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Culicoides Latreille and *Leptoconops* Skuse biting midges of the southwestern United States with emphasis on the Canyonlands of southeastern Utah (Diptera: Ceratopogonidae)

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Culicoides Latreille and *Leptoconops* Skuse biting midges of the southwestern United States with emphasis on the Canyonlands of southeastern Utah (Diptera: Ceratopogonidae)

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Abstract. *Leptoconops* Skuse and *Culicoides* Latreille (Diptera: Ceratopogonidae) biting midges are serious pests of mammals, birds, and reptiles and important vectors of viruses, protozoans, and filarial nematodes. Their collection became an important adjunct to mosquito surveillance using light-baited and CO_2-baited suction traps in Grand County, Utah, United States, during 1999–2016. During 2017–2020, collecting was expanded to California, Nevada, Idaho, Wyoming, Colorado, Arizona, New Mexico, and other parts of Utah using an ultraviolet light suction trap. As a result, five species of *Leptoconops* and 59 species of *Culicoides*, representing *Leptoconops* subgenera *Holoconops* Kieffer and *Leptoconops* Skuse, *Culicoides* subgenera *Amossovia* Glukhova, *Beltranmyia* Vargas, *Diphaomyia* Vargas, *Drymodesmyia* Vargas, *Haematomyidium* Goeldi, *Monoculicoides* Khalaf, *Selfia* Khalaf, *Sensiculicoides* Shevchenko, *Silvaticulicoides* Glukhova, *Silvicola* Mirzaeva and Isaev, and *Wirthomyia* Vargas, and the *Culicoides* Leoni, Limai, Palmerae, Piliferus, Saundersi, and Stonei species groups, were collected. Keys to adult males and females and tables of diagnostic characters are provided for identification of 15 species of *Leptoconops* and 86 species of *Culicoides* collected, reported by others, or likely to occur in the Southwestern United states west of the Continental Divide. Description references, synonymies, diagnoses, geographic and seasonal distributions, and biological summaries from the available literature are provided. Data on relative abundance in light-baited or CO_2-baited traps are provided for the species collected. Intersex specimens and specimens parasitized by mites or mermithid nematodes are tabulated. *Culicoides* (*Drymodesmyia*) *bakeri* Vargas is reported from California (**new United States record**). New state records of other species for Idaho, Nevada, Utah, Colorado, Arizona, and New Mexico of the United States and for the Mexico states of Puebla, San Luis Potosi, and Oaxaca are reported. *Culicoides salihi* Khalaf is assigned to the subgenus *Diphaomyia* of *Culicoides* (**new status**). *Culicoides stellifer* (Coquillett) is reassigned to the subgenus *Haematomyidium* of *Culicoides* (**new status**). *Culicoides travisi* Vargas is assigned to the subgenus *Sensiculicoides* of *Culicoides* (**new status**). *Culicoides luglani* Jones and Wirth is reassigned to the *Culicoides* Limai group (**new status**). Confusion over species limits was evident between *Culicoides cacticola* Wirth and Hubert and *Culicoides torridus* Wirth and Hubert, between *C. travisi* and *Culicoides kibunensis* Tokunaga, between *Culicoides doeringae* Atchley and *Culicoides lophortygis* Atchley and Wirth, between *Culicoides owyheensis* Jones and Wirth and *Culicoides mortivallis* Wirth and Blanton, and between *Culicoides cockerellii* (Coquillett), *Culicoides neomontanus* Wirth, and *Culicoides sierrensis* Wirth and Blanton. Several new species, hybrids, or variants of *Culicoides* are diagnosed but not formally described: two of subgenus *Silvicola*, one of the Palmerae group, two of the Piliferus group, and one unplaced to subgenus or species group.

Key words. Leptoconopinae, Ceratopogoninae, Culicoidini, Nearctic, intersex, vector, new state records, Arizona, California, Colorado, Idaho, Nevada, New Mexico, new United States record.

