ [OSUC], 14 Jun year unknown, R.C. Osburn leg.; **Jackson Co.:** (39.01, -82.61): 1 ♀ [OSUC], 9 Aug 1942, R.W. Strandtmann leg.; **Lawrence Co.:** (38.6, -82.52): 1 ♂ [OSUC], 8 Aug 1942, R.W. Strandtmann leg.; **Logan Co.:** (39.54, -82.41): 1 ♀ [UMSP], 16 Jul 1930, J. Patton leg.; **Lucas Co.:** [MASR]; (41.68, -83.47): 1 ♀ [OSUC], 19 May 2003, M. Arduser leg., *Lupinus perennis*; **Ottawa Co.:** Catawba Island (41.579, -82.836): 1 ♀ [OSUC], 27 Jun 1902, J.G. S. leg.; Put-in-Bay (41.649, -82.816): 1 ♀ [OSUC], 20–30 Jun 1924; 1 ♀ [OSUC], 14 Jul 1935, R.C. Osburn leg.; 1 ♀ [OSUC], 22 Aug 1941, R.C. Osburn leg.; 1 ♀ [OSUC], date unknown, C.H. Kennedy leg.; **Paulding Co.:** Charloe (41.131, -84.434): 1 ♀ [OSUC], 12 May 1951, H.F. Price leg.; **Scioto Co.:** (38.82, -82.99): 1 ♀ [OSUC], 6 Aug 1942, R.W. Strandtmann leg.; 1 ♀ [OSUC], 9 Jun 1943, J.N. Knull, D.J. Knull leg.; **Summit Co.:** Ira (41.182, -81.585): 1 ♀ [OSUC], date unknown, J.S. Hine leg.; **Vinton Co.:** (39.25, -82.49): 1 ♀ [OSUC], 20 Jun 1901; **Williams Co.:** Bryan (41.472, -84.553): 2 ♀ [OSUC], date unknown. **Tennessee: Davidson Co.:** Nashville: [MASR]. **Wisconsin: Burnett Co.:** (43.5, -88.71): 1 ♀ [UMSP], M. Sabourin leg.; **Crawford Co.:** Barnum (43.218, -90.839): 1 ♀ [UMSP], 2 Aug 1922, A.M. Holmquist leg.; **Dane Co.:** Madison (43.094, -89.321): 1 ♀ [OSUC], 25 Jun 1916; **La Crosse Co.:** [MASR]; **Oconto Co.:** Lakewood (45.3, -88.523): 1 ♀ [UMSP], 15 Jul 1948, H.E. Milliron leg.; **Polk Co.:** Tewksbury SACN (45.3031, -92.7312): 1 ♀ [CNBL], 25 May 2017, K. Friedrich leg., vac, *Barbarea vulgaris*; 2 ♀ [CNBL], 8 Jun 2017, K. Friedrich leg., vac, *Ru.* Sp.; 1 ♀ [CNBL], 4 Jun 2018, K. Friedrich leg., vac, *Ru.* Sp. **Canada: Ontario: Middlesex Co.:** London: [MASR].

Other US *Augochloropsis* species

Augochloropsis (*Paraugochloropsis*) *anonyma* Cockerell

Augochlora anonyma Cockerell, 1922: 15 ♀. **Holotype**: ♀ USA, Florida, No Name Key [USNM, catalog #53678 barcode #: 00536758, Type #: 2489]. Images examined by ZP and MA. Online record: http://n2t.net/ark:/65665/347b15a43-e8d1-4195-8eaf-f8ac9cbbec94 (labels read “No Name / Key 3.98 Fla // GN Collins / Collector // CL Pollard / Collector // TypeNo. / 24890 / U.S.N.M. [red label] // Augochlora / anonyma / Ckll. TYPE.”).

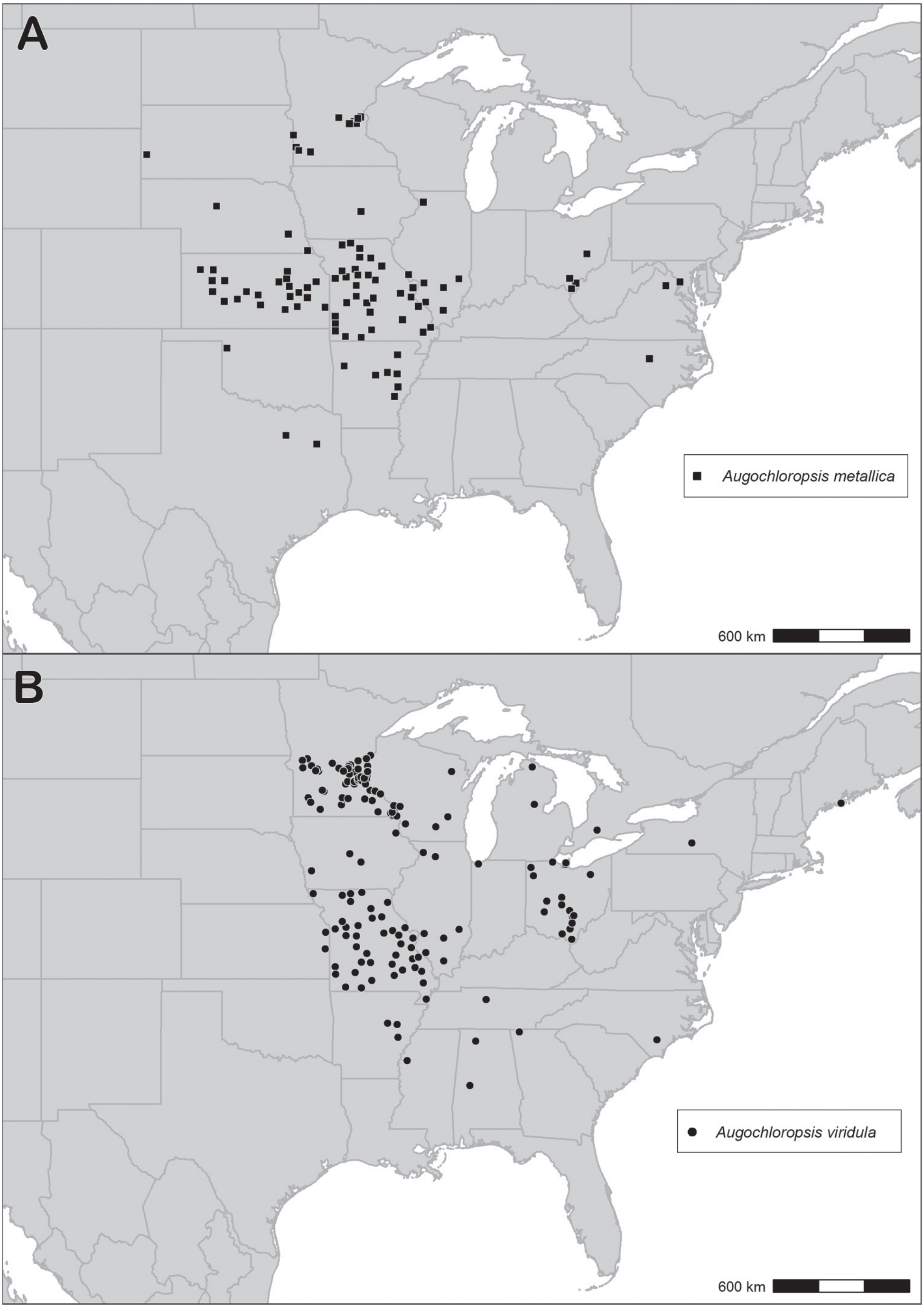

Figure 21. Map of specimens examined for this study **A** *Augochloropsis metallica* **B** *Augochloropsis viridula*. Due to the limited geographic focus of our study, the easternmost extents of the ranges are relatively incomplete.

Augochloropsis cuprea (in Sandhouse 1937 [in part]: key).
Augochloropsis (*Paraugochloropsis*) *anonyma* (in Mitchell 1960: key, redescription of female, first description of male; Hurd 1979: catalog).

Diagnosis. Both sexes of *Augochloropsis anonyma* can be recognized by the short propodeal triangle, which is impressed and narrower than the metanotum (Fig. 17E). *Augochloropsis anonyma* are most likely to be confused with *Augochloropsis viridula*, as they overlap in range, and both have shining integument and poorly developed apical hair fringes on the metasoma. *Augochloropsis anonyma* females can be recognized by the presence of dark pubescence on T2–T4, whereas *Augochloropsis viridula* lacks dark pubescence. In addition, *Augochloropsis anonyma* has the propodeum dorsal surface impressed, shining, and relatively narrow with its medial length slightly less than the medial length of the metanotum (Fig. 17E). In comparison, *Augochloropsis viridula* has the propodeum dorsal surface flat throughout, not impressed, and relatively broad, its medial length dorsally as long (or longer) than the medial length of the metanotum (Fig. 17C).

Augochloropsis anonyma is also similar to *Augochloropsis fulgida* because both share the character of dark hairs on the metasoma (see Fig. 23C, D for *fulgida*). However, the narrow propodeal triangle of *Augochloropsis anonyma* (Fig. 17E) separates these two species, as *Augochloropsis fulgida* has the propodeal triangle broader (visible in Fig. 23C).

Comments. *Augochloropsis anonyma* is known from the far southeastern US, and we have examined material from Florida and Georgia (Fig. 18). Mitchell (1960) reports it occurring as far north as North Carolina.

Augochloropsis (*Paraugochloropsis*) *cuprea* (Smith), stat. nov.

Augochlora cuprea Smith, 1853: 79 ♀. Images examined by ZP and MA (Fig. 22). **Holotype:** ♀ North America [OUMNH]. (Labels read: "[small square with illegible markings] // HOLOTYPE / Augochloropsis / cuprea (Sm) / J.S. Moure 1957 // Probably the Holotype as labelled. No specimen labelled Type in B.M. / C.D. Michener in litt. 13 VIII 1965").
Augochloropsis cuprea (in Sandhouse 1937 [in part]: key).

Comments. The type of *Augochloropsis cuprea* (Fig. 22) was located in the Oxford Museum, and based on the label, it was examined by J.S. Moure in 1957 and C.D. Michener in 1965. The specimen is not clearly labeled as the type, but both Moure and Michener agreed that it was likely the holotype. Sandhouse (1937) appears to have only examined the type by proxy through sawfly taxonomist R. B. Benson and Mitchell (1960) did not examine it.

Augochloropsis cuprea was considered a junior synonym of *Augochloropsis metallica metallica* by both Moure (1960) and Mitchell (1960). However, examination of the type of *Augochloropsis cuprea* reveals that it is distinct from *Augochloropsis metallica* based

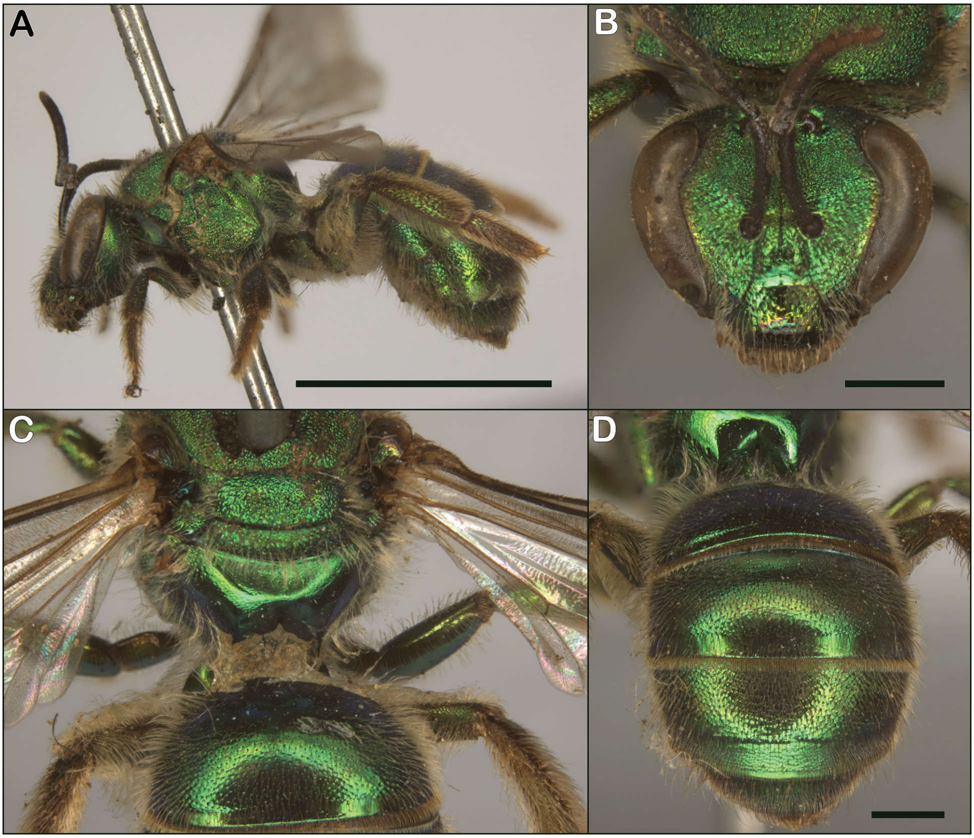

Figure 22. *Augochloropsis cuprea* holotype female **A** lateral view **B** head **C** rear dorsal view of propodeum **D** metasoma. Scale bars: 5 mm (**A**); 1 mm (**B**); 1 mm (**D**). Images provided by Dr. James Hogan (OUMNH).

on the short T2 fringe (Fig. 22D), the relatively short T3 impressed area (Fig. 22D), the presence of some black hairs on the metasoma (Fig. 22A, D), the more shining propodeum (Fig. 22C), and the short posterior carina of the propodeum (Fig. 22C, D). As a result, we recognize the two forms as heterospecific and thus *Augochloropsis cuprea* as a valid species.

The range of *Augochloropsis cuprea* is unclear as Smith (1853) reports the type locality as "North America". We have in our possession a single female from Oklahoma (from Four Canyon Preserve headquarters, Ellis County) that may be a match for *Augochloropsis cuprea*, but this must be considered tentative, especially since the Oklahoma specimen lacks the number of black hairs on the metasoma seen in the type. There is also the possibility that *Augochloropsis cuprea* is a Mexican species, especially since multiple Mexican species share the character of the broadly shiny propodeal triangle. The male remains unknown and additional investigation, with more material, is sorely needed.

Augochloropsis (*Paraugochloropsis*) *fulgida* (Smith), stat. nov.

Augochlora fulgida Smith, 1853: 79 ♀. **Holotype**: ♀ USA, Florida, St. John's Bluff, East Florida [NHMUK014024970]. Images examined by ZP and MA (Fig. 23). Online record: https://data.nhm.ac.uk/object/f5102905-1ee6-44fe-81f5-df87a97b4033 (Labels read "Type / H.T. [circle with red border] // B.M. TYPE / HYM / 14.a.1231 // B.M. TYPE / HYM / augochlora / fulgida / Smith 1853 // fulgida / Type Sm. // E. Doubleday / St. John's Bluff, / E. Florida. // NHMUK 014024970 [label with QR code]").

Augochlora fulgida (in Cockerell 1905: taxonomy).

Augochloropsis cuprea (in Sandhouse 1937 [in part]: key).

Comments. We define *Augochloropsis fulgida* differently than previous workers because examination of the type specimen (Fig. 23) revealed that it does not match the species concept used for *Augochloropsis metallica fulgida* by Mitchell (1960). Even though Mitchell (1960) examined the type, it does not key out correctly in his key or match his description. As it stands, the type of *Augochloropsis fulgida* does not match any *Augochloropsis* species we are familiar with. The type female, from St. John's Bluff Florida (Fig. 18), is most similar to *Augochloropsis anonyma* in that it has erect dark hairs on the metasoma (Fig. 23C, D), but it differs in having a larger and more tessellate propodeal triangle (Fig. 23C) compared to the narrow and shining propodeal triangle in *Augochloropsis anonyma* (Fig. 17E), and the hair fringe on T2 of *Augochloropsis fulgida* appears to be slightly more prominent than in *Augochloropsis anonyma*.

More work is needed to clarify this species as it is currently only known from the type and the male is unknown. However, we have not performed a dedicated search for more material that could match *Augochloropsis fulgida*. It is also a possibility that the type of *Augochloropsis fulgida* is mislabeled and not from Florida or even the United States. However, a more likely explanation is that any *Augochloropsis fulgida* material has been misidentified as *Augochloropsis anonyma* due to the presence of black pubescence on the metasoma.

Augochloropsis (*Paraugochloropsis*) *sumptuosa* (Smith)

Augochlora sumptuosa Smith, 1853: 82 ♀. **Syntype(s?)**: ♀ North America. Type or types missing and presumed lost.

Augochlora lacustris Cockerell, 1922: 14 ♀ (syn. Sandhouse 1937). **Holotype**: ♀ USA, Florida, Lakeland [USNM Type no. 24888]. Images examined by ZP and MA. Online record: http://n2t.net/ark:/65665/32a505d56-7e7d-4fea-ba47-574f3858121f (labels read: "Lakeland, Fla / Nov. 8 1911 // [red label] TypeNo. / 24888 / U.S.N.M. // Augochlora / lacustris / Ckll. TYPE // [yellow label with barcode] USNM ENT 00536780").

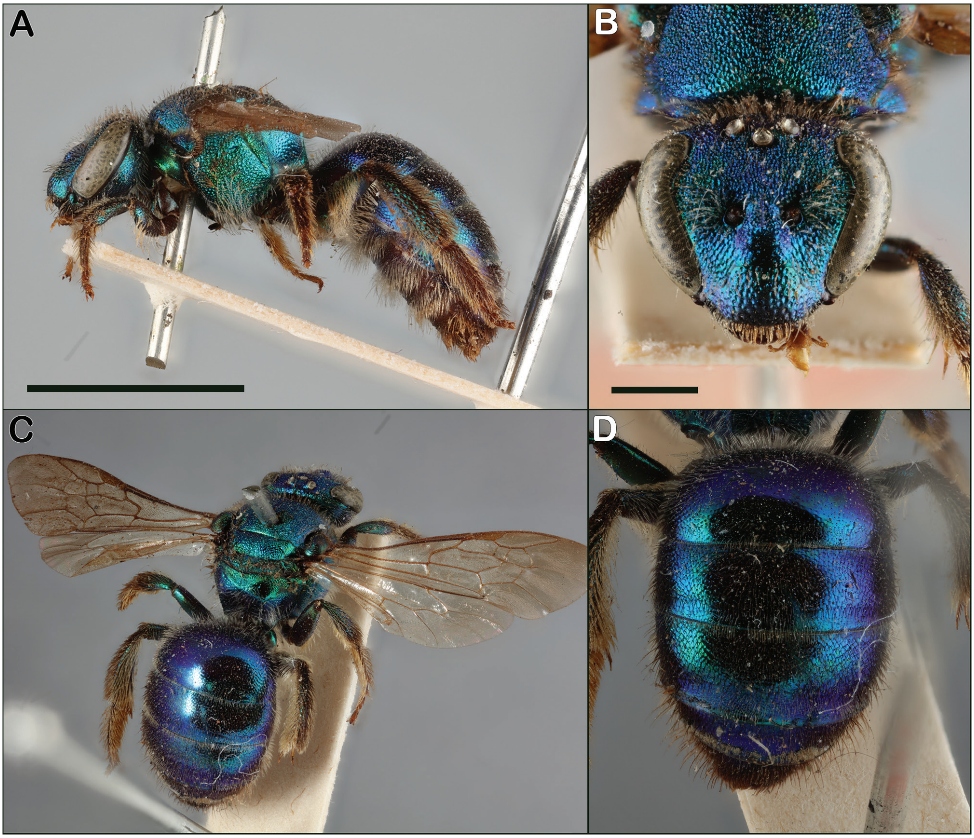

Figure 23. *Augochloropsis fulgida* holotype female **A** lateral view **B** head **C** rear dorsal view **D** metasoma. Scale bars: 5 mm (**A**); 1 mm (**B**). Images provided by Dr. Joseph Monks (NHMUK).

Augochlora floridica Cockerell, 1922: 14 ♂ (syn. Sandhouse 1937). **Holotype**: ♂ USA, Florida, Monticello [USNM Type no. 24889]. Images examined by ZP and MA. Online record: http://n2t.net/ark:/65665/3053e0fc2-b95d-49b6-9630-b55645b3e89d (labels read: "MonticelloFla / Oct. 4–8, 1914 // [red label] Type No. / 24889 / U.S.N.M // Augochlora / floridica Ckll / TYPE. // [yellow label with barcode] USNM ENT / 00536777").

Augochlora sumptuosa (in Robertson 1887: floral record).

Augochlora humeralis (in Smith 1910: biology).

Augochloropsis caerulea (in Sandhouse 1937 [in part]: key).

Augochloropsis (*Paraugochloropsis*) *sumptuosa* (in Mitchell 1960 [in part]: key, redescription; Hurd 1979 [in part]: catalog).

Diagnosis. *Augochloropsis sumptuosa* is most similar to *Augochloropsis humeralis* (refer to the diagnosis of that species to separate them).

Comments. We use *Augochloropsis sumptuosa* in a more restricted sense than previous authors because we have split it into two species: *Augochloropsis sumptuosa* and *Augochloropsis humeralis*. Now, *Augochloropsis sumptuosa* refers to the species occurring in the southeastern United States though the exact range is unknown at this time, and it remains to be seen to what degree, if any, the range of the two species overlaps.

The type or types of *Augochloropsis sumptuosa* have been lost. The type could not be located by Sandhouse (1937) or Mitchell (1960). The last report of possible types is from Cockerell (1897), who stated that "Col. C.T. Bingham" examined syntypes in the Natural History Museum (London, UK). However, there are currently no specimens in the Natural History Museum that could possibly be syntypes (J. Monks, pers. comm., Jun 2021). Despite the missing types, it is our opinion that there is not a need for a neotype because the identity of *Augochloropsis sumptuosa* can be determined from the original description. Specifically, the original description states "the base of the metathorax enclosed by an arched ridge, the enclosed space granulated, the sides of the truncation margined by sharp carinae." This description matches the southeastern species (which has the propodeal triangle surrounded by a weak semicircular carina; Fig. 17D) but not the species found in the Midwest. On this basis, we are retaining the name *Augochloropsis sumptuosa* Smith for the southeastern species. The oldest available name for the midwestern species is *Augochloropsis humeralis* (Patton), the types of which were collected in western Kansas.