Resumen. *Leptoconops* Skuse y *Culicoides* Latreille (Diptera: Ceratopogonidae) los mosquitos picadores de son plagas graves de mamíferos, aves y reptiles y vectores importantes de virus, protozoos y nematodos filariales. Su colección se convirtió en un complemento importante para la vigilancia de mosquitos mediante el uso de trampas de succión con cebo ligero y con cebo de CO_2 en Grand County, Utah, Estados Unidos, durante 1999–2016. Durante 2017–2020, la recolección se expandió a California, Nevada, Idaho, Wyoming, Colorado, Arizona, New Mexico, y otras partes de Utah usando una trampa de succión de luz ultravioleta. Como resultado, cinco especies de *Leptoconops* y 59 especies de *Culicoides*, representando *Leptoconops* subgénero *Holoconops* Kieffer y *Leptoconops* Skuse, *Culicoides* subgénero *Amossovia* Glukhova, *Beltranmyia* Vargas, *Diphaomyia* Vargas, *Drymodesmyia* Vargas, *Haematomyidium* Goeldi, *Monoculicoides* Khalaf, *Selfia*

Khalaf, *Sensiculicoides* Shevchenko, *Silvaticulicoides* Glukhova, *Silvicola* Mirzaeva e Isaev, y *Wirthomyia* Vargas, y los grupos *Culicoides* Leoni, Limai, Palmerae, Piliferus, Saundersi, y Stonei. Se proporcionan claves para machos y hembras adultos y tablas de caracteres de diagnóstico para la identificación de 15 especies de *Leptoconops* y 86 especies de *Culicoides* recolectadas, reportadas de otra manera o que probablemente ocurran en el suroeste de los Estados Unidos al oeste de la Divisoria Continental de América. Se proporcionan referencias descriptivas, sinonimias, diagnósticos, distribuciones geográficas y estacionales, y resúmenes biológicos de la literatura disponible. Se proporcionan datos sobre la abundancia relativa en trampas con cebo ligero o cebo con CO_2 para las especies recolectadas. Se tabulan los especímenes intersexuales y los especímenes parasitados por ácaros o nematodos mermitidos. *Culicoides* (*Drymodesmyia*) *bakeri* Vargas se informa de California (**nuevo registro de Estados Unidos**). Se reportan nuevos registros estatales de otras especies para Idaho, Nevada, Utah, Colorado, Arizona, y Nuevo México de los Estados Unidos y para Puebla, San Luis Potosí, y Oaxaca de los Estados Unidos Mexicanos. *Culicoides salihi* Khalaf se asigna al subgénero *Diphaomyia* de *Culicoides* (**nuevo estatus**). *Culicoides stellifer* (Coquillett) se reasigna al subgénero *Haematomyidium* de *Culicoides* (**nuevo estatus**). *Culicoides travisi* Vargas se asigna al subgénero *Sensiculicoides* de *Culicoides* (**nuevo estatus**). *Culicoides luglani* Jones y Wirth es reasignado al grupo *Culicoides* Limai (**nuevo estatus**). La confusión sobre los límites de especies fue evidente entre *Culicoides cacticola* Wirth y Hubert y *Culicoides torridus* Wirth y Hubert, entre *C. travisi* y *Culicoides kibunensis* Tokunaga, entre *Culicoides doeringae* Atchley y *Culicoides lophortygis* Atchley y Wirth, entre *Culicoides owyheensis* Jones y Wirth y *Culicoides mortivallis* Wirth y Blanton, y entre *Culicoides cockerellii* (Coquillett), *Culicoides neomontanus* Wirth, y *Culicoides sierrensis* Wirth y Blanton. Varias especies nuevas, híbridos o variantes de *Culicoides* se diagnostican, pero no se describen formalmente: dos del subgénero *Silvicola*, uno del grupo Palmerae, dos del grupo Piliferus, y uno no colocado en subgénero o grupo de especies.

Palabras clave. Leptoconopinae, Ceratopogoninae, Culicoidini, Neártico, intersexual, vector, nuevos registros estatales, Arizona, California, Colorado, Idaho, Nevada, Nuevo México, nuevo registro de Estados Unidos.