More work remains to be done on the taxonomy of *Augochloropsis sumptuosa* because we have not critically evaluated the status of two synonyms: *Augochlora lacustris* Cockerell and *Augochlora floridica* Cockerell. They were originally synonymized with *Augochloropsis sumptuosa* by Sandhouse (1937), and Mitchell (1960) agreed with that designation, stating "Examination of the types has failed to reveal any significant difference that would justify the recognition of either *lacustris* or *floridica*." We have examined images of the types, which are clear enough for us to tentatively agree. However, given that we have split *Augochloropsis sumptuosa* into two species and there is potentially a third similar species in Florida, these types should be critically reexamined as part of a reevaluation of the Florida fauna.

Additional unknown *Augochloropsis* species in the United States

We are aware of at least four additional potential species of *Augochloropsis* in the United States. We are listing them here in order to alert readers to their presence, as many have been incorrectly lumped together under existing species, particularly *Augochloropsis metallica*. However, we do not treat them further. We lack sufficient material of these species, and it is unknown whether they are undescribed or not, as they may be described from Mexico or they may be one of the many poorly known species described by Cockerell. The potential species and their locations include:

- Arizona: A species with a broad and shining propodeum in the female (M. Arduser, unpublished).

- Florida: A species similar to *Augochloropsis sumptuosa* seen in material from Archbold Biological Station (M. Arduser, unpublished).
- Texas: A species that has a unique propodeal triangle (Fig. 17F) and an intermediate T2 comb (Fig. 15C) that falls between *Augochloropsis metallica* and *Augochloropsis viridula* (Z. Portman, unpublished; from material in UMSP and OSUC). This species may have contributed to the confusion by previous authors who believed that *Augochloropsis metallica* and *Augochloropsis viridula* were a single variable species.
- Texas: A species similar to *Augochloropsis humeralis* (M. Arduser, unpublished).

Conclusions

Here, we have revised the *Augochloropsis* of the Midwest and made additional changes to the *Augochloropsis* of the broader United States. This work will allow for the confident identification of the species in the midwestern United States and allow the species' ranges to be better understood. However, there are areas of the southern United States (particularly Florida and Texas) where any *Augochloropsis* identifications must be undertaken with great care due to the number of undescribed or unknown species. We estimate there are an additional four species of *Augochloropsis* in the United States that are unknown or undescribed, not counting *Augochloropsis fulgida*, which is only known from the type and has the male now unknown. In addition, more work needs to be done to check the status of some of the current synonyms of *Augochloropsis sumptuosa* and *Augochloropsis humeralis* from Texas and Florida. Even the genus name may change at some point, as Gonçalves et al. (2022) advocate for raising the subgenus *Paraugochloropsis* to genus level.

The taxonomic changes and identification resources provided here will allow for more accurate identification of *Augochloropsis* and the other shiny green Halictinae. However, similar to the situation in *Augochloropsis*, more taxonomic work is still needed in the other shiny green Halictinae. For example the *Agapostemon* of the United States were last revised 50 years ago (Roberts 1972; Janjic and Packer 2003; Sheffield et al. 2021), the *Augochlora* of the United States have never been revised, and the molecular and morphological diversity found in *Augochlorella aurata* suggests it is potentially a cryptic species complex (Ordway 1966; Sheffield et al. 2009). Given the identification issues surrounding what were the former *Augochloropsis metallica* subspecies, it is especially important that researchers cite the taxonomic concepts and identification resources they use and save voucher specimens (see Packer et al. 2018). In addition, we recommend that non-peer-reviewed identification resources should be avoided whenever possible, as they often have errors and lack a version of record. Indeed, many non-peer-reviewed works would not pass peer review, and the widespread use of these error-ridden and out-of-date identification resources (particularly the keys on discoverlife.org) are contributing to the high rates of misidentifications in bees.

Table 1. Comparison of names and species concepts applied over various keys and revisions of *Augochloropsis*. Dashes indicate that the species was not treated by the author.

Robertson 1902	Sandhouse 1937	Dreisbach 1945	Mitchell 1960	Current name
fervida (Smith)	*cuprea* (Smith)	*cuprea* (Smith)	*metallica metallica* (Fabricius)	*metallica* (Fabricius)
–		–		*cuprea* (Smith)
–		–		*fulvofimbriata* (Friese)
viridula (Smith)		*viridula* (Smith)	*metallica fulgida* (Smith)	*viridula* (Smith)
–		–		*fulgida* (Smith)
–		–	*anonyma* (Cockerell)	*anonyma* (Cockerell)
–	*caerulea* (Ashmead)	*humeralis* (Patton)	*sumptuosa* (Smith)	*humeralis* (Patton)
–		–		*sumptuosa* (Smith)

Our work also demonstrates the difficulty, indeed the futility, of attempting to monitor many bee groups that are in taxonomic disarray (Portman and Tepedino 2021; Tepedino and Portman 2021). Here, we have altered the species concept of essentially every *Augochloropsis* species in the United States and split what was formerly *Augochloropsis metallica* into five species (Table 1). This will necessitate that the majority of existing identifications be checked and updated, which is impossible for monitoring schemes or other studies that do not preserve their specimens (Packer et al. 2018), and it demonstrates one of the major issues with digitizing old museum specimens without first updating them to modern taxonomic concepts. While the taxonomic changes made here will no doubt cause headaches as specimens are checked and names updated, this is a predictable consequence of a genus going 60+ years without a revision. The taxonomic issues seen in *Augochloropsis* are not an isolated problem, as demonstrated by the high rate of new species described in recent revisions of the North American bee fauna (e.g., 15 new species of *Epeolus* (Onuferko 2018); 20 new species of "red-tailed" *Lasioglossum* (Gardner and Gibbs 2020)). This high rate of new species discovery and taxonomic changes will continue in bee genera and subgenera that either lack revisions or have not been revised in the last 50 years (e.g., *Melissodes*, *Nomada*, *Sphecodes*, many *Andrena*, etc.), particularly since prior taxonomic research on those groups predates molecular tools and high-resolution images.

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RESEARCH ARTICLE

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Establishment of two new *Anaplecta* species (Blattodea, Blattoidea, Anaplectidae) based on morphological and *COI* data with an additional description of *Anaplecta furcata* Deng & Che, 2020

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Abstract

Based on morphological characteristics, including male and female genitalia, combined with DNA barcodes, two new species, *Anaplecta circinalis* Deng & Che, **sp. nov.** and *Anaplecta bihamata* Deng & Che, **sp. nov.**, are described in detail. Additional information on the female genitalia of *Anaplecta furcata* Deng & Che, 2020 is also provided. Photographs of external morphology and caudal anatomy of these species, as well as a key to the Chinese *Anaplecta* species, are provided.

Keywords

Cockroaches, *COI*, DNA barcodes, female genitalia, morphology, new species, taxonomy

Introduction

At present, 112 species of *Anaplecta* have been recorded, widely distributed in Asia, North America, South America, Africa and Oceania (21 species in China) (Beccaloni 2014; Deng et al. 2020; Zhu et al. 2022). As taxonomic research progresses, both morphological characters including male and female genitalia and DNA barcodes have been applied to the identification of *Anaplecta* species (Deng et al. 2020; Zhu et al. 2022). This has enriched the knowledge of the *Anaplecta* fauna, which shows a rich diversity.

The effective discernment of species using male genitalia was verified in Deng et al. (2020) although subtle intraspecific variation occurred in male genitalia of some *Anaplecta* species. Three cryptic *Anaplecta* species were revealed in Zhu et al. (2022), where they combined male and female genitalia with DNA barcodes. This confirmed the importance of female genitalia in species delimitation of this genus.

Recently, after collecting cockroach specimens in Fujian, Yunnan, Guangdong and Hunan provinces in China, two new *Anaplecta* species were discovered based on morphological characters. This result was then further verified here by using DNA barcodes. In addition, an exhaustive description of the female genitalia of *Anaplecta furcata* was also provided herein.

Materials and methods

Morphological study

Sixty-eight specimens from Fujian, Yunnan, Guangdong and Hunan provinces were examined in this study. The genitalia terminology used in this paper mainly follows McKittrick (1964), Roth (1990) and Deng et al. (2020), while veins terminology follows Li et al. (2018).

The measurements are based on the specimens examined. The genitalia were processed with 10% NaOH at 65 °C for 30–35 min for digestion of soft tissues. The genitalia segments were dissected and stored in glycerol, then observed with a Motic K400 stereomicroscope. These segments were then preserved with the remainder of the specimen in ethyl alcohol. Photographs of the genitalia and body were taken with a Leica M205A stereomicroscope and edited with Adobe Photoshop CS6. All type materials are deposited at the Institute of Entomology, College of Plant Protection, Southwest University, Chongqing, China (SWU).

Abbreviations in this paper are as follows:

L1, L2, L3	sclerites of the left phallomere;
L2d	L2 dorsal;
L2v	L2 ventral;
L2vm	median sclerite;
M	media veins;
R1, R2, R3	sclerites of the right phallomere;
CuA	cubitus anterior;
CuP	cubitus posterior.

PCR amplification and sequencing

Four specimens were used for cytochrome oxidase subunit I (*COI*) sequencing in this study. Total DNA was extracted from the muscle of legs according to the HiPure Tissue DNA Mini Kit (Magen Biotech, Guangzhou). Primers for polymerase chain reaction (PCR) were *COI*-F (5'-CAACYAATCATAAAGANATTGGAAC-3') and *COI*-R (5'-TAAACTTCTGGRTGACCAAARAATCA-3') (a simple adjustment based on Folmer 1994; Yang et al. 2019). The amplification conditions were as follows: initial denaturation 2 min at 98 °C, followed by 35 cycles of 10 s at 98 °C, 10 s annealing at 49–50 °C, 15 s extension at 72 °C, and a final extension of 2 min at 72 °C; the samples were then held at 8 °C. The PCR products were sequenced by Tsingke Biotechnology Co., Ltd. (Beijing, China).

Molecular analyses

A total of 62 *COI* sequences were analyzed in this study: four newly-sequenced sequences of our newly described *Anaplecta* species and 55 published sequences of 20 Chinese *Anaplecta* species, and three sequences of *Periplaneta* Burmeister, 1838 (as outgroup) downloaded from GenBank (Table 1). The alignment was then manually corrected by translation into amino acids in MEGA 7 (Kumar et al. 2016). The genetic divergence value was quantified based on the Kimura 2-parameter (K2P) distance model (Kimura 1980). Maximum likelihood (ML) analysis was implemented in IQ-TREE (Nguyen et al. 2015) with 1000 replicates for bootstrap values, after choosing optimal partitioning scheme and substitution models (*COI*_pos 1, GTR+I+G; *COI*_pos 2 and *COI*_pos 3, HKY+I+G) in PartitionFinder v.2.1.1 (Lanfear et al. 2017) with the corrected Akaike Information Criterion (AICc).

Results

Morphological delimitation based on external morphology and genitalia

After observing the external morphological and genital characteristics of 42 *Anaplecta* samples from Fujian, Yunnan, Guangdong and Hunan provinces, two new morphospecies and one known species, *Anaplecta furcata*, were identified. One morphospecies can be distinguished by its curled L2vm from other Chinese *Anaplecta* species; while the other is characterized by its hook-shaped L2vm and R1.

Molecular analysis based on *COI*

In this study, the sequenced length of *COI* excluding the primer was approximately 658bp. Four new *COI* sequences have been deposited in GenBank with accession numbers OP306075 to OP306078 (Table 1). Interspecific *COI* genetic divergence

Table 1. Samples of *Anaplecta* species used in the maximum likelihood analyses.

Species	Location (voucher number, gender)	Literature source	GenBank Accession Number
A. circinalis sp. nov.	Pu'er, Yunnan (Anapcircm, ♂)		OP306078
A. circinalis sp. nov.	Pu'er, Yunnan (Anapcircf, ♀)		OP306077
A. bihamata sp. nov.	Shaoyang, Hunan (Anapbiham, ♂)		OP306076
A. bihamata sp. nov.	Shaoyang, Hunan (Anapbihaf, ♀)		OP306075
A. bicruris		Zhu et al. (2022)	OL790029, OL790030, OL790036
A. spinosa		Zhu et al. (2022)	OL790028, OL790038
A. ungulata		Zhu et al. (2022)	OL790031, OL790053, OL790048
A. anomala		Zhu et al. (2022)	OL790032, OL790050
A. serrata		Zhu et al. (2022)	OL790033, OL790047, OL790046
A. bombycina		Zhu et al. (2022)	OL790037, OL790049, OL790034, OL790052
A. longihamata		Zhu et al. (2022)	OL790035, OL790051
A. paraomei		Zhu et al. (2022)	OL790039, OL790045, OL790041, OL790042
A. condensa		Zhu et al. (2022)	OL790040, OL790043, OL790044
A. truncatula		Zhu et al. (2022)	OL790054, OL790055
A. omei		Zhu et al. (2022)	OL790056, OL790057, OL790058
A. omei		Deng et al. (2020)	MT800287
A. corneola		Zhu et al. (2022)	OL790063
A. corneola		Deng et al. (2020)	MT800293, MT800296
A. cruciata		Zhu et al. (2022)	OL790061
A. cruciata		Deng et al. (2020)	MT800303, MT800304
A. basalis		Zhu et al. (2022)	OL790060
A. basalis		Deng et al. (2020)	MT800305, MT800309
A. nigra		Deng et al. (2020)	MT800306
A. staminiformis		Zhu et al. (2022)	OL790062
A. staminiformis		Deng et al. (2020)	MT800297, MT800299
A. arcuata		Zhu et al. (2022)	OL790065
A. arcuata		Deng et al. (2020)	MT800307, MT800308
A. strigata		Zhu et al. (2022)	OL790064
A. strigata		Deng et al. (2020)	MT800291, MT800292
A. furcata		Deng et al. (2020)	MT800301,MT800302
A. bicolor		Zhu et al. (2022)	OL790059
A. bicolor		Deng et al. (2020)	MT800310
Periplaneta americana		Jones et al. (2013)	KC617846
Periplaneta fuliginosa		Beeren et al. (2015)	KM577133
Periplaneta australasiae		Yue et al. (2014)	KF640069

ranged from 5.54% (*A. longihamata* and *A. condensa*) to 27.53% (*A. truncatula* and *A. ungulata*) (Table 2). Interspecific *COI* genetic divergence ranges among the two new morphospecies (*A. bihamata* sp. nov. and *A. circinalis* sp. nov.) and other *Anaplecta* species are 13.97–27.53%, and 18.85–24.85% respectively (Table 2). ML analysis revealed that conspecific samples including two new morphospecies (*A. bihamata* sp. nov. and *A. circinalis* sp. nov.) gathered together well to constitute monophyletic groups (Fig. 1), which solidly supported our morphological results.

Taxonomy

Based on the morphology and ML analysis, we confirmed two new species: *Anaplecta circinalis* Deng & Che, sp. nov. and *Anaplecta bihamata* Deng & Che, sp. nov.

Table 2. Interspecific genetic distance calculated by the K2P model using *COI* sequences in MEGA.

	species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	***A. bihamata* sp. nov.**																					
2	*A. staminiformis*	0.1397																				
3	*A. bicruris*	0.1686	0.1827																			
4	*A. spinosa*	0.1835	0.1764	0.1653																		
5	*A. longihamata*	0.2177	0.2460	0.2134	0.2222																	
6	*A. condensa*	0.2121	0.2370	0.2160	0.2131	**0.0554**																
7	*A. paraomei*	0.2003	0.2220	0.2037	0.2169	0.0832	0.0881															
8	*A. omei*	0.1966	0.2202	0.2192	0.2065	0.0779	0.0937	0.0699														
9	*A. corneola*	0.2078	0.2115	0.1972	0.1975	0.1425	0.1447	0.1437	0.1513													
10	*A. nigra*	0.1899	0.1904	0.1943	0.2150	0.2318	0.2365	0.2146	0.2277	0.2108												
11	*A. basalis*	0.1734	0.1875	0.1918	0.1909	0.2417	0.2400	0.2176	0.2202	0.2133	0.2132											
12	*A. bicolor*	0.2265	0.2215	0.1939	0.2025	0.2211	0.2209	0.2104	0.2207	0.2070	0.2399	0.2246										
13	*A. anomala*	0.2123	0.2119	0.2159	0.2065	0.2106	0.2154	0.1981	0.1974	0.2157	0.2220	0.2342	0.1972									
14	*A. strigata*	0.2123	0.2236	0.2077	0.2012	0.2032	0.2100	0.2095	0.2035	0.2004	0.2094	0.2104	0.2071	0.0868								
15	*A. serrata*	0.2027	0.2287	0.2090	0.2198	0.2366	0.2526	0.2213	0.2144	0.2353	0.2141	0.2124	0.2438	0.1986	0.1852							
16	***A. circinalis* sp. nov.**	0.2014	0.2175	0.2179	0.1885	0.2427	0.2485	0.2236	0.2196	0.2416	0.2368	0.2063	0.2282	0.2145	0.2019	0.2051						
17	*A. bombycina*	0.2487	0.2423	0.2201	0.2050	0.2269	0.2310	0.2247	0.2198	0.2141	0.2176	0.2530	0.2471	0.2263	0.2216	0.2373	0.2263					
18	*A. arcuata*	0.1970	0.2339	0.2367	0.2310	0.2258	0.2355	0.2197	0.2291	0.2442	0.2128	0.2364	0.2239	0.2089	0.2100	0.2495	0.2027	0.1925				
19	*A. furcata*	0.2201	0.2357	0.2133	0.2208	0.2199	0.2419	0.2376	0.2178	0.2284	0.2126	0.2275	0.2128	0.2124	0.2084	0.2059	0.2192	0.1887	0.1867			
20	*A. truncatula*	0.2025	0.2161	0.2008	0.1961	0.2387	0.2274	0.2187	0.2219	0.2400	0.2395	0.2031	0.2393	0.2405	0.2398	0.2348	0.2099	0.2494	0.2456	0.2334		
21	*A. cruciata*	0.2087	0.2167	0.2201	0.2258	0.2352	0.2233	0.2359	0.2107	0.2475	0.2291	0.2292	0.2354	0.2228	0.2370	0.2383	0.2230	0.2615	0.2342	0.2362	0.2546	
22	*A. ungulata*	0.2337	0.2644	0.2720	0.2411	0.2424	0.2503	0.2509	0.2536	0.2349	0.2284	0.2250	0.2569	0.2276	0.2068	0.2628	0.2435	0.2504	0.2374	0.2454	**0.2753**	0.2571

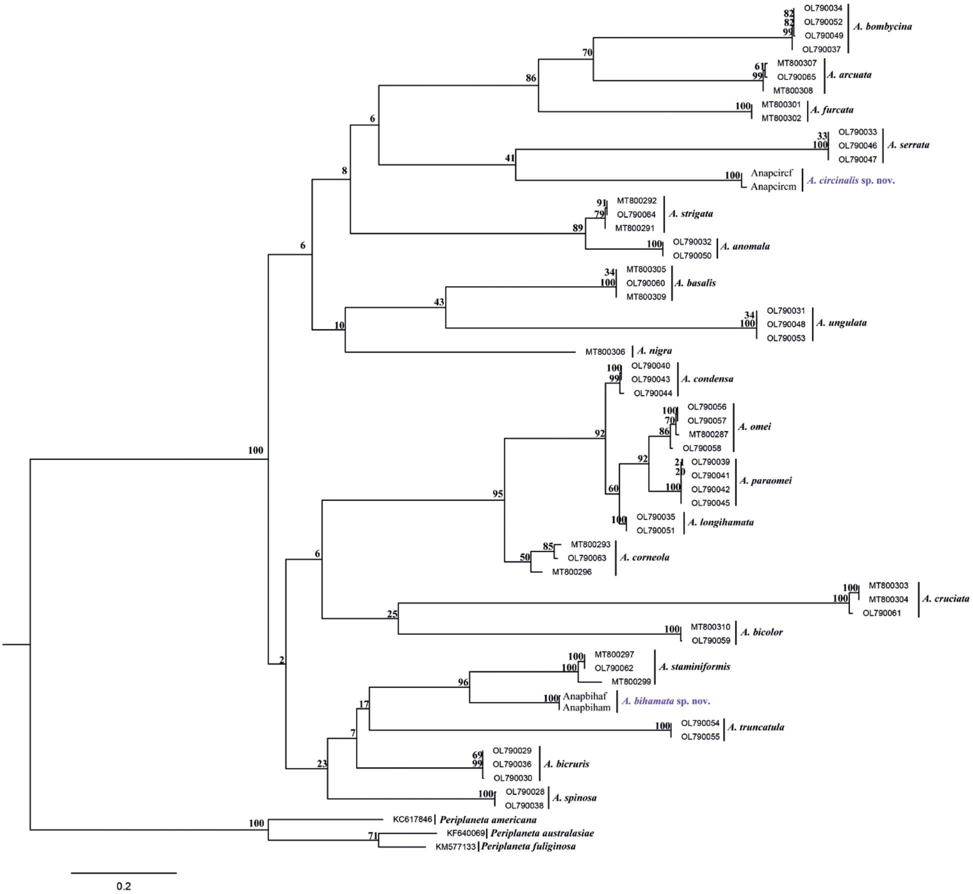

Figure 1. Maximum likelihood (ML) tree derived from *COI* sequences implemented in IQ-TREE with 1000 replicates for bootstrap values.

Key to species of *Anaplecta* in China

[*A. simplex* Shiraki, 1931 is not included because we were unable to collect a sample and only wings were described by the author.]