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Introduction

Cursed in various languages as ponk, punkies, no-see-ums, sand flies, chitras, mý, chaquistles, rin, moose-flies, maruins, purrujas, jejenes, serapiche, brûlots, tsi'ii' da'aneezi', five-O's, and cedar or pinyon gnats, biting midges of the genera *Leptoconops* Skuse and *Culicoides* Latreille (Diptera: Ceratopogonidae) are notorious blood-sucking pests and vectors of various human and animal disease agents (Atchley and Wirth 1975; Crane et al. 1983; Linley at al. 1983; Linley 1985; Holbrook 1988; Kramer et al. 1990; Mellor et al. 1990; Halouzka and Hubálek 1996; Borkent and Spinelli 2007; EFSA 2009; Santiago-Alarcon et al. 2012b; Carpenter et al. 2013) for which they are often underestimated (Sick et al. 2019). During his travels through Mexico, Gadow (1908) graphically described how the "chaquistles … settle upon the skin and burn it like red-hot grains of sand … which left a red inflamed spot … which turned the camp into a perfect hell."

In the Canyonlands of the Colorado River Basin of Utah, USA, several species—most notably those of *Leptoconops*—can be so locally abundant and aggressive as to make outdoor activities unbearable. Residents and visitors who spend much time in the region—especially in May and June—often become too familiar with these tiny pests that can crawl through regular mosquito netting and ignore some common insect repellents, sometimes compelling forced marches and abandonment of campsites (personal experience).

There have been several regional surveys of biting midges west of the Continental Divide of North America. Townsend collected in 1891 on the Continental Divide in New Mexico, from which he described *Tersesthes torrens* Townsend 1893 (now *Leptoconops torrens* [Townsend]). Stanford (1931) collected human-biting flies in Sevier County, Utah, and reported *Culicoides variipennis* (Coquillett) (now either *Culicoides occidentalis* Wirth and Jones or *Culicoides sonorensis* Wirth and Jones). Knowlton and Hardy collected in Cache County, Utah, in 1938, from which Fox (1946) described *Culicoides utahensis* Fox. Knowlton and Fronk (1950) reported *Leptoconops kerteszi* Kieffer and eight species of *Culicoides* from Utah. Knowlton and Kardos (1951) added *Culicoides hieroglyphicus* Malloch to the Utah list. Wirth (1952a) did an extensive study of the Ceratopogonidae of California that included 3 species of *Leptoconops* and 22 species of *Culicoides*. A survey of the *Culicoides* of Salt Lake County, Utah, collected 12 species (Bullock 1952; Rees and Bullock 1954). Atchley did two extensive surveys: one of the *Culicoides* of New Mexico that collected 23 species (Atchley 1967), and a targeted survey of species belonging to subgenus *Selfia* Khalaf of *Culicoides* that collected six predominantly southwestern North American species (Atchley 1970). Jorgensen (1969) surveyed the *Culicoides* of southeastern Washington and collected 13 species. Romney (1971) intensively surveyed the fauna of desert rock pool habitats in Grand and San Juan counties, Utah, and found *Leptoconops* and *Culicoides* immatures. Wirth and Atchley (1973) reviewed the North American *Leptoconops* and recognized nine western species. Clastrier and Wirth (1978) revised the North American *Leptoconops* Kerteszi group and recognized 12 western species distinct from Palearctic *L. kerteszi*. Intense studies in the Santa Rosa Mountains of southern California were conducted over several years, collecting 7 species of *Leptoconops* and 19 species of *Culicoides*, of which 5 had been undescribed (Mullens and Dada 1992a, b).

Despite this activity, many areas of western North America have not been surveyed, and little is known of the natural variation of many of the species, particularly those known from only a limited geographic area. The southwestern United States also presents a great variety of habitats, often surrounded and isolated by rugged landscapes and inhospitable desert. Immatures of most biting midge species, especially in the genus *Culicoides*, typically are found in association with surface or near-surface water or moist habitats such as treeholes or rotting cacti (Blanton and Wirth 1979; Zimmer et al. 2014), which are frequently both rare and quite localized in the xeric southwest, thus providing some guidance regarding where to sample. Furthermore, this island biogeography provides abundant opportunity for population isolation, inbreeding, and speciation. In particular, eastern Utah had never been intensively surveyed for biting midges, and the variety of habitats and potential for geographic isolation provided many new distribution records and several species new to science.