1 Disk of pronotum bicolored **2**

– Disk of pronotum unicolored **6**

2 Disk dark and faded gradually or sharply towards the posterior end.............. **3**

– Disk dark with some markings.. **4**

3 Tegmina yellowish brown, 1/3 of the base black (except the lateral margins)... .... ***A. basalis* Bey-Bienko, 1969**

– Tegmina completely yellowish brown (except the lateral margins).................. .... ***A. bicolor* Deng & Che, 2020**

4 Disk with a pair of blurred longitudinal darker areas...................................... .... ***A. bicruris* Zhu & Che, 2022**

– Disk with a lighter blurred centre **5**

5 Tegmina unicolored .... ***A. strigata* Deng & Che, 2020**

– Tegmina bicolored, 1/3 of the base darker than remaining parts (except lateral margins and anal field) .... ***A. anomala* Zhu & Che, 2022**

6 Tegmina with obvious markings **7**

– Tegmina without obvious markings **9**

7 Tegmina yellowish brown, with a nearly oval brown spot at CuP .... ***A. ungulata* Zhu & Che, 2022**

– Tegmina yellowish brown, with a subrectangular black spot at base **8**

8 R1 needle-shaped .... ***A. truncatula* Zhu & Che, 2022**

– R1 arc-shaped .... ***A. nigra* Deng & Che, 2020**

9 Male paraprocts with dense spines on curly posterior margin **10**

– Male paraprocts not as above **13**

10 Intercalary sclerite small, nearly filamentous .... ***A. condensa* Zhu & Che, 2022**

– Intercalary sclerite large, strip-shaped or sheet-like **11**

11 Right first valvifer arm long, lateral edges folded up .... ***A. longihamata* Zhu & Che, 2022**

– Right first valvifer arm short, lateral edges not folded up **12**

12 The posterior margin of anterior arch hip-shaped .... ***A. paraomei* Zhu & Che, 2022**

– The posterior margin of anterior arch smooth .... ***A. omei* Bey-Bienko, 1958**

13 L1 with a long and curved filamentary structure **14**

– L1 with a short and robust uncinate structure .... ***A. cruciata* Deng & Che, 2020**

14 R1 degraded or merged with L2vm **15**

– R1 well developed, not merged with L2vm **18**

15 Male paraprocts specialized, stripe-shaped, with spines on posterior margin .... ***A. spinosa* Zhu & Che, 2022**

– Male paraprocts unspecialized **16**

16 The apex of L2v bifurcated, sheet-like **17**

– The apex of L2v not bifurcated, shaped like ‘3’ .... ***A. bombycina* Zhu & Che, 2022**

17 One sclerite of R2 serrated .... ***A. serrata* Zhu & Che, 2022**

– All sclerites of R2 without serration **18**

18 L2vm slender .... ***A. arcuata* Deng & Che, 2020**

– L2vm broad .... ***A. circinalis* Deng & Che, sp. nov.**

19 R1 curved **20**

– R1 straight, cylindrical .... ***A. staminiformis* Deng & Che, 2020**

20 R1 highly sclerotized, horn-shaped **21**

– R1 sightly sclerotized, arc-shaped .... ***A. furcata* Deng & Che, 2020**

21 Right phallomere without special horny structure .... ***A. bihamata* Deng & Che, sp. nov.**

– Right phallomere with special horny structure .... ***A. corneola* Deng & Che, 2020**

Anaplecta circinalis Deng & Che, sp. nov.

https://zoobank.org/90ED9DF4-AEE9-4927-8EE8-835ACD03312A

Figs 2A–I, 4A–C

Type material. ***Holotype*:** China • male; Yunnan Prov., Pu'er County, Xiniuping Scenic Area of Pu'er National Park; 26°36.14'N, 101°5.53'E; 1602 m; 29 Jun. 2021; Jia-Wei Zhang & Jin-Lin Liu leg; SWU-B-AN-0175. ***Paratypes*:** China • 9 males & 14 females; same data as holotype; SWU-B-AN-0176 to 0198.

Diagnosis. This species can be easily separated from other Chinese *Anaplecta* species by its curled left phallomere (L2vm).

Etymology. The specific epithet *'circinalis'* is derived from the Latin word *circinalis*, referring to the curled L2vm.

Description. ***Measurements* (mm)**. **Male:** Pronotum length × width: 1.0–1.3 × 1.8–1.9, tegmina length: 5.0–5.2, overall length: 5.8–6.1. **Female:** Pronotum length × width: 1.2–1.4×1.7–2.0, tegmina length: 4.7–5.1, overall length: 5.6–6.2.

Coloration. Body dark yellowish brown, eyes black, antennae dark brown. Head yellowish brown (Fig. 2A, B, D). Pronotum dark yellowish brown, lateral borders nearly hyaline (Fig. 2C). Tegmina yellowish brown, lateral borders nearly hyaline (Fig. 2E). Wings with costal field and appendicular field light brown, other parts light brown, veins dark brown (Fig. 2H). Center of abdominal sterna yellowish brown, gradually darkening to edges. Cerci and legs yellowish brown.

Head and thorax. Interocular space slightly greater than distance between antennal sockets. Third and fifth maxillary palpi equal in length, longer than fourth; fifth maxillary palpus subelliptical and thicker than other segments (Fig. 2D). Pronotum subelliptical, anterior margin arched, hind margin nearly straight (Fig. 2C).

Tegmina with indistinct veins; the radius posterior veins of hind wings slightly indistinct, CuP and CuA merging into one venation (Fig. 2E, H). Front femur type B_2 (Fig. 2G), pulvilli absent, tarsal claws symmetrical, arolia present.

Male abdomen and genitalia. Supra-anal plate nearly symmetrical, sheet-like (Fig. 2F). Subgenital plate asymmetrical, interstylar margin arched, with a pair of anterior extensions (Fig. 2I). The left styli more robust than the right. Styli with length about 1/3 of interstylar space (Fig. 2I). Phallomere complex, L1 small, with slender and curved filamentary structure. L2v elongated, slightly bifurcated. L2vm broad, slightly thickened and curved. L2d slender and bifurcated. L3 slender, uncinate part blunt (Fig. 2J). R1 absent. R2 irregular, sheet-like, slightly sclerotized. R3 simple, sheet-like (Fig. 2K).

Female abdomen and genitalia. Supra-anal plate nearly symmetrical. Paraprocts (pp.) broad, not extending to the posterior margin of supra-anal plate. Intercalary sclerite (intc.s) nearly stripe-shaped, slightly curved. First valvifer arm short. First valve (v.I) robust. Second valve (v.II) small, basally fused. Third valve (v.III) broad. The anterior margin of anterior arch (aa.) symmetrical, slightly sclerotized, extending forward in a flaky shape with a deep concavity in the middle. Basivalvula (bsv.) nearly flattened, elliptical (Fig. 4A, B). Laterosternal shelf (ltst.sh) slightly sclerotized, lateral margin straight (Fig. 4C).

Distribution. China (Yunnan).

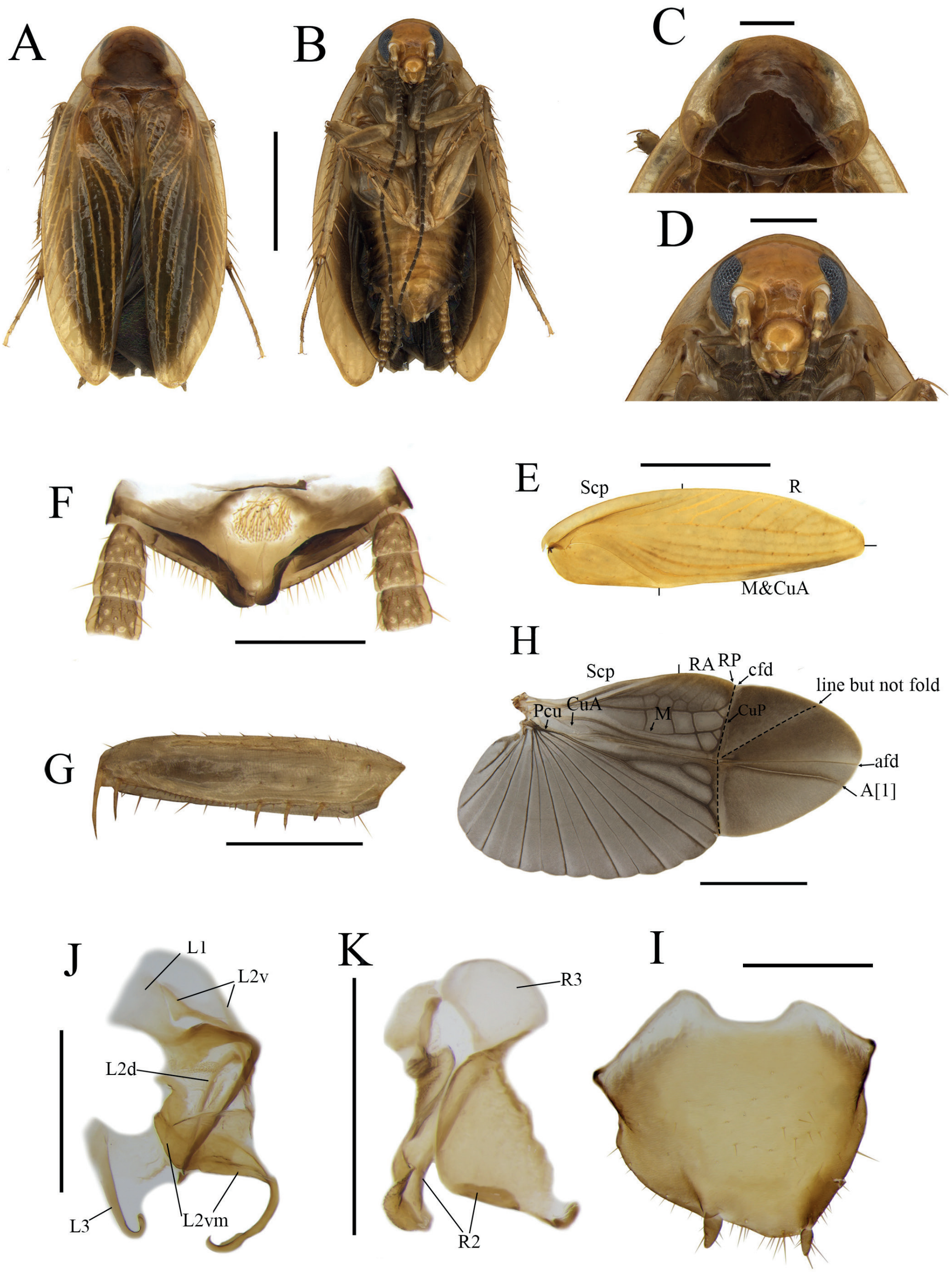

Figure 2. *Anaplecta circinalis* Deng & Che, sp. nov. holotype, male SWU-B-AN-0175 **A** habitus, dorsal view **B** habitus, ventral view **C** pronotum, dorsal view **D** head, ventral view **E** tegmen **F** supra-anal plate, ventral view **G** front femur **H** wing **I** subgenital plate, dorsal view **J** left phallomere **K** right phallomere, dorsal view. Abbreviations: **afd** anal fold, **A[1]** anterior anal vein, **cfd** cubitus fold, **CuA** cubitus anterior, **CuP** cubitus posterior, **L1, L2, L3** sclerites of the left phallomere, **L2d** L2 dorsal, **L2v** L2 ventral, **L2vm** median sclerite, **M** median, **Pcu** postcubitus, **R** radius, **RA** radius anterior, **RP** radius posterior, **R2, R3** sclerites of the right phallomere, **ScP** subcostal posterior. Scale bars: 2 mm (**A–E, G, H**); 0.5 mm (**F, I–K**).

Anaplecta bihamata Deng & Che, sp. nov.

https://zoobank.org/01866CE9-D683-4CB2-94C1-5DB812542B74
Figs 3A–I, 4D–F

Type material. ***Holotype*****:** China • male; Hunan Prov., Shaoyang City, Chengbu County, Ten Miles Flat Monitoring Station; 26°14.12'N, 110°25.52'E; 821 m; 22 May 2021; Jing Zhu leg; SWU-B-AN-0199. ***Paratypes*****:** China • 7 males; SWU-B-AN-0200 to 206; same collection data as holotype • 1 male; SWU-B-AN-0207; Guangdong Prov., Shaoguan City • 2 males and 1 female; SWU-B-AN-0208 to 0210; Ruyuan County, Nanling Nature Reserve Xiaozhu Parking Lot; 24°54.10'N, 113°2.53'E; 695 m, 18 May 2021; Wei Han & Li-Min Qiao leg. • 1 male; SWU-B-AN-0211; Hunan Prov., Yongzhou City, Ningyuan County, Mt. Jiuyi, Yellow River Village; 25°9.8'N, 111°34.17'E; 629 m, 6 Jun. 2021; Jing Zhu leg. • 3 males; SWU-B-AN-0212 to 214; Fujian Prov., Wuyishan City, Sisin Integrated Observation Site; 27°35.30'N, 117°46.4'E; 450 m, 23 Jun. 2021; Wei Han & Jing Zhu leg.

Diagnosis. This species can be easily separated from other Chinese *Anaplecta* species by its hook-shaped L2vm and R1.

Etymology. The specific epithet is derived from the Latin word *hamatus*, referring to both L2vm and R1 being hook-like.

Description. ***Measurements*** **(mm)**. **Male:** Pronotum length × width: 1.2–1.4 × 1.9–2.0, tegmina length: 5.8–6.4, overall length: 6.8–7.3. **Female:** Pronotum length × width: 1.1–1.4 × 1.9–2.2, tegmina length: 5.4–5.6, overall length: 6.2–6.7.

Coloration. Body yellowish brown, eyes black, antennae dark brown. Head yellowish brown (Fig. 3A, B, C). Pronotum and tegmina yellowish brown, lateral borders nearly hyaline (Fig. 3D, E). Wings with costal field and appendicular field infuscated, other parts light brown, with veins dark brown (Fig. 3E, H). Abdominal sterna, cerci and legs yellowish brown (Fig. 3B).

Head and thorax. Interocular space slightly greater than distance between antennal sockets. Fourth and fifth maxillary palpi equal in length, shorter than third maxillary palpus; fifth maxillary palpus triangular and thicker than others (Fig. 3C). Pronotum subelliptical (Fig. 3D). Tegmina with indistinct veins; wings with radial veins slightly indistinct, CuP and CuA merging into one venation (Fig. 3E, H). Front femur type B_2 (Fig. 3G), pulvilli absent, tarsal claws symmetrical, arolia present.

Male abdomen and genitalia. Supra-anal plate symmetrical, sheet-like (Fig. 3F). Subgenital plate subelliptical, with an anterior extension in the left and the posterior margin slightly arched (Fig. 3I). Styli small, cylindrical, styli with length about ⅓ of interstylar space (Fig. 3I). Phallomere complex, L1 small, with slender and curved filamentary structure. L2v elongated, bifurcated at apex and highly sclerotized at terminal. L2vm broad with curved hook at the left (Fig. 3K). L3 robust and medium, uncinate part with apex blunt (Fig. 3J). R1 hooked, the proximal part sharply tapered and highly sclerotized (Fig. 3L). R2 irregular, slightly sclerotized. R3 short, simple sheet-like (Fig. 3M).

Female abdomen and genitalia. Supra-anal plate nearly symmetrical. Paraprocts (pp.) broad, extending to the posterior margin of supra-anal plate. Intercalary sclerite

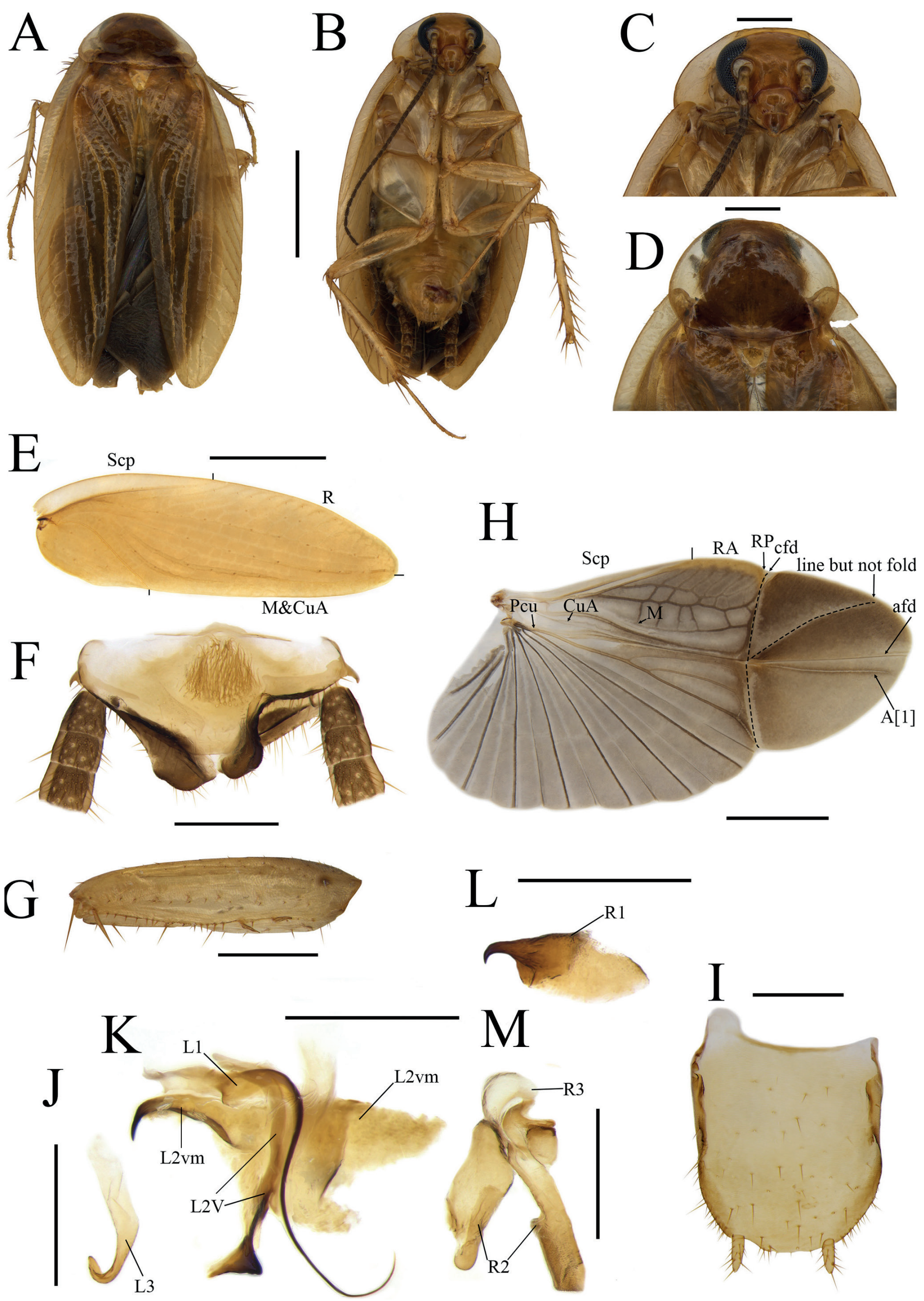

Figure 3. *Anaplecta bihamata* Deng & Che, sp. nov. holotype, male SWU-B-AN-0177 **A** habitus, dorsal view **B** habitus, ventral view **C** pronotum, dorsal view **D** head, ventral view **E** tegmen **F** supra-anal plate, ventral view **G** front femur **H** wing **I** subgenital plate, dorsal view **J, K** left phallomere **L, M** right phallomere, dorsal view. Abbreviations: **afd** anal fold, **A[1]** anterior anal vein, **cfd** cubitus fold, **CuA** cubitus anterior, **CuP** cubitus posterior, **L1, L2, L3** sclerites of the left phallomere, **L2v** L2 ventral, **L2vm** median sclerite, **M** median, **Pcu** postcubitus, **R** radius, **RA** radius anterior, **RP** radius posterior, **R1, R2, R3** sclerites of the right phallomere, **ScP** subcostal posterior. Scale bars: 2 mm (**A–E, G, H**); 0.5 mm (**F, I–M**).

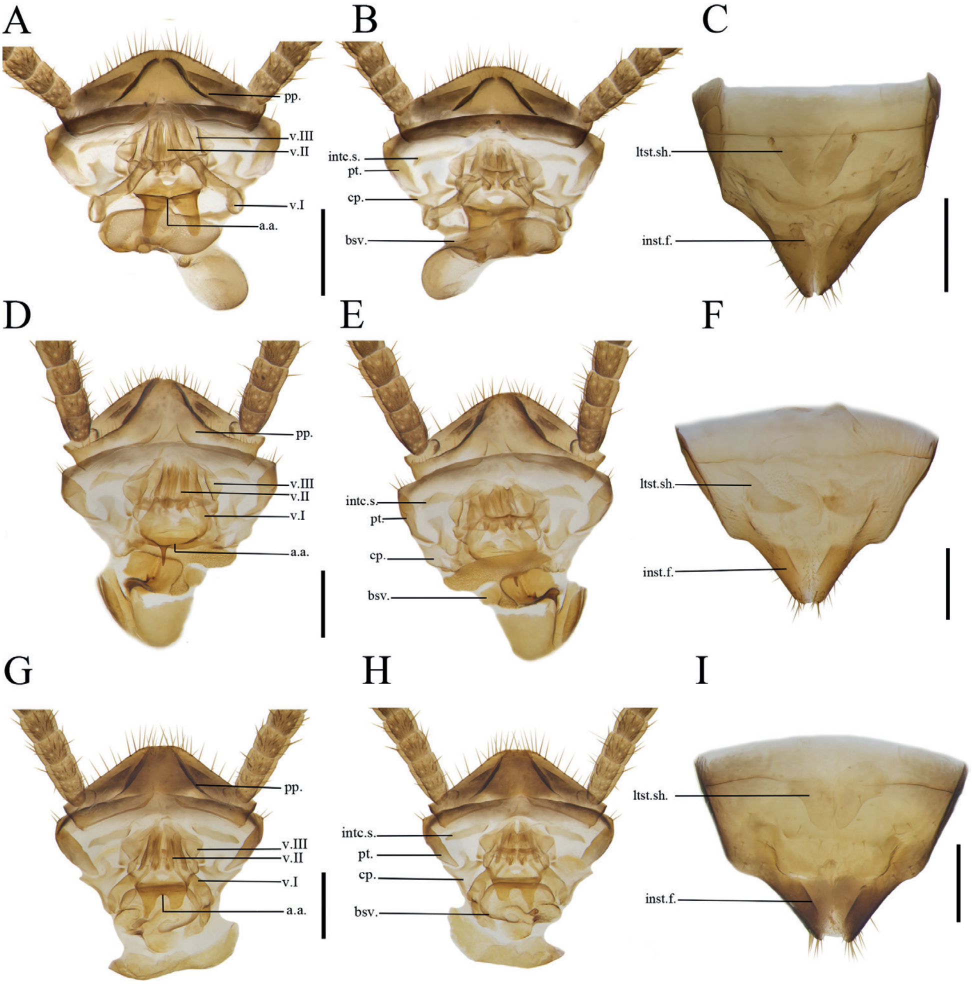

Figure 4. A–C *Anaplecta circinalis* Deng & Che, sp. nov. paratype, female SWU-B-AN-0176 **D–F** *Anaplecta bihamata* Deng & Che, sp. nov. paratype, female SWU-B-AN-0178 **G–I** *Anaplecta furcata* female SWU-B-B-A060471 **A, D, G** supra-anal plate, ventral view **B, E, H** supra-anal plate, dorsal view **C, F, I** subgenital plate, dorsal view. Abbreviations: **a.a.** anterior arch, **bsv.** basivalvula, **cp.** crosspiece, **pt**. paratergites, **intc.s.** intercalary sclerite, **inst.f.** Intersternal fold, **ltst.sh.** laterosternal shelf, **pp.** paraprocts, **sp.** spermatheca, **v.I** first valve, **v.II** second valve, **v.III** third valve. Scale bars: 2 mm.

(intc.s) short, nearly stripe-shaped, slightly curved. First valvifer arm short. First valve (v.I) robust. Second valve (v.II) small, basally fused. Third valve (v.III) broad. The anterior margin of anterior arch (aa.) slightly sclerotized, with a near spine-shaped protrusion and dense tiny punctuations. Basivalvula (bsv.) nearly flat (Fig. 4D, E). Laterosternal shelf (ltst.sh) slightly sclerotized lateral margin straight (Fig. 4F).

Distribution. China (Hunan, Fujian, Guangdong).

Anaplecta furcata **Deng & Che, 2020**
Fig. 4G–I

Anaplecta furcata Deng & Che in Deng et al. 2020: 93–95.

Description. ***Measurements*** **(mm)**. **Female:** pronotum length × width: 1.1–1.4 × 1.9–2.2, tegmina length: 5.4–5.6, overall length: 6.2–6.7.

Female abdomen and genitalia. Supra-anal plate nearly symmetrical. Paraprocts broad, extending to the posterior margin of supra-anal plate. Intercalary sclerite (intc.s) nearly stripe-shaped. First valve (v.I) robust. Second valve (v.II) small, basally fused. Third valve (v.III) broad. The anterior margin of anterior arch (aa.) slightly sclerotized, extending forward in a flaky shape with a deep concavity in the middle. Basivalvula (bsv.) broad, some areas with dense punctuations. Laterosternal shelf (ltst.sh) slightly sclerotized, lateral margin slightly curved.

Material examined. China • 2 females; SWU-B-AN-0215 to 216; Guangxi Prov., Jinxiu County, Mt. Dayao; 24°8.43'N, 110°11.70'E; 944 m; 7 Jul. 2015; Lu Qiu & Qi-Kun Bai leg.

Distribution. China (Guangxi).

Acknowledgements

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RESEARCH ARTICLE

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Systematic notes on three troglobitic *Anapistula* (Araneae, Symphytognathidae) spiders from China, with the descriptions of two new species

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Abstract

Three cave-dwelling spider species belonging to the family Symphytognathidae Hickman, 1931, i.e., *Anapistula sanjiao* **sp. nov.** (♂♀), *A. walayaku* **sp. nov.** (♂♀), and *A. panensis* Lin, Tao & Li, 2013 (♂♀), are reported from southwest China. DNA sequences and detailed illustrations of the habitus, male palps and epigynes are provided, and their distributions are mapped. Their phylogenetic position within symphytognathids and relationships were tested and assessed using previously published phylogenetic analyses on symphytognathoids. The results showed that they form a clade with *A. choojaiae* Rivera-Quiroz, Petcharad & Miller, 2021 from Thailand.

Keywords

Cave spider, description, molecular analysis, symphytognathids, taxonomy

Introduction

The genus *Anapistula* Gertsch, 1941 includes 26 described species. It is the second-most speciose genus of the Symphytognathidae Hickman, 1931, with more than half of the species widespread in the tropical and subtropical regions of the Oriental and Neotropical realms (WSC 2022). Eighteen known *Anapistula* species have been collected from the leaf litter, soil or mosses (Gertsch 1941; Forster 1958, 1959; Forster and Platnick 1977; Baert and Jocqué 1993; Saaristo 1996; Harvey 1998; Ono 2002; Rheims and Brescovit 2003; Tong and Li 2006; Rubio and González 2010; Lin et al. 2013; Dupérré and Tapia 2017; Rivera-Quiroz et al. 2021), seven live in caves (Harvey 1998; Rheims and Brescovit 2003; Cardoso and Scharff 2009; Lin et al. 2009; Lin et al. 2013), and only one was found at a cave entrance (Rheims and Brescovit 2003).

The type species, *Anapistula secreta* Gertsch, 1941, is widely distributed from the USA to Colombia, the Bahamas and Jamaica (Dupérré and Tapia 2017). The first described Asian *Anapistula* species is *A. jerai* Harvey, 1998 from Malaysia and Indonesia (Harvey 1998). Additional Asian species include *Anapistula appendix* Tong & S. Li, 2006 (China), *Anapistula choojaiae* Rivera-Quiroz, Petcharad & Miller, 2021 (Thailand), *Anapistula ishikawai* Ono, 2002 (Japan), *Anapistula orbisterna* Lin, Pham & S. Li, 2009 (Vietnam), *Anapistula panensis* Lin, Tao & Li, 2013 (China), *Anapistula zhengi* Lin, Tao & Li, 2013 (China) (Ono 2002; Tong and Li 2006; Lin et al. 2009; Lin et al. 2013; Rivera-Quiroz et al. 2021). Considering the two new species described here, the genus now consists of 28 species, half of which are described only from one sex. There are four species represented only by males, and 10 species in which only females are known.

The aims of this paper are: 1) to report three cave-dwelling *Anapistula* species from China, two of them new to science, and 2) to verify their sex pairing and resolve their phylogenetic relationships within symphytognathids. We used a combination of newly generated sequences and others available from GenBank to build a molecular phylogeny of the Symphytognathidae to confirm the generic placement of our new species.

Materials and methods

Specimen sampling

Specimens studied here were collected from caves in Yunnan and Guizhou provinces, in southwest China, on or during 26 April 2010, 24 June 2016, 10–24 August 2018, and 24 August 2020. All of the specimens were captured by hand and stored in 95% ethanol at –20 °C.

Molecular data

To test relationships within symphytognathids and the taxonomic position of the three *Anapistula* species, eight individuals were selected from the examined materials for molecular data collection. Their legs and prosoma were used to extract genomic DNA and sequence five gene fragments: 16S, 18S, 28S, COI and H3. The abdomens and male palps were kept as vouchers. All of the molecular data were obtained from specimens collected at the type localities, although not from the type specimens themselves. Whole genomic DNA was extracted from tissue samples with the TIANamp Micro DNA Kit (TIANGEN) following the manufacturer's protocol for animal tissue. The five gene fragments were amplified in 25μL reactions. Primer pairs and PCR protocols are given in Table 1. Raw sequences were edited and assembled using BioEdit v.7.2.5 (Hall 1999). New sequences from this study were deposited in GenBank (Table 2). All molecular vouchers and examined materials are stored in the Natural History Museum of Sichuan University in Chengdu (NHMSU), China.

We used these sequences and a selection from previously sequenced taxa to assemble a phylogeny of symphytognathid spiders. In total, 50 species of symphytognathoids representing the families Theridiosomatidae, Mysmenidae, Anapidae, and Symphytognathidae were used. Two tetragnathid species were used as outgroups. We used the MAFFT v.7.450 online server (https://mafft.cbrc.jp/alignment/server/) with default parameters to align the sequences of the three Chinese *Anapistula* species. All sequences were concatenated in Sequence Matrix v.1.7.8 (Vaidya et al. 2011). We used PartitionFinder2 (Lanfear et al. 2017) to identify the best-fit models of molecular evolution for each locus. GTR+I+G was selected for COI, H3, 18S and 28S, and GTR+G was selected for 16S.

The maximum parsimony (MP) tree was constructed using MEGA X (Kumar et al. 2018) with TBR (Tree-Bisection-Reconnection) branch swapping and 2000 bootstrap replicates with default parameters. Bayesian phylogenetic inference (BI) was performed using MrBayes v.3.2.7 (Ronquist et al. 2012) through the Cipres Science Gateway (Miller et al. 2010) using four Markov Chain Monte Carlo (MCMCs) chains with default heating parameters for 50,000,000 generations or until the average standard deviation of split frequencies was less than 0.01. The Markov chains were sampled every 1000 generations, and the first 25% of sampled trees were burn-in. The program Tracer v.1.7.1 (Rambaut et al. 2018) was used to analyse the performance of our BI analyses.

Table 1. The loci, primer pairs, and PCR protocols used in this study.

Locus	Annealing temperature/time	Direction	Primer	Sequence 5'→3'	Reference
16S	46.45 °C/30 s	F	16sb2_12864	CTCCGGTTTGAACTCAGATCA	Hormiga et al. 2003
		R	LR-J-13360	GTAAGGCCTGCTCAATGA	Feng et al. 2019
	47 °C/30 s	F	16S-A	CGCCTGTTTATCAAAAACAT	Palumbi et al. 1991
		R	16S-B	CTCCGGTTTGAACTCAGATCA	
18S	52.1 °C/30 s	F	18s_1F	TACCTGGTTGATCCTGCCAGTAG	Giribet et al. 1996
		R	18s_1000R	GTGGTGCCCTTCCGTCAATT	Balczun et al. 2005
28SD2	54.9 °C/30 s	F	28sa	GACCCGTCTTGAAACACGGA	Rix et al. 2008
		R	LSUR	GCTACTACCACCAAGATCTGCA	
COI	48.95 °C/30 s	F	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
		R	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	
	46 °C/30 s	F	LCO1490	GGTCAACAAATCATAAAGATATTGG	Simon et al. 1994
		R	COI-Nancy	CCCGGTAAAATTAAAATATAAACTTC	
H3	48 °C/30 s	F	H3af	ATGGCTCGTACCAAGCAGACVGC	Colgan et al. 1998
		R	H3ar	ATATCCTTRGGCATRATRGTGAC	
	50 °C/30 s	F	H3nf	ATGGCTCGTACCAAGCAGAC	
		R	H3nr	ATRTCCTTGGGCATGATTGTTAC	

Table 2. GenBank accession numbers for new DNA sequence data from three *Anapistula* species.

Species	Identifier	Sex/Stage	16S	18S	28S	COI	H3
Anapistula panensis	HA020	♀/adult	–	OP120815	OP120929	OP117477	OP131579
	HA020	♂/juvenile	–	OP120816	OP120930	OP117478	OP131580
Anapistula sanjiao sp. nov.	HA125	♂/adult	–	OP120819	OP120933	OP117481	OP131583
	HA125	♀/adult	–	OP120818	OP120932	OP117480	OP131582
Anapistula walayaku sp. nov.	HA138	♂/adult	OP133563	OP120822	OP120936	OP117484	OP131586
	HA138	♀/adult	–	OP120820	OP120934	OP117482	OP131584
	HA138	♀/juvenile	OP133562	OP120821	OP120935	OP117483	OP131585
	HA106	♀/adult	OP133561	OP120817	OP120931	OP117479	OP131581

Morphological data

Specimens were studied in ethanol using a Leica M205 C stereomicroscope. Habitus and copulatory organs were photographed with a Canon EOS 60D wide zoom digital camera (8.5 megapixels) mounted on an Olympus BX 51 compound microscope. Male palps and epigynes were examined after dissection and treated with lactic acid before being embedded in Hoyer's Gum and placed on an ultra-thin slide to take photos of the dorsal and ventral sides. The digital photos were montaged using Helicon Focus v.3.10 (Khmelik et al. 2006) image stacking software. All measurements are in millimetres. Leg measurements are given as follows: total length (femur, patella, tibia, metatarsus, tarsus).

Nomenclature of the genital structures was based on Dupérré and Tapia (2017) and Rivera-Quiroz et al. (2021) for *Anapistula*. Abbreviations in the text and figures are as follows:

Male palp

Co	conductor;
C1	anterior projection of conductor;
C2	posterior projection of conductor;
Cy	cymbium;
E	embolus;
Pa	palpal patella;
Sd	sperm duct;
Te	palpal tibia.

Epigyne

A	epigynal atrium;
MD	median duct of vulva;
Fd	fertilization duct;
Lb	lateral branch of the MD;
Llb	distal lobe of lateral branch;
S	spermatheca.

Institutional acronyms

IZCAS	Institute of Zoology, Chinese Academy of Sciences, Beijing, China;
NHMSU	Natural History Museum of Sichuan University, Chengdu, China.

Results

Phylogenetic analysis

The MP analysis of the full dataset recovered a single most parsimonious tree topology (Fig. 1). This tree shows symphytognathoids are monophyletic but with low support. Theridiosomatidae, Mysmenidae and Symphytognathidae are monophyletic, also with low support. Here we note that *Theridiosoma gemmosum* (L. Koch, 1877) (indicated by a red in the orange box in Fig. 1) is nested within the Symphytognathidae. Anapidae contains the polyphyletic Micropholcommatinae and an undescribed Theridiosomatidae species (indicated by a red star in the blue box in Fig. 1). A clade composed of four *Anapistula* species (three species in red font and *A. choojaiae* in Fig. 1) were highly supported as monophyletic. These results support our taxonomic classification.

The result of BI is consistent with MP for some major clades, but there are some differences (Fig. 2). In the BI tree, Mysmenidae is highly supported compared to Theridiosomatidae, Anapidae and Symphytognathidae. However, an undescribed Theridiosomatidae species (marked by a red star in the blue box of Fig. 2) occurs between Anapidae and Symphytognathidae, and Micropholcommatinae is nested in Anapidae. Three Chinese and one Thai *Anapistula* species form a separate, highly supported clade in the BI topology. As a sister group, the clade of *Anapistula* is delimited to include: (*A. choojaiae* (*A. walayaku* sp. nov. (*A. sanjiao* sp. nov. + *A. panensis*))). Both the MP and BI analyses found the three Chinese and one Thai *Anapistula* species formed a clade sister to the remaining symphytognathids. The available molecular evidence seems sufficient to justify the taxonomic placement of the two new and one known *Anapistula* species.

Taxonomy

Family Symphytognathidae Hickman, 1931

Genus *Anapistula* Gertsch, 1941

Anapistula Gertsch, 1941: 2.

Type species. *Anapistula secreta* Gertsch, 1941 by original designation, from the Bahamas.

Diagnosis. *Anapistula* differs from other genera of Symphytognathidae by: the presence of four lateral eyes in diads (most common) or the eyes are reduced to indistinct spots or absent (median eyes present in *A. boneti* Forster, 1958: figs 15, 16); the chelicerae are fused near the base, with two promarginal teeth; the cephalic area is

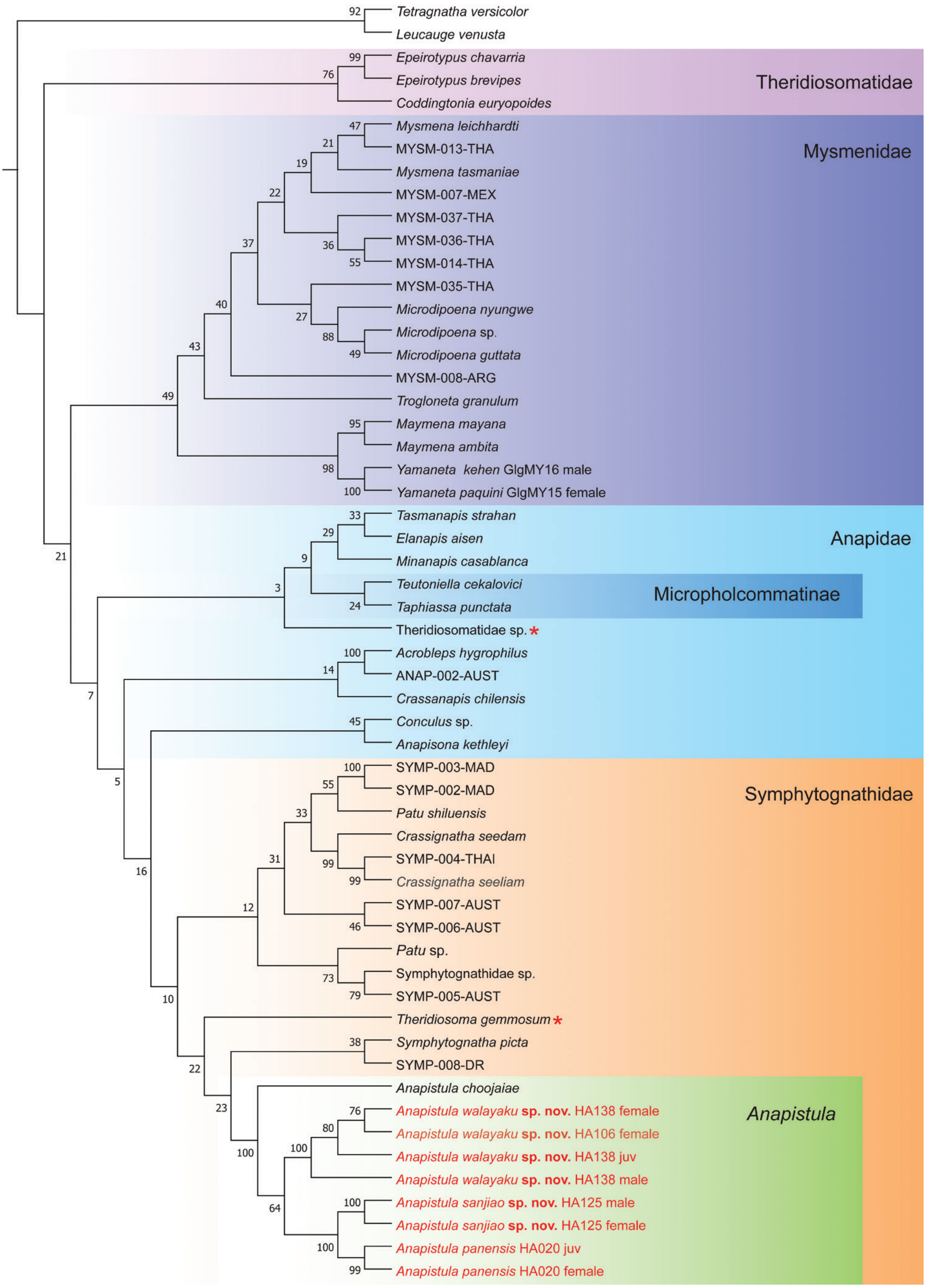

Figure 1. Tree topology obtained by maximum parsimony in MEGA-X using a modified version of Rivera-Quiroz et al. (2021) plus three Chinese *Anapistula* species (red font). Numbers at nodes indicate bootstrap support. Symphytognathidae is in the orange box and *Anapistula* in the green box. Note the paraphyly of Anapidae, the high support of *Anapistula* in Symphytognathidae, and the placement of Theridiosomatidae sp. (red star) within Anapidae and *Theridiosoma gemmosum* (red star) within Symphytognathidae.

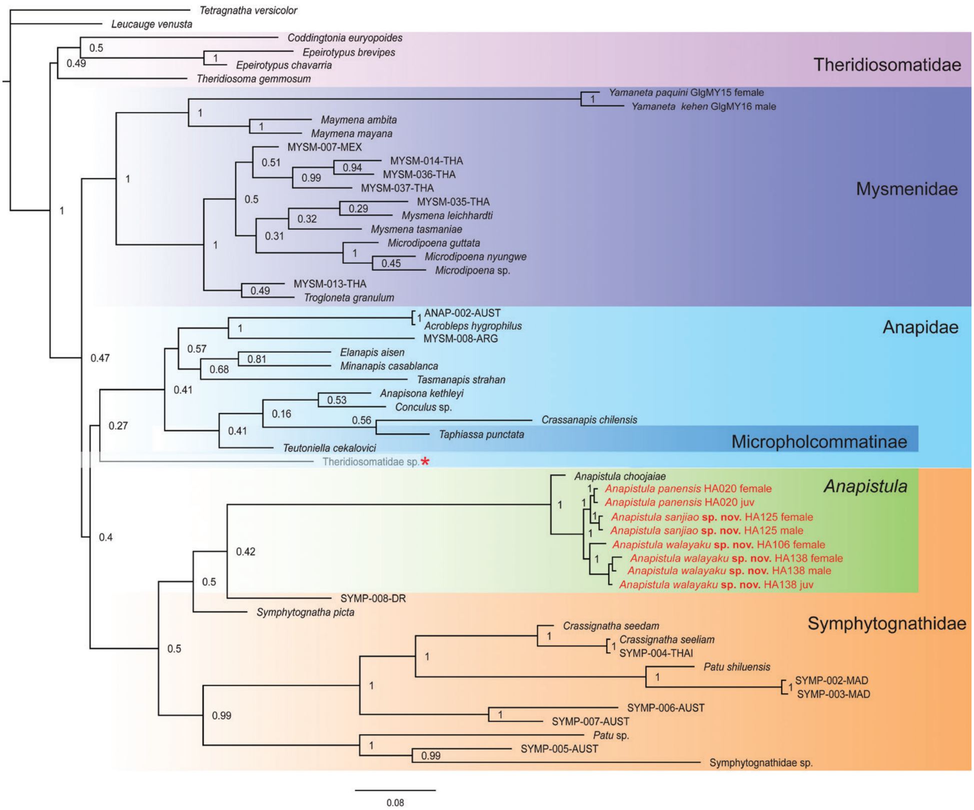

Figure 2. Tree topology from Bayesian analysis. Numerical values at nodes indicate posterior probabilities; other conventions as in Fig. 1. Note the high support of *Anapistula* in Symphytognathidae, and the monophyly of four *Anapistula* species; the low support of Anapidae, the nesting of Micropholcommatinae, and the placement of Theridiosomatidae sp. (red star) sister to Micropholcommatinae.

slightly raised (strongly raised in *A. boneti*); a smooth carapace; and a sub-spherical abdomen without a colulus. Males are diagnosed by lacking clasping spines on tibia II, a cymbium without teeth or denticles but with long setae and apical lobes, a conductor, a short embolus (length less than ½ the diameter of the bulb), and a sperm duct coiled ca 1.5 times. Females are diagnosed by lacking palps, round spermathecae connected by a T- or Y-shaped epigynal median duct, and the absence of a scape and parmula (see Forster and Platnick 1977: fig. 19; Harvey 1998: figs 2, 4, 9, 14, 19; Dupérré and Tapia 2017: fig. 33; Rivera-Quiroz et al. 2021: figs 8d, 9c).

Composition in Asia. *Anapistula appendix* (♀, China), *A. choojaiae* (♂♀, Thailand), *A. ishikawai* (♀, Japan), *A. jerai* (♂♀, Malaysia, Borneo, and Indonesia), *A. orbisterna* (♀, Vietnam), *A. panensis* (♂♀, China), *A. sanjiao* S. Li & Lin, sp. nov. (♂♀, China), *A. walayaku* S. Li & Lin, sp. nov. (♂♀, China), and *A. zhengi* (♂♀, China).