This paper reports on a series of surveys for biting midges using light-baited or CO_2-baited suction traps or human bait intensively in Grand County and occasionally in other parts of Utah, New Mexico, Arizona, California, Nevada, Idaho, and Wyoming. Its purposes are to add to our knowledge of species diversity and distributions, help resolve some taxonomic issues, provide a tool for identifying the regional species, pull together the scattered literature for each species, and provide brief summaries of what is known of their biology for ecologists, entomologists, and other biologists who encounter them.

Furthermore, little or nothing is known of the immature forms and habitats (Table 19), vertebrate hosts (Table 20), pathogens, and vector capabilities of most species. This paucity of information severely limits our ability to understand and control important *Culicoides*-vectored diseases such as bluetongue and epizootic hemorrhagic disease (Pfannenstiel et al. 2015). In addition, *Culicoides*-vectored avian diseases, which are only slightly known, may have significant influence on the survivorship and population dynamics of many bird species. Only a few of the species known from the western United States have been shown to have vector competency—most notably *C. sonorensis* (many references, see its species account), but also *Culicoides obsoletus* (Meigen) (Meiswinkel et al. 2004; Mehlhorn et al. 2007; Foxi et al. 2016), *Culicoides crepuscularis* Malloch (Bennett and Fallis 1960; Fallis and Bennett 1961a; Hibler 1963; Robinson 1971), *Culicoides haematopotus* Malloch (Hibler 1963; Robinson 1971; Atkinson 1988), *Culicoides kibunensis* Tokunaga (Bernotienė et al. 2019; Žiegytė et al. 2021), and *Culicoides bottimeri* Wirth (Weinmann et al. 1979; Mullens et al. 2006); however, more species are likely to be found to be important vectors as they are more thoroughly studied.

I have tried to briefly summarize the available biological information for each species; thus, if data are lacking from the biology summaries in the species accounts and as indicated in Table 19, it is likely we know little more and have considerable need for further research. Further studies using other collection methods, such as emergence-trapping, sweep-netting, and laboratory-rearing will undoubtedly produce much more information about habitats, life cycles, and ecological relationships and discover more new species and distribution records. Though the original research in this paper was limited to the adult stages, it is hoped it will help with further studies of the biology of this abundant, widespread, diverse, and important group.

Materials and Methods

Collection of insects. Adult biting midges were collected at 65 sites in Utah (Tables 1, 2) and 14 sites in other states (Table 3). Regular collections were made in the Moab Mosquito Abatement District, Grand County, Utah, from 13 May to 1 October 1999, 4 April to 17 October 2000, 7 March to 31 October 2001, 2 April to 15 November 2002, 20 March to 2 October 2003, and 9 March to 9 November 2004. Collections continued irregularly in the Moab District during 2005–2016; and outlying areas of Utah, Colorado, Wyoming, Idaho, Nevada, California, and Arizona were sampled during 2017–2020.

Light traps and CO_2-baited traps were used within Grand County. The regular collections were from Moab and Spanish Valleys (1205–1390 m elevation) and the Colorado River corridor (1205–1220 m elevation). Outlying areas of Grand County included the University of Utah Rio Mesa Field Station (formerly Entrada Ranch) (38.799°N 109.181°W, 1280 m elevation) 41 km northeast of Moab, 8 June 1999, 4 and 21 June, 8 and 10 July 2001, and 18 and 19 May 2002, and Hunter Canyon (38.5068°N 109.5890°W, 1265 m elevation) 8 km south-southeast of Moab, 22 June 2003.

Only ultraviolet light traps (UVLT) and human bait were used outside of Grand County (Tables 2 and 3). In addition, Riley Nelson provided a UVLT collection made by J. E. Lee and A. J. Nelson in Garfield County, Utah, at Calf Creek Campground 7–8 July 2003, 37.795°N 111.413°W, 1632 m elevation (included in Table 2).