Distribution in Asia. China (Hainan, Guizhou, and Yunnan), Japan, Vietnam, Thailand, Malaysia, Borneo and Indonesia.

Anapistula sanjiao S. Li & Lin, sp. nov.

https://zoobank.org/7A23C5A8-EB67-46B6-A26E-D0C18CE53952
Figs 3A, D, G, J, 4A–E, 7A–D

Type material. ***Holotype*** ♀ and ***paratypes*** 1♂ 2♀ (NHMSU-HA125), **China:** Yunnan Province, Kunming City, Yiliang County, Jiuxiang Township, Dazhezong Village, Sanjiao Cave (25.13439°N, 103.39932°E, 1833 m), 24.VIII.2018, Y. Lin, Y. Li & Y. Shu leg.; 1♂ and 1♀ (NHMSU-HA125) used for sequencing, GenBank accession numbers given in Table 2, same data as for preceding.

Etymology. The new species is named after the type locality; noun.

Diagnosis. The male of this new species is similar to that of *A. zhengi* in the overall shape of the palp and in having C1 and C2 roughly as sharp as *A. zhengi* but differs in the length of C1 with respect to C2 and the presence of a small median projection between C1 and C2 (cf. Figs 4A, 7A to Lin et al. 2013: figs 6, 7). The female can be distinguished from most *Anapistula* species by the Y-shaped MD and its width greater than half the diameter of one spermatheca. The configuration of the vulva of *Anapistula sanjiao* sp. nov. seems most similar to that of *A. choojaiae* but differs by the smaller size of the spermathecae compared to the width of the MD, and the ends of the Llb are located beyond the anteromargin of the spermathecae (cf. Figs 4E, 7D to Rivera-Quiroz et al. 2021: fig. 9c).

Description. Male: carapace ovoid, pale yellow with smooth surface and two central short setae (Fig. 3A). Lateral eyes degenerated into white eyespots, almost invisible (Fig. 3A). Chelicerae with two promarginal teeth. Labium rectangular, fused to sternum (Fig. 3D). Sternum peltate, slightly longer than wide, smooth, slightly convex, with sparse short setae, truncated posteriorly (Fig. 3D). Legs same colour as carapace. Abdomen sub-spherical, darker than prosoma and legs, cuticle with sparse long setae and weakly sclerotized patches (Fig. 3A, D). Spinnerets and anal tubercle pale yellow. Somatic measurements: body length 0.58, carapace 0.28 long, 0.24 wide, 0.20 high; sternum 0.20 long, 0.18 wide; length of legs: I 0.90 (0.24, 0.08, 0.22, 0.14, 0.22), II 0.76 (0.18, 0.10, 0.12, 0.10, 0.18), III 0.66 (0.12, 0.08, 0.16, 0.10, 0.20), IV 0.86 (0.22, 0.10, 0.20, 0.16, 0.18); leg formula I-IV-II-III; abdomen 0.35 long, 0.34 wide, 0.38 high.

***Palp*:** weakly sclerotized (Figs 4A, B, 7A, B). Femur long, ca 2.2× length of patella, slightly constricted in ventral middle. Patella nearly cubic. Tibia oblate, ca 1.4× length of patella. Cymbium wraps around bulb prolaterally, with long setae at distal margin (Figs 4A, 7A). Sheath like conductor divided into two distal, sharp projections (C1 and C2 in Figs 4A, B, 7A, B); C1 longer than C2. Sperm duct (Sd) completes ca 1.8 loops in the bulb. Embolus sharp, protrudes from lower retrolateral edge of bulb, extends to retrolateral side of C1. End of embolus does not extend beyond CI. Embolic end no exceeds the C1 (Figs 4A, B, 7A, B).

Female: habitus as in male, except without palps (Fig. 3G, J). Somatic measurements: body length 0.60, carapace 0.28 long, 0.25 wide, 0.24 high; sternum 0.22 long, 0.20 wide; length of legs: I 1.10 (0.32, 0.12, 0.24, 0.20, 0.22), II 0.86 (0.26, 0.10,

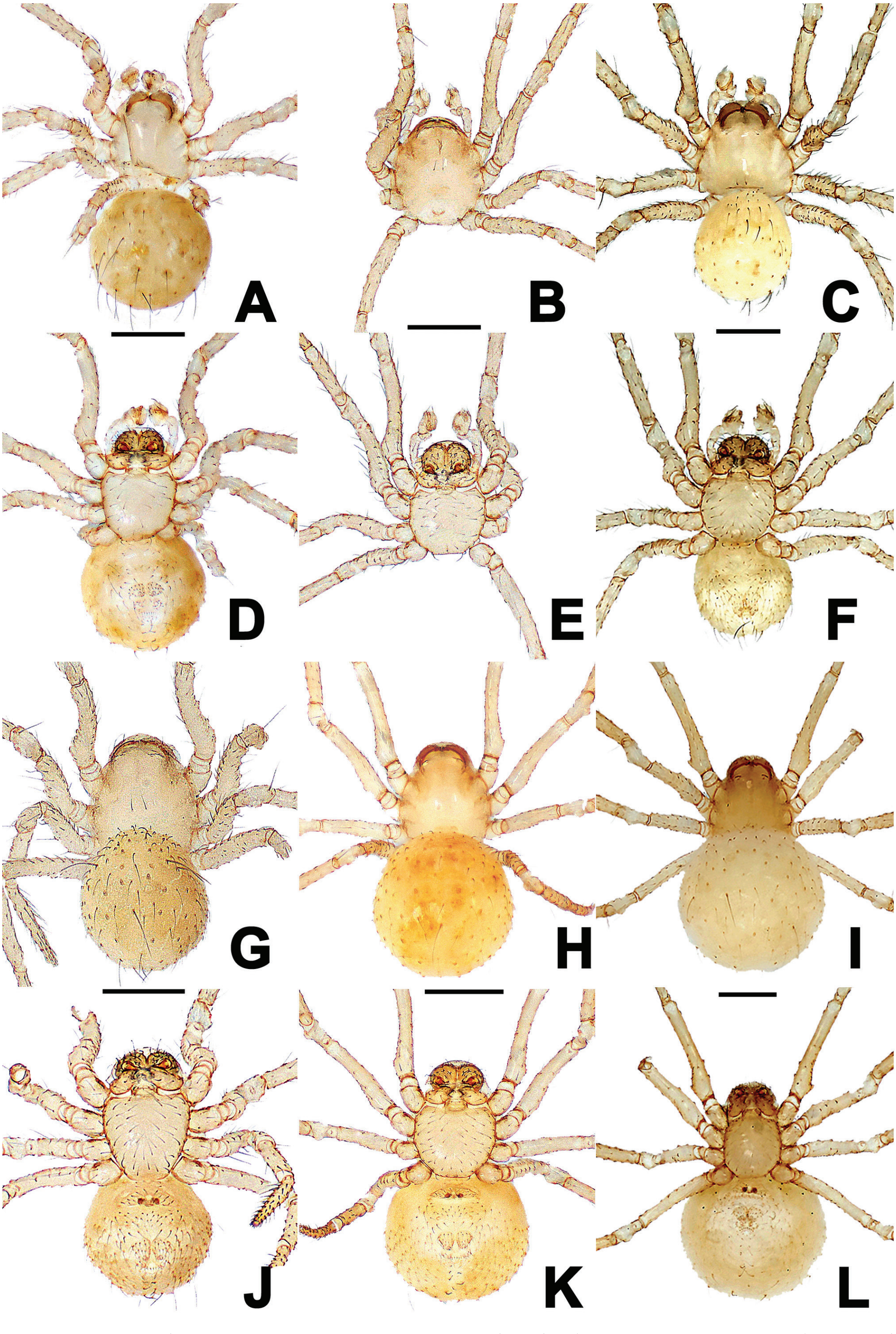

Figure 3. *Anapistula sanjiao* sp. nov. (**A, D, G, J**), *Anapistula walayaku* sp. nov. (**B, E, H, K**), and *Anapistula panensis* (**C, F, I, L**) **A, C** male habitus, dorsal **D, F** male habitus, ventral **B** male prosoma, dorsal **E** male prosoma, ventral **G–I** female habitus, dorsal **J–L** female habitus, ventral. Scale bars: 0.20 (**A–L**).

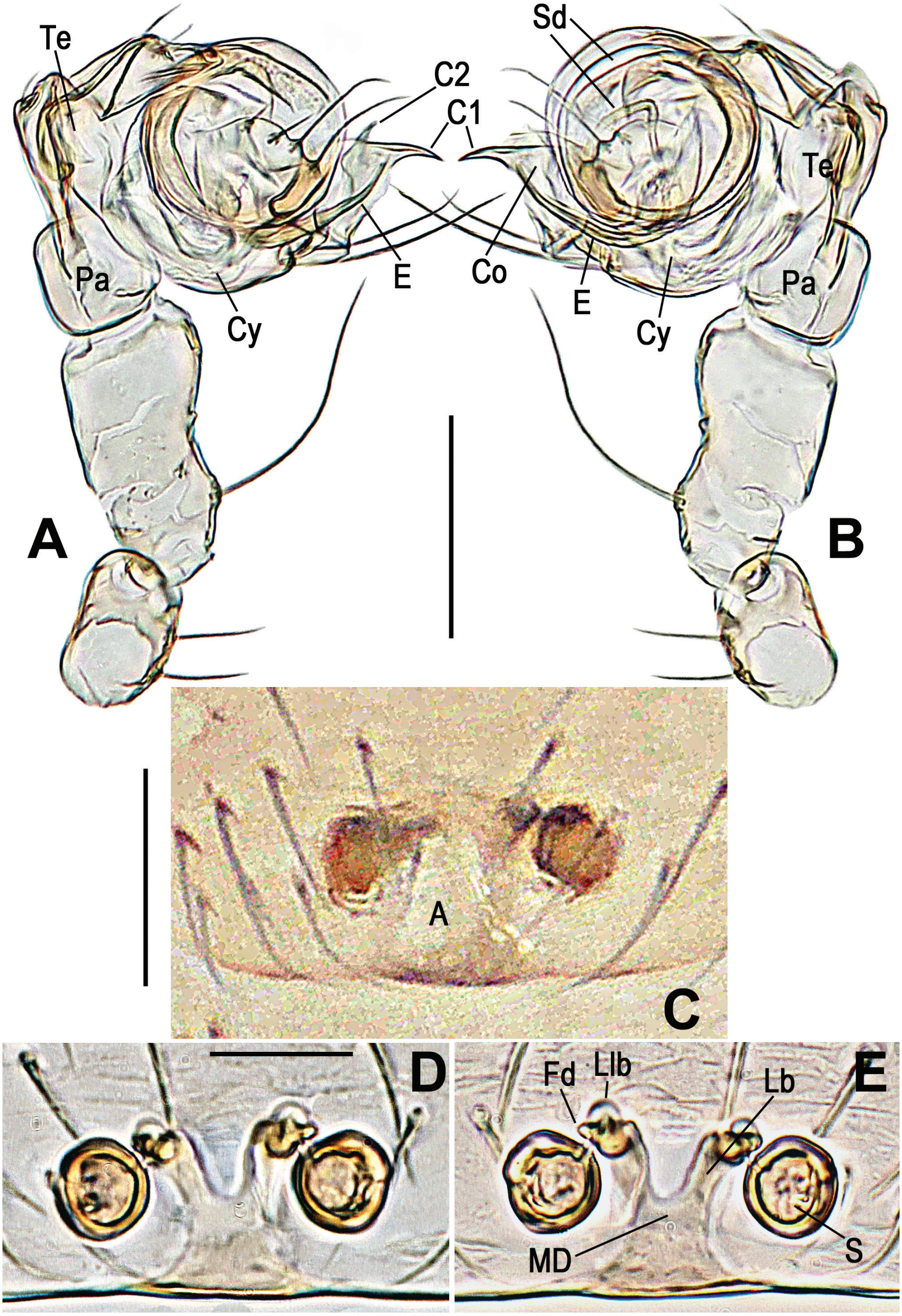

Figure 4. *Anapistula sanjiao* sp. nov. **A** male palp, prolateral **B** male palp, retrolateral **C** epigyne, ventral **D** vulva, ventral **E** vulva, dorsal. Abbreviations: A = epigynal atrium; Co = conductor; C1 = anterior projection of conductor; C2 = posterior projection of conductor; Cy = cymbium; E = embolus; Fd = fertilization duct; Lb = lateral branch of the MD; Llb = distal lobe of lateral branch; MD = median duct of vulva; Pa = palpal patella; S = spermatheca; Sd = sperm duct; Te = palpal tibia. Scale bars: 0.10 (**A–E**).

0.20, 0.12, 0.18), III 0.76 (0.22, 0.08, 0.16, 0.12, 0.18), IV 0.88 (0.20, 0.10, 0.24, 0.16, 0.18); leg formula I-IV-II-III; abdomen 0.36 long, 0.0.32 wide, 0.40 high.

***Epigyne*:** flat, without scape. Internal structures faintly visible via cuticle (Fig. 4C). Atrium long, subtriangular. Spermathecae spherical, strongly sclerotized relative to rest of body (Fig. 3J). MD as wide as diameter of spermatheca (Figs 4E, 7C). Lb diverging from the MD, forming a "Y" shape (Figs 4E, 7D). Lb as long as MD, wide as ca ½ of MD. Llb small, nodular, at distal end of Lb (Figs 4E, 7D).

Natural history. The species lives in the crevices of cave entrance walls and in rubble on the cave floor.

Distribution. China (Yunnan) (Fig. 10).

Anapistula walayaku S. Li & Lin, sp. nov.

https://zoobank.org/2AC52BB0-C4EB-49BE-80B6-0324F4FD7BEC
Figs 3B, E, H, K, 5A–E, 8A–D

Type material. ***Holotype*** ♀ and ***paratypes*** 1♂ 6♀ (NHMSU-HA138), **China:** Yunnan Province, Nujiang Lisu Autonomous Prefecture, Lushui County, Daxingdi Township, Walayaku Cave (26.13198°N, 098.86149°E, 910 m), 10.VIII.2018, Y. Lin, Y. Li & Y. Shu leg.; 2♀ (NHMSU-HA106) from **China:** same data as for the holotype, 24.VI.2016, Y. Li leg. (NHMSU-HA106); 1♂, 1♀, 1 juv. (NHMSU-HA138), and 1♀ (NHMSU-HA106) used for sequencing, GenBank accession numbers given in Table 2, same data as for preceding.

Etymology. The new species is named after the type locality; noun.

Diagnosis. The male of *A. walayaku* sp. nov. is similar to that of *A. panensis* Lin, Tao & Li, 2013 by the relatively small bulb and the ventrally extended cymbium, but it differs by the short, blunt C2 (cf. Figs 5B, 8B to Figs 6B, 9B), the concave margin at the expanded part of the cymbium (cf. Figs 5A, B, 8A, B to Figs 6A, B, 9A, B) and the straight embolic tip (vs. bent) (cf. Figs 5A, 8A to Figs 6A, 9A). The female differs from most *Anapistula* species by the rounded atrium and the wide MD forming a Y-shape with the Lb (Figs 5C, E, 8C). It seems similar to *A. choojaiae* but can be distinguished by the narrower base of the MD and having an earlobe-shaped Llb (cf. Figs 5E, 8D to Rivera-Quiroz et al. 2021: figs 8d, 9c).

Description. Male: Carapace nearly round in male, ovoid in female, pale centrally and pale brown marginally, smooth surface and two central short setae (Fig. 3B). Lateral eyes vestigial, barely visible (Fig. 3B). Chelicerae with two promarginal teeth. Labium rectangular, fused to sternum (Fig. 3E). Sternum peltate, as long as wide, smooth, slightly convex, with sparse, short setae (Fig. 3E). Legs same colour as carapace (Figs 3B, E). Abdomen unknown. Spinnerets and anal tubercle pale. Somatic measurements: body length unknown. Carapace 0.32 long, 0.28 wide, 0.24 high; sternum 0.20 long, 0.20 wide; length of legs: I 1.00 (0.28, 0.12, 0.24, 0.14, 0.22), II 0.82 (0.20, 0.10, 0.18, 0.12, 0.22), III 0.76 (0.18, 0.10, 0.16, 0.10, 0.22), IV 0.80 (0.20, 0.08, 0.20, 0.14, 0.18); leg formula I-IV-II-III.

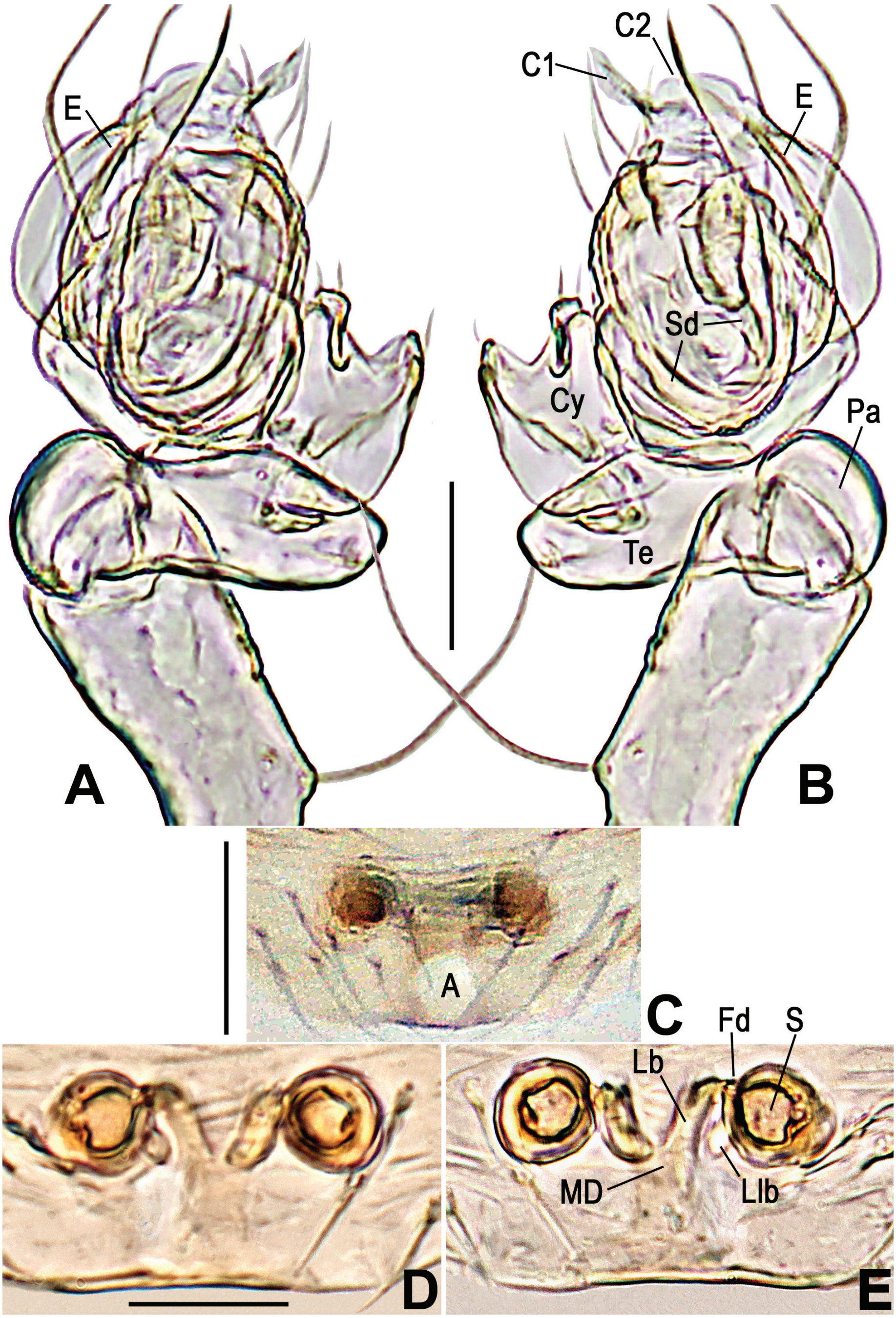

Figure 5. *Anapistula walayaku* sp. nov. **A** male palp, prolateral **B** male palp, retrolateral **C** epigyne, ventral **D** vulva, ventral **E** vulva, dorsal. Abbreviations: A = epigynal atrium; C1 = anterior projection of conductor; C2 = posterior projection of conductor; Cy = cymbium; E = embolus; Fd = fertilization duct; Lb = lateral branch of the MD; Llb = distal lobe of lateral branch; MD = median duct of vulva; Pa = palpal patella; S = spermatheca; Sd = sperm duct; Te = palpal tibia. Scale bars: 0.10 (**A–E**).

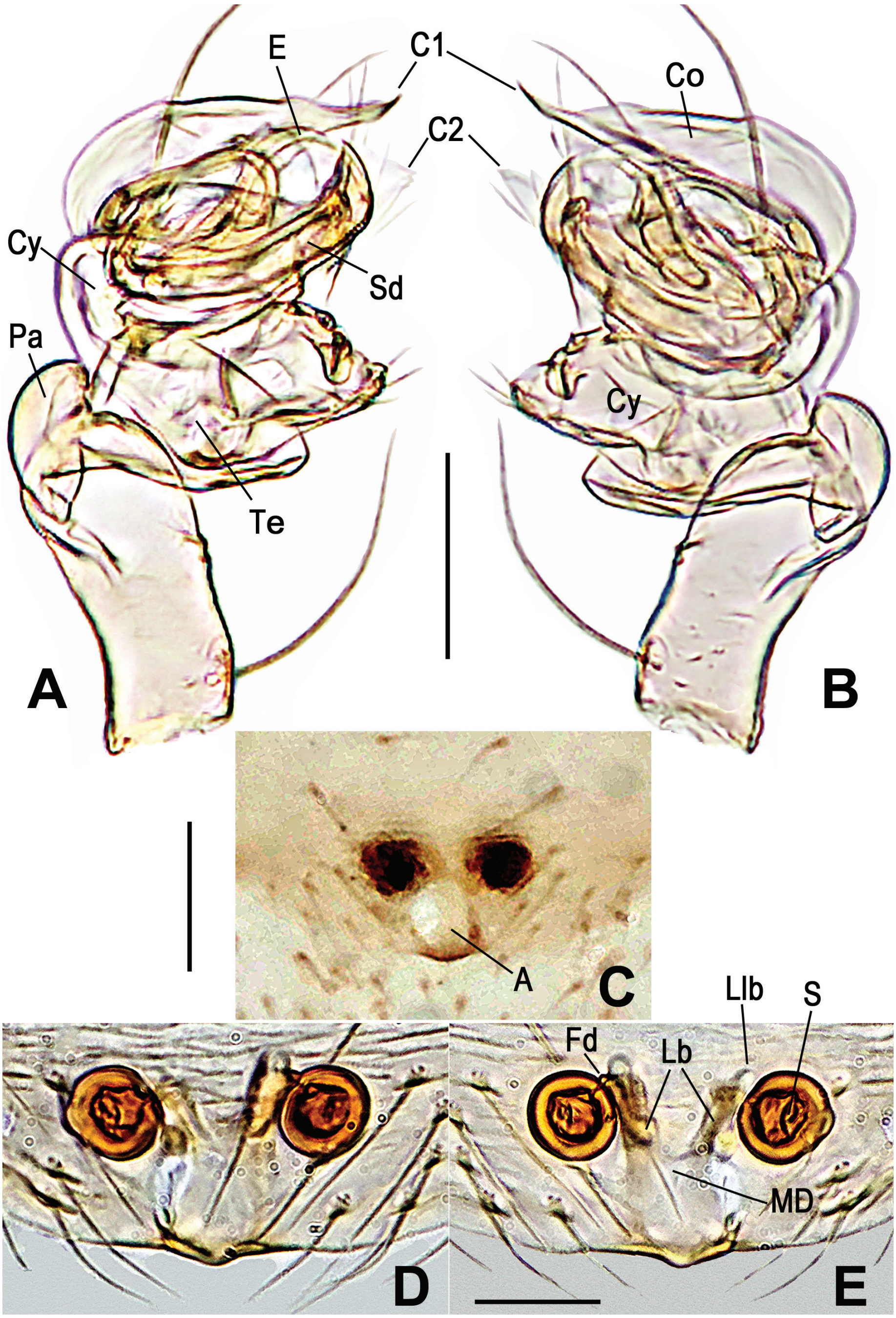

Figure 6. *Anapistula panensis* **A** male palp, prolateral **B** male palp, retrolateral **C** epigyne, ventral **D** vulva, ventral **E** vulva, dorsal. Abbreviations: A = epigynal atrium; Co = conductor; C1 = anterior projection of conductor; C2 = posterior projection of conductor; Cy = cymbium; E = embolus; Fd = fertilization duct; Lb = lateral branch of the MD; Llb = distal lobe of lateral branch; MD = median duct of vulva; Pa = palpal patella; S = spermatheca; Sd = sperm duct; Te = palpal tibia. Scale bars: 0.10 (**A–E**).

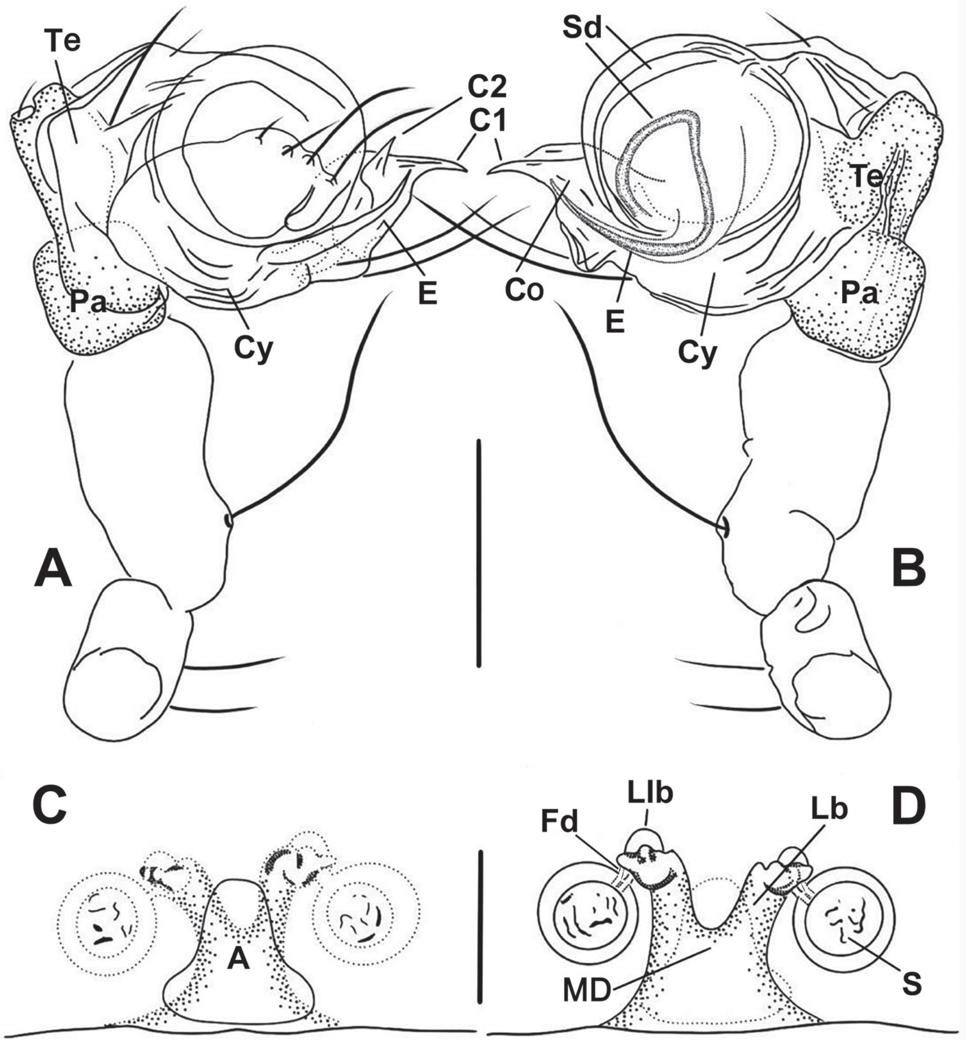

Figure 7. *Anapistula sanjiao* sp. nov. **A** male palp, prolateral **B** male palp, retrolateral **C** vulva, ventral **D** vulva, dorsal. Abbreviations: A = epigynal atrium; Co = conductor; C1 = anterior projection of conductor; C2 = posterior projection of conductor; Cy = cymbium; E = embolus; Fd = fertilization duct; Lb = lateral branch of the MD; Llb = distal lobe of lateral branch; MD = median duct of vulva; Pa = palpal patella; S = spermatheca; Sd = sperm duct; Te = palpal tibia. Scale bars: 0.10 (**A–D**).

***Palp*:** small and weakly sclerotized. Femur swollen distally, with a long seta at retrolateral base. Patella short, as long as ½ length of tibia. Tibia contracted proximally, lacking setae. Cymbium with 4 retrolateral short and 3 dorsal long setae. Paracymbial rim concave, with 3 short setae (Figs 5B, 8B). Conductor sheet shaped, with two projections (C1 and C2), C1 sharp, C2 broad, blunt distally. Embolus long, needle shaped, located posterior to conductor, its end nearly reaches apex of C2. Sperm duct coiled ca 1.8 times inside bulb (Figs 5A, B, 8A, B).

Female: prosoma pear-shaped, palps absent, others as in male (Fig. 3H, K). Abdomen sub-spherical, yellow, dorsally darker than ventrally, cuticle with sparse, short setae and weakly sclerotized spots (Fig. 3H, K). Somatic measurements: body length 0.64, carapace 0.32 long, 0.24 wide, 0.24 high; sternum 0.24 long, 0.24 wide; length of legs: I 0.96 (0.30, 0.12, 0.20, 0.18, 0.16), II 0.86 (0.28, 0.08, 0.18, 0.18, 0.14), III 0.70 (0.18, 0.08, 0.16, 0.14, 0.14), IV 0.82 (0.20, 0.06, 0.22, 0.14, 0.20); leg formula I-IV-II-III; abdomen 0.44 long, 0.40 wide, 0.44 high.

***Epigyne*:** flat, covered with sparse, long setae, without scape. Atrium nearly round, as broad as width of inner MD. Spermathecae spherical, separated by ca 1.2× their diameter, obviously sclerotized (Figs 3K, 5C, 8D). Lateral branch diverging from MD forming "Y" (Figs 5D, E, 8C, D), as wide as ½ MD, same long as ⅔ of MD. Lateral branch runs along dorsal surface of spermathecae and ends in a short, transparent Llb. Fertilization ducts very short, nearly invisible (Figs 5D, E, 8C, D).

Natural history. This species was found in the crevices of stalagmites and stalactites in the dark zone of a cave.

Distribution. China (Yunnan) (Fig. 10).

Anapistula panensis Lin, Tao & S. Li, 2013

Figs 3C, F, I, L, 6A–E, 9A–D

Anapistula panensis Lin, Tao & Li, 2013: 53, figs 1–5 (♂♀).

Type material. ***Holotype*** ♂ and ***paratypes*** 1♂ 50♀ (IZCAS) from **China:** Guizhou Province, Liupanshui City, Pan County, Zhudong Township, Shiliping Village, Shenxian Cave (25.62367°N, 104.75653°E, 1687 m), 15.IV.2007, J. Liu & Y. Lin leg. Examined.

Other material examined. 51♀ 18 juvs (NHMSU-HA020) from **China:** same data as type locality, 26.IV.2010, Y. Lin & Q. Zhao leg.; 1♂ 67♀ 20 juvs (NHMSU-QX003) same data as type locality, 24.VIII.2020, Y. Lin et al. leg.; 1♀ 1 juv (NHMSU-HA020) used for sequencing, GenBank accession numbers given in Table 2, same data as for preceding.

Diagnosis. The male of *A. panensis* is similar to that of *A. choojaiae* in the shape of the palp and in having C1 and C2 roughly equal in length, but it differs by a narrower C1 and a wider C2, a longer embolus, and having three setae on the paracymbium (vs. two; cf. Figs 6A, B, 9A, B; Lin et al. 2013: figs 1, 2 with Rivera-Quiroz et al. 2021: figs 7c, 9a, b). The female differs from most *Anapistula* species by the Y-shaped epigynal median duct; it shares this character with *A. orbisterna*, *A. secreta*, *A. bifurcate*, *A. tonga*, *A. choojaiae*, *A. equatoriana*, *A. zhengi*, *A. sanjiao* sp. nov. and *A. walayaku* sp. nov. *Anapistula panensis* differs from all of these by the width and length of the MD, the length of the lateral branches, and the shape and relative size of the atrium (Figs 6C–E, 9C, D and Lin et al. 2013: figs 3, 4 vs. Forster and Platnick 1977: fig. 19; Harvey 1998: figs 9, 19; Rivera-Quiroz et al. 2021: figs 8d, 9c; Dupérré and Tapia 2017: fig. 33; Lin et al. 2013: figs 8, 9).

Redescription. Male: habitus as in Fig. 3C, F. Body yellow. Legs pale yellow. Carapace nearly round, cephalic area moderately elevated. Four vestigial eyes in diads.

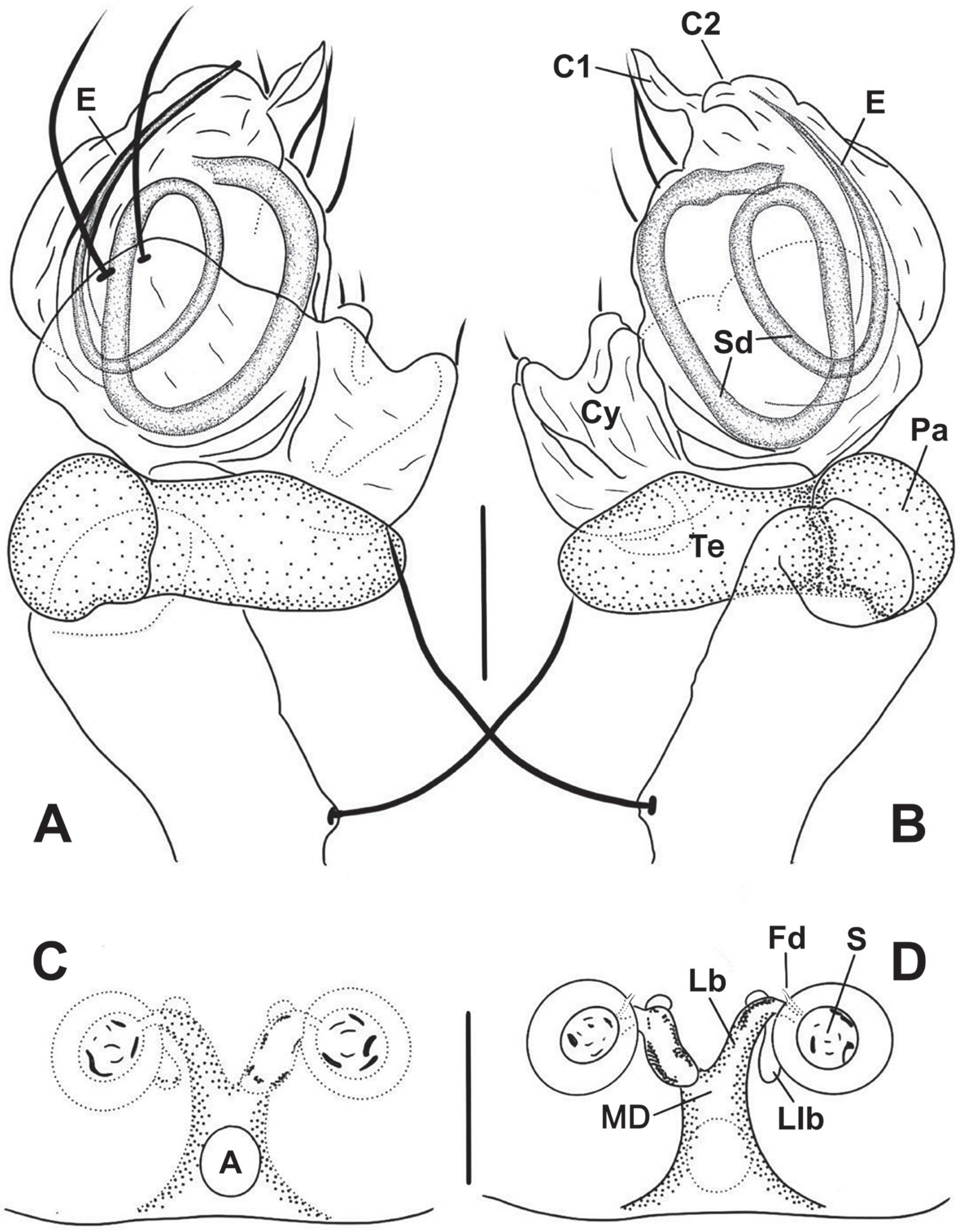

Figure 8. *Anapistula walayaku* sp. nov. **A** male palp, prolateral **B** male palp, retrolateral **C** vulva, ventral **D** vulva, dorsal. Abbreviations: A = epigynal atrium; C1 = anterior projection of conductor; C2 = posterior projection of conductor; Cy = cymbium; E = embolus; Fd = fertilization duct; Lb = lateral branch of the MD; Llb = distal lobe of lateral branch; MD = median duct of vulva; Pa = palpal patella; S = spermatheca; Sd = sperm duct; Te = palpal tibia. Scale bars: 0.10 (**A–D**).

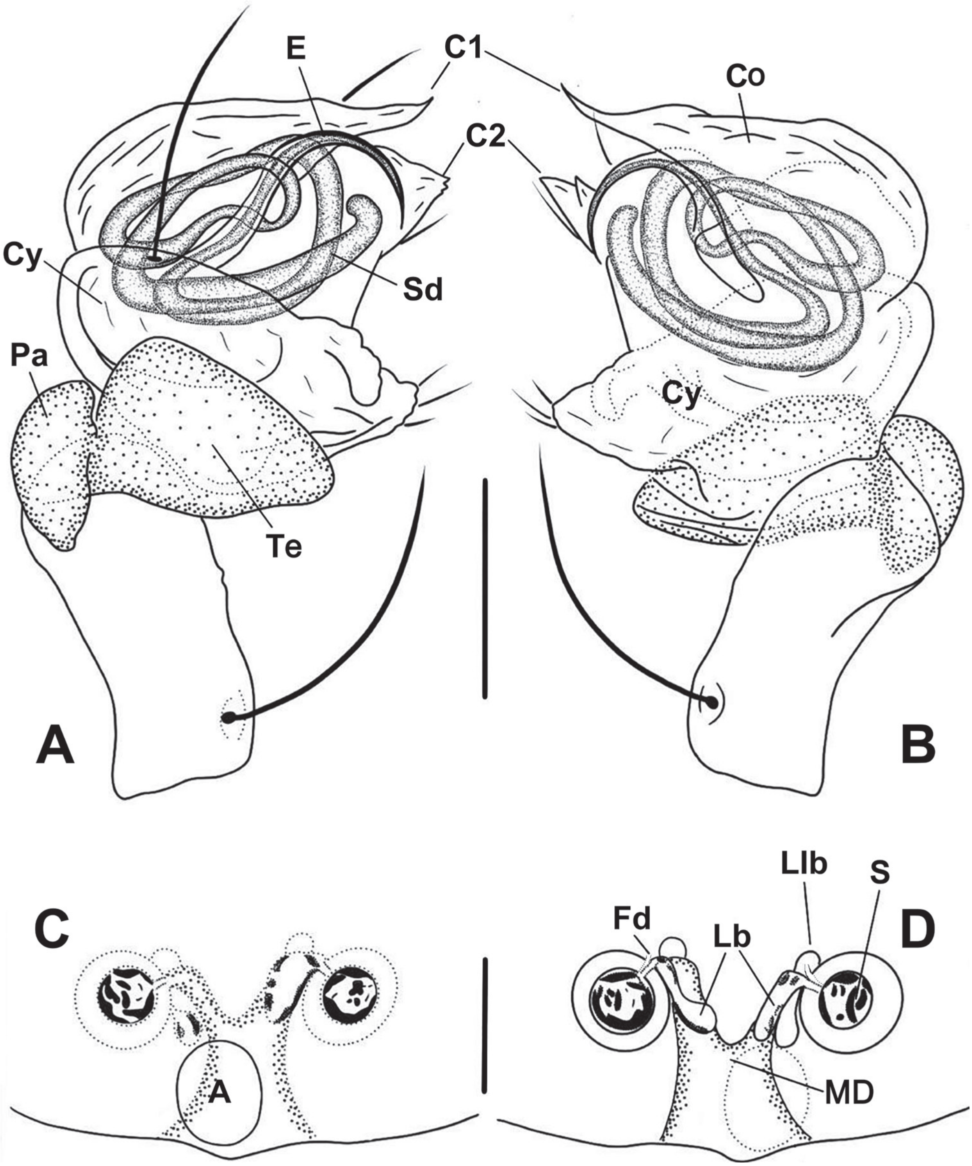

Figure 9. *Anapistula panensis* **A** male palp, prolateral **B** male palp, retrolateral **C** vulva, ventral **D** vulva, dorsal. Abbreviations: A = epigynal atrium; Co = conductor; C1 = anterior projection of conductor; C2 = posterior projection of conductor; Cy = cymbium; E = embolus; Fd = fertilization duct; Lb = lateral branch of the MD; Llb = distal lobe of lateral branch; MD = median duct of vulva; Pa = palpal patella; S = spermatheca; Sd = sperm duct; Te = palpal tibia. Scale bars: 0.10 (**A–D**).

Chelicerae distinctly sclerotized and fused basally, concave at inner margins, with two promarginal teeth. Endites as long as wide. Labium rectangular, length ca equal to ⅓ of width, fused to sternum. Sternum flat, with sparse setae, truncated posteriorly. Femur I and II swollen retrolatero-basally, tiny serrations and granulations on surface. Patellae I–IV each with a distal-dorsal seta. Abdomen ovoid dorsally, higher than long, covered with sparse, grey, long setae, posterior expanded beyond spinnerets. Colulus absent. Somatic measurement: body length 0.56, carapace 0.28 long, 0.28 wide, 0.24 high; sternum 0.20 long, 0.24 wide; abdomen 0.32 long, 0.28 wide, 0.36 high; length of legs: I 1.18 (0.34, 0.14, 0.26, 0.14, 0.30), II 0.96 (0.28, 0.12, 0.18, 0.12, 0.26), III 0.80 (0.20, 0.10, 0.16, 0.10, 0.24), IV 0.98 (0.30, 0.12, 0.18, 0.16, 0.22); leg formula I-IV-II-III.

***Palp*:** small and weakly sclerotized. Femur slightly swollen distally, with a long seta at retrolateral base. Patella short, semilunar shaped. Tibia contracted proximally, broad distally. Cymbium transparent, with 7 retrolateral short and 2 dorsal long setae. Conductor sheet shaped, with two projections (C1 and C2), C1 sharp, C2 lamellar, nearly invisible. Embolus short, needle shaped, posterior to conductor. Sd coiled ca 2 times inside bulb (Figs 6A, B, 9A, B).

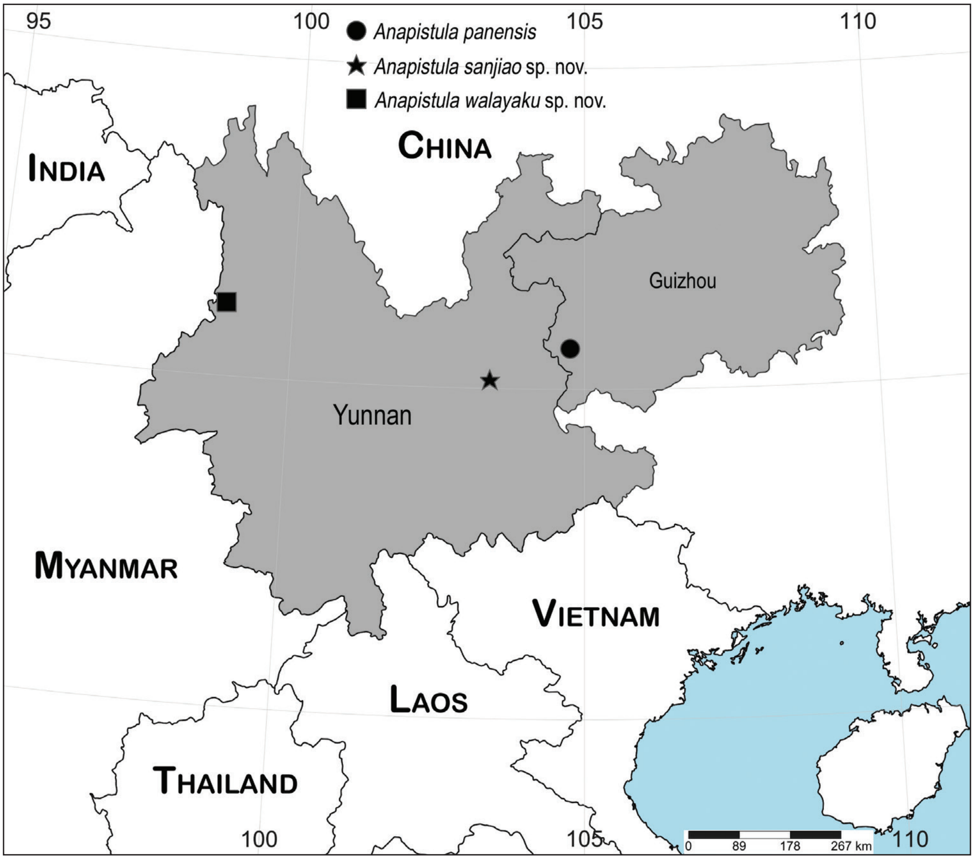

Figure 10. Distribution records of three Chinese cave-dwelling *Anapistula* species.

Female: habitus see Fig. 3I, L. Carapace darker yellow than abdomen. Palps absent, others as in male. Somatic measurements: body length 0.68, carapace 0.28 long, 0.28 wide, 0.24 high; sternum 0.20 long, 0.18 wide; abdomen 0.50 long, 0.52 wide, 0.52 high; length of legs: I 1.18 (0.36, 0.14, 0.24, 0.20, 0.24), II 1.08 (0.30, 0.14, 0.24, 0.18, 0.22), III 0.82 (0.18, 0.12, 0.16, 0.16, 0.20), IV 1.12 (0.30, 0.14, 0.26, 0.18, 0.24); leg formula I-IV-II-III.

***Epigyne*:** flat, without scape. Atrium ovoid, narrower than space between spermathecae. Spermathecae spherical, separated by ca 1.3× their diameter, obviously sclerotized (Figs 3L, 6C, 9C). Lateral branches diverging from MD, forming Y-shape (Figs 6D, E, 9C, D), as wide as ⅓ of MD, as long as MD (Fig. 6E; Lin et al. 2013: figs 3, 4). Fertilization ducts very short, translucent, nearly invisible, Llb appear as tiny bumps distally on lateral branches (Figs 6D, E, 9C, D).

Natural history. This species spins a small, flat circular web in the crevices of stalagmites or stalactites in caves.

Distribution. China (Guizhou) (Fig. 10).

Discussion

The taxonomy of symphytognathoids is inadequate due to their small size and difficulty in collection. However, the worldwide species diversity of this family has increased from 37 species in eight genera to 98 species in ten genera in the past 20 years (WSC 2022). Recent studies have reported 48 species from Asia (Ono 2002; Tong and Li 2006; Lin and Li 2009; Lin et al. 2009, 2013; Miller et al. 2009; Shinkai 2009; Miller et al. 2014; Lin 2019; Li et al. 2020, 2021; Rivera-Quiroz et al. 2021) and 11 species from South America (Rheims and Brescovit 2003; Brescovitet al. 2004; Rubio and González 2010; Dupérré and Tapia 2017).

The symphytognathoids were first proposed as a morphological group by Griswold et al. (1998), who postulated that this spider group consisted of the monophyletic families Theridiosomatidae, Mysmenidae, Symphytognathidae and Anapidae. However, the monophyly of Symphytognathidae and its relationships to the other three families are complex and inconsistent in different phylogenetic studies. Symphytognathidae has been used repeatedly as a representative clade to test the phylogenetic relationships of specific groups, such as "symphytognathoids" (Rix et al. 2008; Lopardo et al. 2011; Feng et al. 2019), the Orbiculariae (Lopardo and Hormiga 2008; Fernández et al. 2014; Rivera-Quiroz et al. 2021) and all Araneae (Dimitrov et al. 2012; Wheeler et al. 2017; Kulkarni et al. 2020) using different molecular approaches and analyses. However, these studies were limited by missing data, including species and markers. The taxonomic status and validity of most symphytognathoid genera and species have not been tested with molecular phylogenetic methods, and the systematics of the family Symphytognathidae is pending.

In this study, we tested the monophyly of Symphytognathidae, but support values were low, probably due to the limited number of representative taxa. Our MP analysis failed to recover the monophyly of Anapidae. In contrast to the results of Rivera-Quiroz et al. (2021), our MP and BI analyses resolved the position of the Micropholcommatinae as within the Anapidae.

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Cincticostella ebura sp. nov., a new species of mayfly (Ephemeroptera, Ephemerellidae) from Thailand

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Abstract

A new species of ephemerellid mayfly, *Cincticostella ebura* **sp. nov.**, is described based on larvae collected in a stream from Nan Province, Thailand. This new species is classified in the *nigra* complex of the genus *Cincticostella* based on morphological and COI phylogeny evidence. The new species is closely related to *C. nigra* (Uéno, 1928) and *C. funki* Martynov, Selvakumar, Palatov & Vasanth, 2021 based on body colour pattern. Investigation of the chorionic structure of the new species showed similar details to those of other species within this species complex. The phylogeny also placed this species into a monophyletic group with *C. nigra* (Uéno, 1928), *C. elongatula* (McLachlan, 1875) and *C. fusca* Kang & Yang, 1995.

Keywords

COI, ephemerellid mayfly, *insolta* complex, integrative taxonomy, *nigra* complex

Introduction

The genus *Cincticostella* was established by Allen (1971) as a subgenus of *Ephemerella* Walsh, 1862, and was subsequently raised to generic level (Allen 1980). *Cincticostella* species are distributed in the eastern Palearctic and Oriental regions. The larvae are characterised by 1) anterolateral projections of the pronotum and mesonotum rounded and flat (contrary to sharp and acute projections in *Ephacerella*), and 2) a widened and flattened maxillary canine with reticulated ventral margin (Kluge 2004) or reduced to a denticulate blade (Jacobus and McCafferty 2008). Within the genus, some characters were used to distinguish and classify the different species into several species groups. For example, Allen (1975) divided the genus into two species complexes consisting of *insolta* and *nigra* complexes. These two species complexes are differentiated by a head with a pair of tubercles and expansion of the mid and hind femora with chalazae in the *insolta* complex, characters which are absent in the *nigra* complex. Allen (1980) proposed the subgenus *Rhionella* to accommodate the *insolta* complex, but this was refuted by Jacobus and McCafferty (2008) based on their phylogenetic reconstruction.

Recently, Martynov et al. (2021) proposed a *gosei* complex, separated from the *nigra* complex by several characters, such as segments I and II of the labial palp relatively narrow and elongated, moderate anterolateral emargination of the labrum and especially, the maxillary palp absent. Therefore, three species complexes are currently considered: the *nigra*, *insolta* and *gosei* complexes.

Currently, 22 species are recognised in the world, of which 17 are found in the Oriental region (Xie et al. 2009; Martynov et al. 2019; Auychinda et al. 2020a; Martynov et al. 2021). According to Martynov et al. (2021) the *insolta* complex comprises eight species, the *nigra* complex 13 species, and the *gosei* complex a single species. The genus *Cincticostella* has the highest diversity of the family Ephemerellidae in the Oriental region, but only three species are currently known in Thailand: *C. femorata* (Tshernova, 1972) and *C. insolta* (Allen, 1971) that belong to the *insolta* complex and *C. gosei* (Allen, 1975) from the *gosei* complex (Martynov et al. 2021).

In 2019, we collected larval material from Nan Province, Thailand. These specimens were morphologically identified and were found to share many characters with the East Palearctic species, *C. nigra* (Uéno, 1928) and Oriental species, *C. funki* Martynov, Selvakumar, Palatov & Vasanth, 2021. However, some characters were different and together with the distinct geographic or ecological distribution, we therefore classified these specimens as a new species and the first recorded species of the *nigra* complex in Thailand. The morphological characters of the mature larvae are described, including the chorionic structures, which were investigated by scanning electron microscopy (SEM). In addition, the COI gene of the new species was sequenced and a phylogenetic tree was reconstructed using our sequences and some *Cincticostella* COI sequences available in the GenBank database. Species delimitation was also based on the genetic distances using Kimura 2-parameter (K2P) analysis (Alexander et al. 2009; Tenchini et al. 2018).

Materials and methods

Specimen analysis

Larvae were collected using a D-frame kick net in the riffles of fast-flowing areas. The specimens were preserved in 95% ethanol and a whole larva was selected and dissected for morphological observation. The morphological characters were observed by permanent slide preparation using Euparal as a medium and observed by light microscopy. The eggs were also dissected from a late female larva. The chorionic structure was investigated by drying the eggs, coating them with gold, and observing them by SEM with a FEI Quanta 450. Final plates were prepared with Adobe Photoshop® CC 2020. Holotype and paratype specimens of the new species are deposited in the collections of the Zoological Museum at Kasetsart University in Bangkok, Thailand [**ZMKU**] and the Museum of Zoology in Lausanne, Switzerland [**MZL**].

Molecular analysis

Thoracic muscles were dissected for DNA extraction. Total genomic DNA was extracted with a genomic DNA extraction kit (NucleoSpin, Macherey-Nagel, Germany) following the manufacturer's protocol. The COI amplification was performed using LCO1490 and HCO2198 (Folmer et al. 1994). The polymerase chain reaction (PCR) conditions and procedure were performed as described previously (Auychinda et al. 2020c). Purification and sequencing were conducted by Macrogen, Inc. (South Korea). A Bayesian tree for ephemerellid mayflies was constructed for *Teloganopsis* spp., *Torleya* spp., available *Cincticostella* species (GenBank and BOLD system) and our sequences (658 bp) for the new species (MW633484), and one specimen of *C. insolta* (MW633483). We also added a specimen of *C. femorata* (Tshernova, 1972) from Chiang Mai Province, Thailand that was deposited in MZL (GBIFCH00763740_A01), and its COI was also extracted, sequenced, analysed and deposited in the GenBank database (MW633485). *Teloganella umbrata* Ulmer, 1939 was used as an outgroup. The protocol for tree construction follows Auychinda et al. (2020c).

Taxonomy

Order Ephemeroptera
Family Ephemerellidae Klapálek, 1909
Genus *Cincticostella* Allen, 1971

***Cincticostella ebura* sp. nov.**
https://zoobank.org/99170F17-D407-4F9B-AF3C-72E18192A2A4
Figs 1–5, 6c

Material examined. ***Holotype*:** Male mature larva in ethanol, Thailand, Nan Province, Bo Kluea District, Mae Nam Wa stream, 19°16'22.6"N, 101°10'48.2"E, 848 m, 26.XI.2019, C. Auychinda leg. [**ZMKU**]. ***Paratypes*:** 30 larvae in ethanol, one on slide, same data as holotype [**ZMKU**]; 4 larvae in ethanol, same data as holotype [**MZL** GBIFCH00977588].

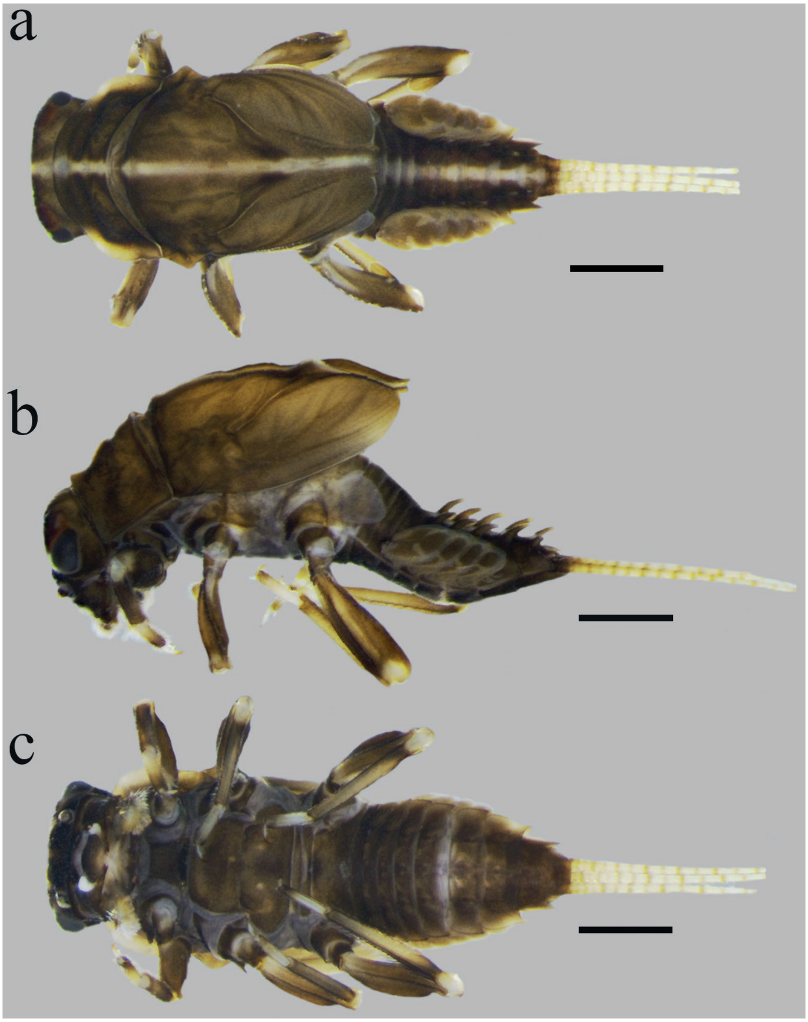

Figure 1. *Cincticostella ebura* sp. nov. **a** larval habitus in dorsal view **b** in lateral view and **c** in ventral view. Scale bars: 1 mm.

Description. Mature larva (in alcohol, Fig. 1; living, Fig. 6c). Body length (without cerci) 5.5–6.0 mm; cerci 6.0–8.5 mm; body brownish-black with a conspicuous dorsal median pale line from the head to tergum X (Figs 1a, 6c).

Head. Black without tubercles, prominent bright ocelli; antennae three times longer than head length. Labrum densely covered with long fine setae, apicolateral angles rounded; apicomedially with deep emargination; ratio of emargination length to maximum labrum length = 1: 4.7 (Fig. 2a). Mandibles stout with numerous, hair-like setae on 2/3 proximal of dorsal and lateral surfaces (Fig. 2b, c). Left mandible: outer incisor composed of three acute teeth; inner incisor with one main stout and one inner vestigial tooth; prostheca with a bunch of hair-like setae on the inner side (Fig. 2b). Right mandible: outer incisor composed of two pointed teeth; inner incisor composed of two apically pointed teeth, orientated perpendicularly to the outer incisor; prostheca consisting of numerous hair-like setae (Fig. 2c) Hypopharynx: lingual surface covered with short setae, most abundant in apical part; superlinguae with numerous hair-like setae, apices rounded, posterolateral part concave (Fig. 2d). Labium with narrow elliptical glossae, almost four times longer than broad and covered with numerous short fine setae; paraglossae broad, semicircular, with surfaces covered with numerous simple setae. Labial palp three-segmented; segments I and II stout and equal in length, outer margin covered with hair-like setae, segment III spine-like in shape, 2.5 times longer than broad at the base (Fig. 2e). Maxillae slender; maxillary palpi long (0.46 mm), covered with tiny setae and three-segmented, length ratio from basal to apical segments = 4: 4: 1 (Fig. 2f), apex of segment II with long hair-like setae, segment III cone-shaped and with tiny short setae apically (Fig. 2h); apex of maxilla widened, surface with numerous long, hair-like setae; maxillary canine reduced to a small denticulated blade and less than half as long as crown, inner margin of galea-lacinia with 3–4 rows of simple setae (Fig. 2f, g).

Thorax. Black with distinct white median line. Pronotum rectangular without clear anterolateral projections. Mesonotum with rounded anterolateral projections, outer margins not notched (Fig. 1a); mounted on slide, this character looks more angular (Fig. 4a); a pair of sub-median tubercles in the middle, a single posterior prominent median tubercle (Fig. 1b), posteriorly between fore wing pads with a pair of well-developed projections, angular with deep cleft (Figs 1a, 4a–b). Prothoracic sternum trapezoidal,

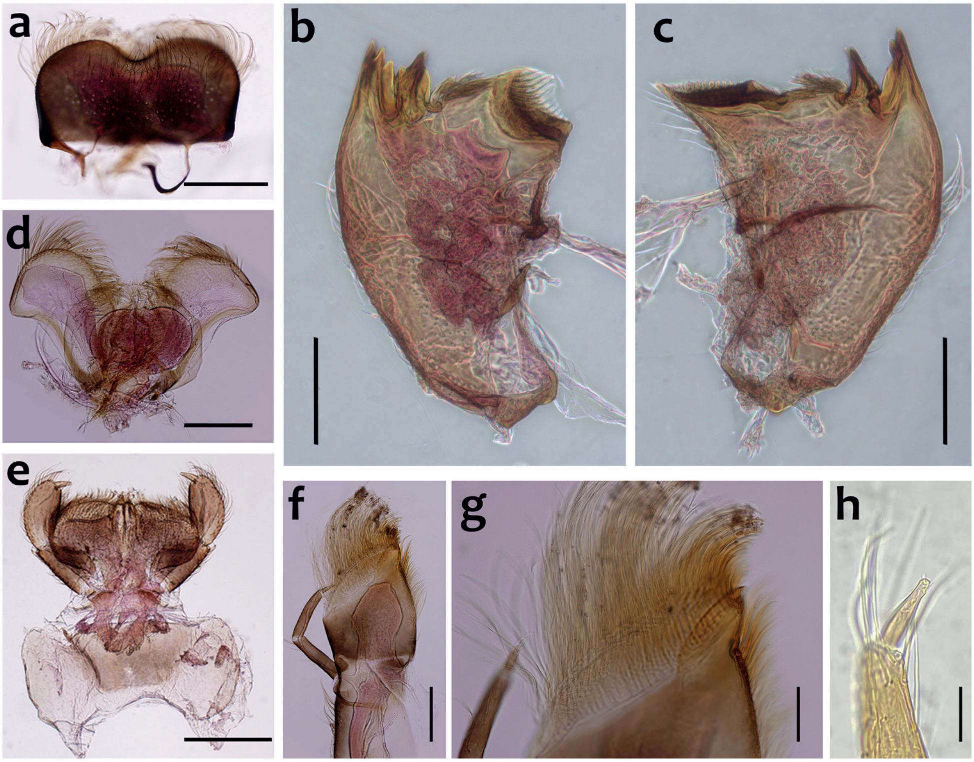

Figure 2. *Cincticostella ebura* sp. nov. **a** labrum **b** left mandible **c** right mandible **d** hypopharynx **e** labium **f** maxilla **g** galea-lacinia **h** segment III of maxillary palp. Scale bars: 0.2 mm (**a–f**); 0.05 mm (**g**); 0.035 mm (**h**).

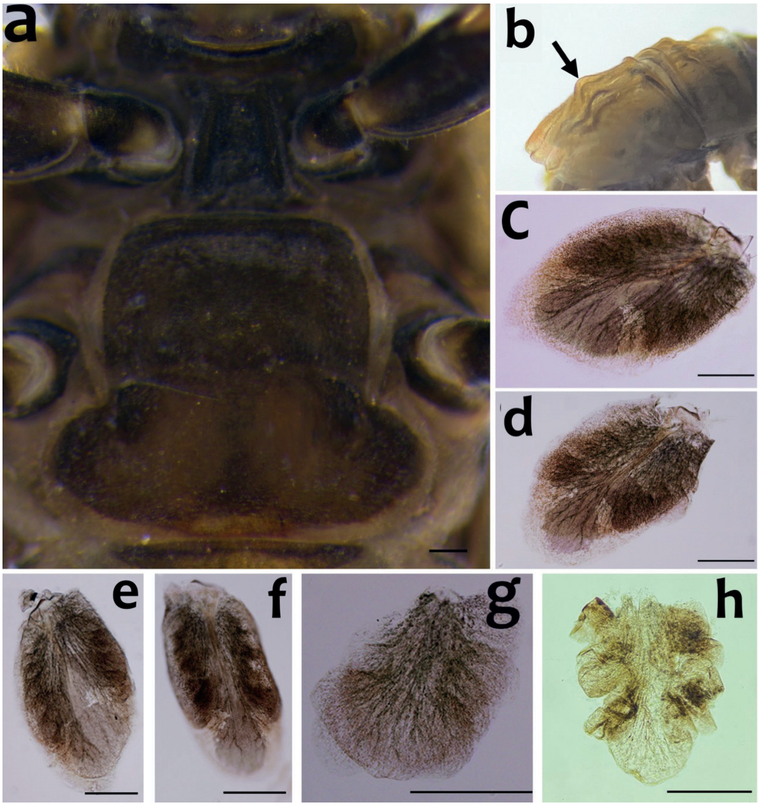

Figure 3. *Cincticostella ebura* sp. nov. **a** prosternum and mesosternum **b** pairs of tubercles (arrow) on mesothorax of early stage; **c–f** gills of segment III–VI **g** ventral lamella of gill of segment VII **h** ventral lamella of gill of segment VI. Scale bars: 0.2 mm.

mesothoracic basisternum rectangular, mesothoracic furcastemum broader than basisternum, oval transversely (Fig. 3a). Forefemora moderately dilated, ventral margin with fine setae, dorsal margin with spatulate setae most abundant in distal part, distal part of the dorsal surface with a transversal discontinuous row of 6–8 spatulate setae perpendicular to the femur (Fig. 4 c, i, j). Midfemora moderately expanded, dorsal margin smooth and with a row of short stout setae abundant in distal part (Fig. 4e). Hind femora moderately expanded, longer than mid femora, dorsal margin smooth, with a row of short stout setae from median to distal part (Fig. 4f). All claws similar, strongly hooked without apical setae, each with an acute basal and subapical tooth (Fig. 4d).

Abdomen. Terga I–X each with a pair of posteromedian projections, well developed into strong tubercles of terga IV–VIII (Figs 1b, 4g); posterolateral projections of tergum VIII less developed (Fig. 4h); posterior margins of each tergum with bifurcate stout setae (Fig. 4k). Gills present on segments III–VII (Fig. 3c–h), all gills consistent with the diagnostic character of the genus *Cincticostella*: gill III without medial transverse band of weakened membrane; ventral lamella of gills III–V bifurcated (Fig. 3c–e),

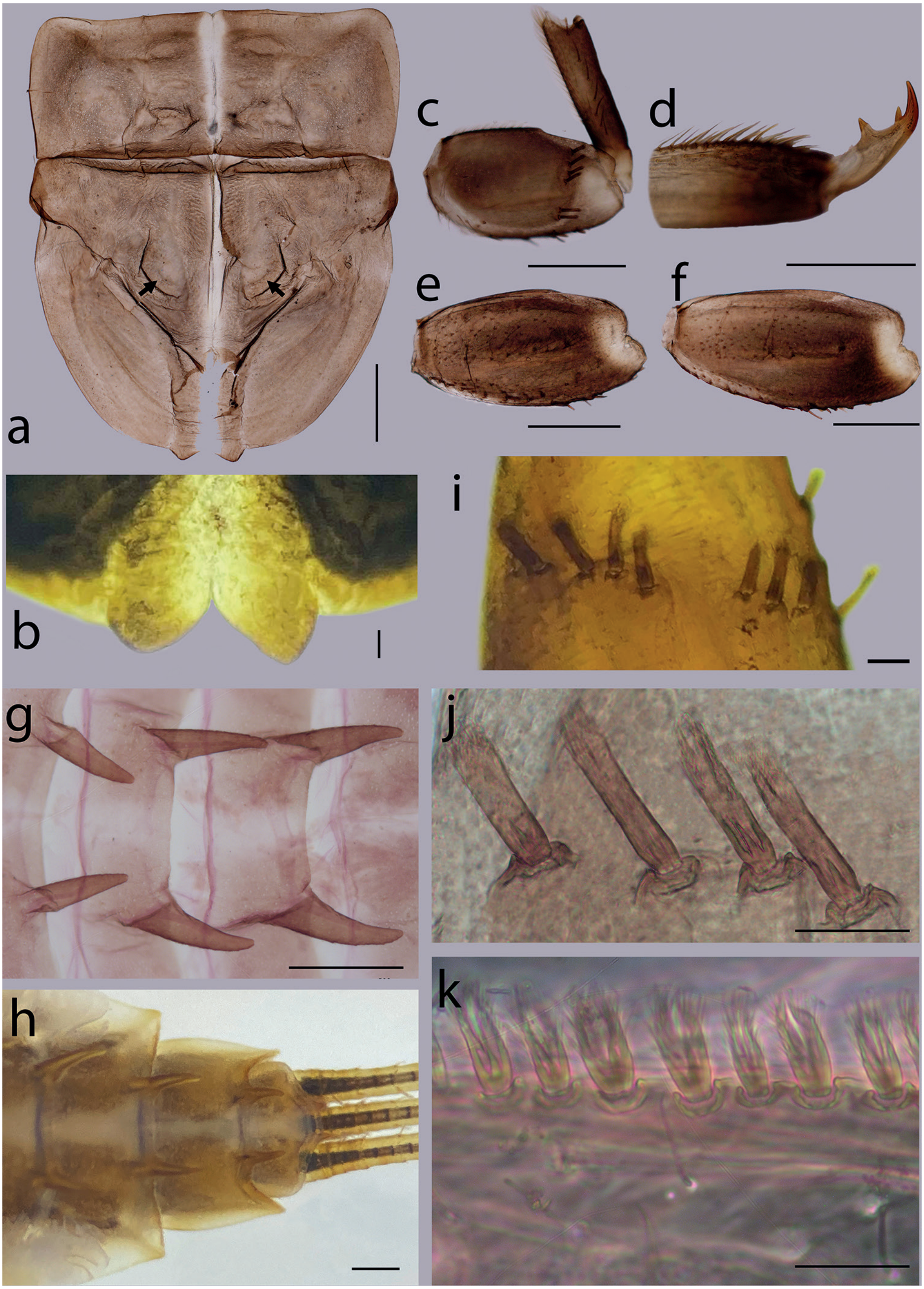

Figure 4. *Cincticostella ebura* sp. nov. **a** thorax in dorsal view, a pair of tubercles was indicated by arrows **b** posterior projection of mesonotum **c** foreleg **d** foretarsal claw **e** mid-femur **f** hind-femur **g** abdominal terga V–VII **h** abdominal terga VIII–X **i, j** setae on apically dorsal forefemoral surface **k** setae on posterior margin of abdominal terga. Scale bars: 0.2 mm (**a, b, c, e, f, g, h**); 0.05 mm (**d, j**); 0.01 mm (**k**).

gill VI–VII non-bifurcate with marginal processes (Fig. 3f–h). Caudal filaments with whorls of dense setae on each segment.

Eggs. Dissected from mature larva (Fig. 5). Ovoid, length ca 125 µm, width ca 110 µm; one pole covered with a dome-shaped polar cap, chorionic surface reticulated, almost hexagonal in formation, with a central spot (Fig. 5a, b). Equator with 4–6 micropyles, sperm guide circular and smooth (Fig. 5c). Rounded knob terminated coiled threads (KCT) especially abundant at the part opposite the polar cap (Fig. 5d).

Adults. Unknown.

Remarks. The pair of sub-median tubercles in the middle of mesonotum of early stages is prominent and variable in number, 2 or 4 tubercles (Fig. 3b) which is similar to other Ephemerellidae such as *Notacanthella commodema* (Allen, 1971) in which the tubercle numbers reduce and are more flattened in later stages (Auychinda et al. 2020b). On the contrary, the posterior median tubercle is distinct in all larval stages of the new species. Although, *C. funki* has no distinct prominent tubercle on their posterior median mesothorax in later stages, this tubercle is distinct in the small larval stages (A. Martynov, pers. comm.)

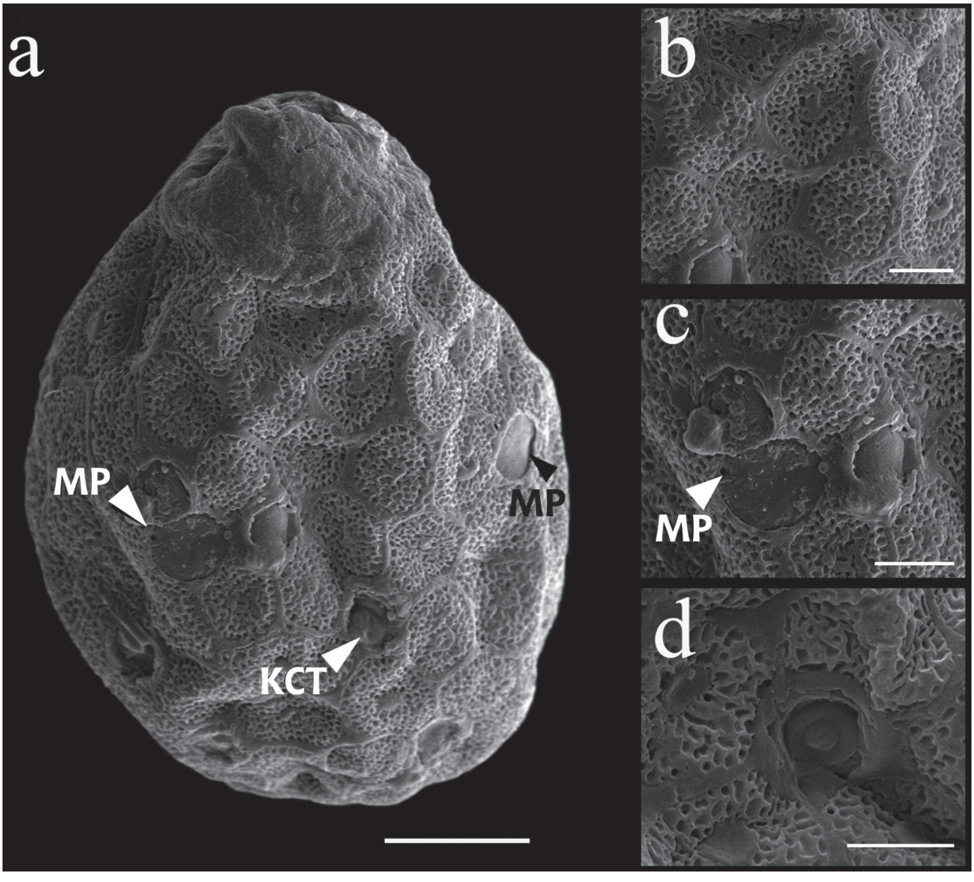

Figure 5. *Cincticostella ebura* sp. nov. **a** an overview of egg **b** chorionic surface **c** chorionic surface with micropyles **d** chorionic surface with KCT. Scale bars: 0.02 mm (**a**); 0.01 mm (**b–d**).

Diagnosis. The larva of *Cincticostella ebura* sp. nov. has a well-marked white median line along its body that can be used to separate it from other *Cincticostella* species. However, this pattern is also present in *C. nigra* (Uéno, 1928) and *C. funki* Martynov, Selvakumar, Palatov & Vasanth, 2021, and the body shape is quite similar (Uéno 1928; Ishiwata 2003; Martynov et al. 2021). Although, claws of *C. ebura* sp. nov. and *C. funki* are hooked with an acute basal and subapical tooth, this character is absent in *C. nigra*, where a row of 6–8 teeth of unequal size can be found (Uéno 1928, fig. 9h–i) or 5–8 denticles of tarsal claws (Ishiwata 2003). In addition, the dorsal surface of the mid- and hind femora of *C. ebura* sp. nov. possess clavate setae while in *C. nigra*, these setae are absent (Ishiwata 2003, figs 48, 52). Furthermore, *C. ebura* sp. nov. can be distinguished from *C. nigra* and *C. funki* based on the combination of following characteristics: 1) small denticulate blade maxillary canine; 2) maxillary palp segment III cone-shaped; 3) all abdominal terga with long pairs of tubercles, especially on terga IV to VIII, on tergum X small and pointed;

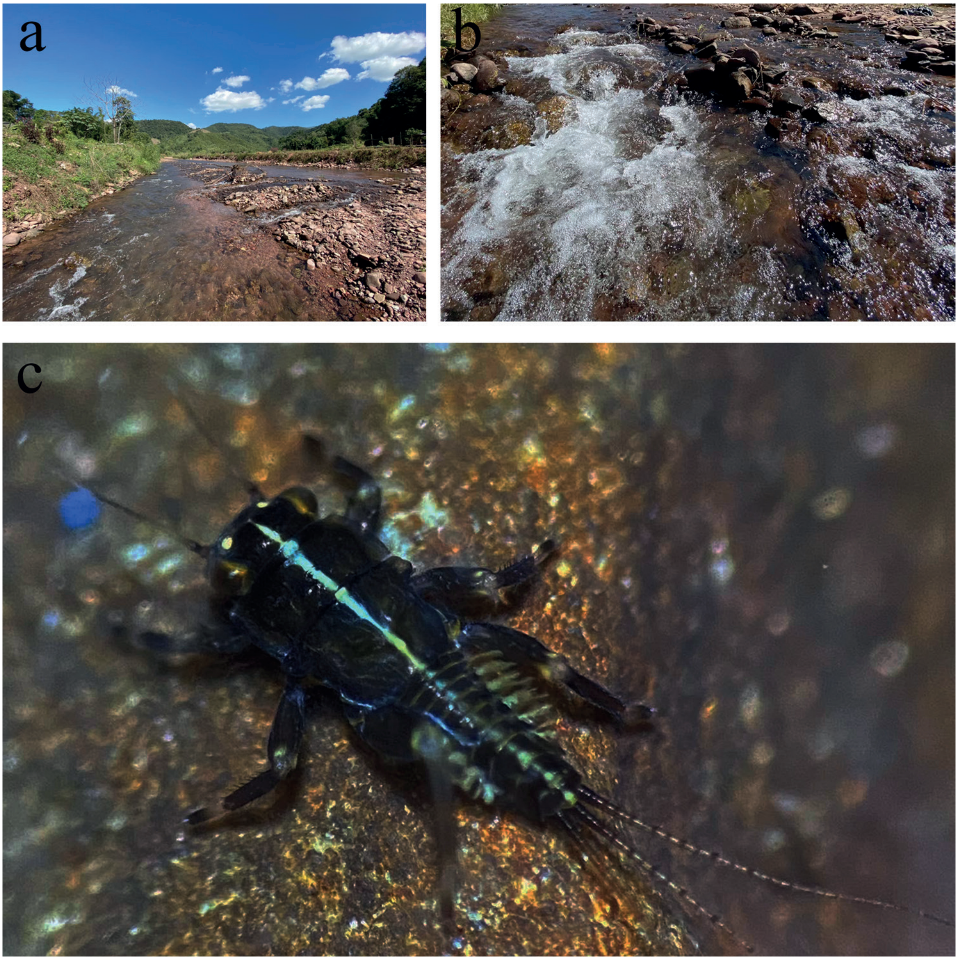

Figure 6. a The Mae Nam Wa stream, Bo Kluea district, Nan Province **b** microhabitat of the larvae of *Cincticostella ebura* sp. nov. **c** *Cincticostella ebura* sp. nov. larva (living).

4) anterolateral projection of the pronotum absent; 5) mature larvae length is almost less than two times of *C. funki*; 6) mesonotum with single prominent median posterior tubercle and posteriorly with a pair of well-developed angular projections; and 7) a transverse discontinuous row of stout setae and without extra setae on surface of forefemora.

Etymology. The specific epithet 'ebura', which means ivory, is a reference to the pairs of long and curve tubercles on the abdominal posteromedian margins.

Habitat and ecology. The type locality of *Cincticostella ebura* sp. nov. is the Mae Nam Wa stream, Nan Province, Thailand (Fig. 6a). The larvae were collected by hand-picking and D-frame net kicking methods from cobble and pebbles within moderate-to fast-flowing current of run/riffle areas (Fig. 6b). This study site also shows a high taxa richness of Ephemerelloidea larvae, as other species, including *C. insolta* (Allen, 1971), *Notacanthella quadrata* (Kluge & Zhou, 2004), *N. commodema* (Allen, 1971), *Dudgeodes* sp. and *Vietnamella nanensis* Auychinda, Sartori & Boonsoong, 2020, co-occurred with the larvae of *C. ebura* sp. nov.

Distribution. Nan Province, northern Thailand.

Molecular analysis

The Bayesian phylogenetic tree reconstruction of COI showed that *Cincticostella* forms a monophyletic lineage which is distinctly separated from the other ephemerellid mayflies, with high probability branch support (Fig. 7). Our reconstruction contained ten species of *Cincticostella*, and the interspecific genetic distances ranged from 15–26%. *Cincticostella ebura* sp. nov. differed from other species by a range of 21 to 26% (Table 1).

Table 1. Pairwise genetic distances (COI) between species of *Cincticostella* using the Kimura 2-parameter.

Species	K2P genetic distances								
	1	2	3	4	5	6	7	8	9
1. *C. ebura* sp. nov.									
2. *C. nigra*	0.22								
3. *C. elongatula*	0.24	0.15							
4. *C. levanidovae*	0.24	0.24	0.24						
5. *C. tornata*	0.23	0.25	0.25	0.26					
6. *C. femorata*	0.23	0.24	0.24	0.20	0.16				
7. *C. gosei*	0.23	0.21	0.25	0.23	0.22	0.23			
8. *C. insolta*	0.22	0.25	0.23	0.22	0.22	0.22	0.22		
9. *C. orientalis*	0.26	0.26	0.26	0.25	0.22	0.25	0.23	0.23	
10. *C. fusca*	0.21	0.22	0.24	0.23	0.22	0.24	0.23	0.24	0.23

Discussion

Our morphological evaluation of *C. ebura* sp. nov, especially body coloration, revealed some similarities with *C. nigra* and *C. funki*. However, these three species inhabit different geographic areas, as *C. nigra* is only reported from the East Palaearctic (Uéno

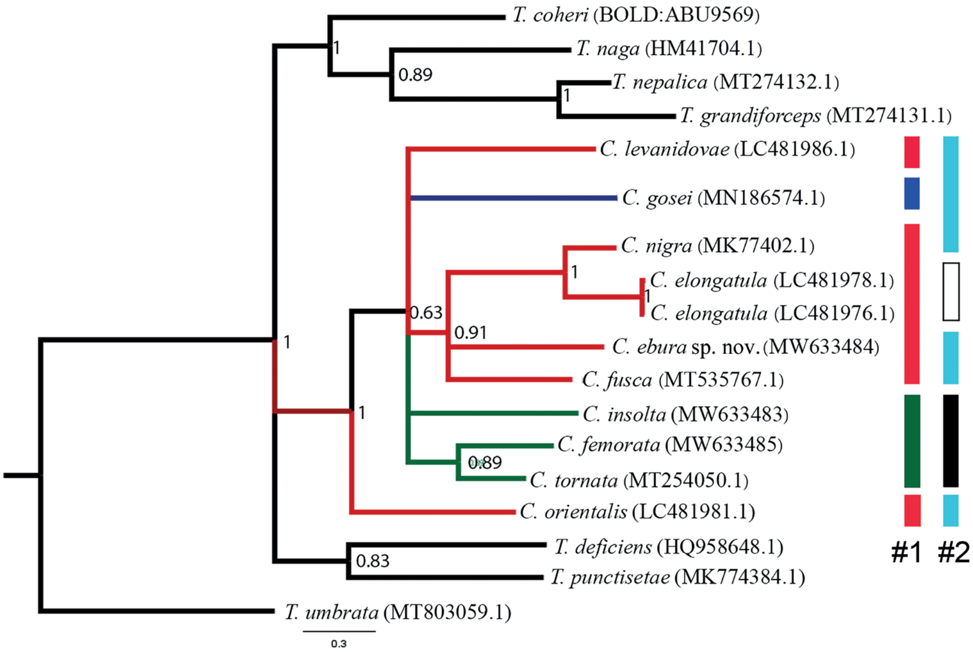

Figure 7. Bayesian inference of COI sequences of some ephemerellid mayflies including *Teloganopsis*, *Torleya* and *Cincticostella* with probability branch support and GenBank accession numbers, or BOLD numbers, in brackets. The color bars indicate the species complex of the genus *Cincticostella*. The first column (#1) is the species complex following Martynov et al. (2021): red = *nigra* complex, blue = *gosei* complex and green = *insolta* complex. The second column (#2) follows Kluge (2021): sky blue = *Cincticostella*/g4, black = *Rhionella* and blank box = uncertain placement (*Ephemerella*/fg3 INCERTAE SEDIS). *Teloganella umbrata* (Ephemerelloidea; Teloganellidae) was chosen as an outgroup.

1928; Ishiwata 2003), while *C. funki* and *C. ebura* sp. nov. both have an Oriental distribution in northern India and northern Thailand, respectively. In addition, ecological factors are also different between the habitats of *C. ebura* sp. nov. and *C. funki*. The larvae of *C. ebura* sp. nov. were collected from a stream which temperature was 18–20 °C in sampling period at 848 m a.s.l. *Cincticostella funki* inhabits in lower water temperature and higher altitude, 12 °C in the sampling period and 1285 m a.s.l. (Martynov et al. 2021).

The egg chorionic structure shows a similar pattern to that of the other *Cincticostella* species, including *C. levanidovae*, *C. elongatula*, *C. nigra*, *C. fusca*, *C. orientalis*, *C. colossa* and *C. femorata* (Kang and Yang 1995; Ishiwata 2003; Jacobus and McCafferty 2008; Zheng and Zhou 2021). It has hexagonal ridges with marks at the centre; the marks vary both in shape and in number therefore can be used to identify species complex of this genus. The dichotomous key to species using chorionic structure is presented below. However, *C. ebura* sp. nov. cannot be separated from *C. colossa*, *C. fusca* and *C. orientalis* by the shape and number of the marks. The egg size can be helpful because *C. ebura* sp. nov. has the smallest egg compared to the others.

From our results, *C. ebura* sp. nov. belongs to the *nigra* complex according to Martynov et al. (2021), or *Cincticostella*/g4 sensu Kluge (2021) based on morphological and molecular evidence. Although this genus has a high number of species, only four of them are found in Thailand, *C. ebura* sp. nov. being the first species from the *nigra* complex to be reported from Thailand.

Our molecular results support the placement of *C. ebura* sp. nov. into the *nigra* complex. In addition, our analysis supports the placement of *C. elongatula* (McLachlan, 1875) by Martynov et al. (2021) into the *nigra* complex. Our tree topology displays several polytomies and did not show the species complexes proposed by both Kluge (2021) and Martynov et al. (2021). However, our reconstruction (Fig. 7) seems to indicate that the *insolta* complex may well be a monophyletic lineage corresponding to the subgenus *Rhionella*.

In our reconstruction, *C. orientalis* (Tshernova, 1952) was recovered as the sister clade of all *Cincticostella* species, whereas Martynov et al. (2021) include it in the *nigra* complex. Our results also support *C. orientalis* as a valid species and not a synonym of *C. levanidovae* (Tshernova, 1952) as proposed by Tshernova et al. (1986) and by Kluge (2021). The species complexes relationship may be solved when more molecular data, both nuclear and mitochondrial DNA, becomes available (Ogden et al. 2019).

Key to the mature nymphs of *Cincticostella* species in Thailand

1 Mid- and hind femora expanded; head with a pair of tubercles **2**

– Mid- and hind femora not expanded; head without tubercles **3**

2 Pronotum with broad and extended anterolateral projection around head capsule .... ***C. femorata***

– Pronotum with moderately anterolateral projection… .... ***C. insolta***

3 Body black without median pale line; maxillary without palpi .... ***C. gosei***

– Body black with median pale line along the body; maxillary with three-segmented palpi .... ***C. ebura* sp. nov.**

Key to known egg structures of *Cincticostella* species (excluding *C. gosei*)

1 Chorion covered with broken reticulation (Ishiwata, 2003, figs 7, 8) .... ***C. levanidovae***

– Chorion covered with not broken reticulation **2**

2 Chorionic surface with one tubercle (rarely two) at the centre of hexagonal ridge **3**

– Chorionic surface with a variety of tubercles (1–5) at the centre of hexagonal ridge (Kang and Yang 1995, figs 11, 12, 14, 15; Ishiwata 2003, figs 15, 16) . ... ***C. colossa*, *C. fusca*, *C. orientalis* and *C. ebura* sp. nov.**

3 Egg relatively large, surface seems to be rough (length 162–168 μm, width 116–120 μm) (Ishiwata 2003, figs 3, 4, 11, 12) .... ***C. elongatula* and *C. nigra***

– Egg relatively small, surface seems to be smooth (length 152 μm, width 114.6 μm) (Zheng and Zhou 2021, fig. 8) .... ***C. femorata***

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