The sampled areas included a variety of habitats including riparian areas and associated permanent and seasonal wetlands of ephemeral and permanent streams and rivers, flood areas, farm and ranchlands, canyons, desert dune and scrub, riparian and juniper woodlands, pinyon-juniper-aspen-Douglas fir, aspen-ponderosa pine, aspen-fir-spruce, aspen-spruce, and aspen-Douglas fir-lodgepole pine forests, and various rural and suburban human habitats.

The only attempt to collect or rear immature *Culicoides* was from mud collected on 10 September 2020 from nonvegetated sunlit alkaline pools in a stream bed 47 km north-northeast of Moab, Grand County, at 38.96339°N 109.33585°W and 1315 m elevation. About 0.9 kg of the top 2 cm of moist, saturated, and submerged mud was collected with a trowel and placed into trays inside a knitted nylon mesh bag, from which the emergent adult midges were collected directly into 95% ethanol using an ethanol-wetted cotton-tipped swab.

No systematic attempts were made to collect midges in the act of biting; however, opportunistic human-biting collections were made directly into alcohol using an alcohol-wetted cotton-tipped swab at several locations in Grand, Kane, San Juan, and Washington counties, Utah, and in Grant County, New Mexico (Tables 1–3) and are reported in the species accounts.

Six different combinations of trap types with light and dry ice bait were used to attract and collect biting midges, with no single traps using light and dry ice simultaneously. Unmodified 120V New Jersey suction traps (Hausherr's Machine Works, Toms River, NJ) with insecticide-treated killing jars were used at three locations (Table 1) during 1999–2002 and equipped with either a 25W incandescent light without dry ice (NJLT) or 1 kg of dry ice without a light (NJT +CO_2). Portable Centers for Disease Control (CDC) style suction traps with fine-mesh collecting bags were used at many locations (Tables 1–3) equipped in four configurations: 1 kg of dry ice without a light (CDC T +CO_2 w/o L) during 1999–2016; a 6V 1W incandescent light without dry ice (CDC LT or ILT) (American Biophysics Corporation, East Greenwich, RI) during 1999–2001; a 6V 4W UV light (John W. Hock Company, Gainesville, FL) without dry ice (UVLT) during 2002–2016; and a homemade 12V 6W UV light without dry ice (UVLT) during 2017–2020. Traps were set at 1400–1700 hours, hung so their entrances were 1–2 m above the ground, and collected at 0700–0900 hours the following morning. When possible, as many as 20 traps were set—some with light, some with CO_2 bait—in various locations in the Moab and Spanish Valleys each week of the season during 1999–2004.

When West Nile virus (WNV) (Flaviviridae) was detected in Grand County in the fall of 2003, surveillance methods were changed, with the result that 98% of trapping from 2004–2016 used only CO_2 bait. Widespread trapping continued in 2004; however, trapping during 2005–2016 was mostly limited to prolific mosquito habitats, which had limited and already known biting midge diversity. During 2017–2020 only a 12V UVLT and human bait were used for collecting.

Preparation of specimens. Specimens were killed by freezing or with triethylamine, transferred into 70% ethanol, and then either preserved in 70% ethanol or placed into 95% ethanol for later mounting on microscope slides. When plain-wing *Culicoides* females (subgenus *Selfia*) were numerous, the collection was cleared as a group with a commercial mixture of 74% lactic acid, 15% acetic acid, and 6% phenol (BioQuip Products, Inc.) so those with sclerotized spermathecae could be selected for alcohol preservation or slide-mounting. Specimens selected were rinsed and preserved in 100% ethanol as soon as they were recognized because prolonged immersion in the clearing fluid causes the wings to curl or the specimens to burst and stick together.

Permanent slides were made using the phenol-balsam method of Wirth and Marston (1968) with some minor changes. After soaking in 95% ethanol, specimens for slide-mounting were soaked in 100% ethanol for an hour or so and then placed in a saturated solution of phenol in 100% ethanol for several hours or overnight until sufficiently cleared. Each specimen was then transferred to a drop of a 1:1 mixture of the saturated phenol and liquid Canada balsam on a microscope slide. Using a small hypodermic needle as a scalpel (30 gauge or smaller is good): a wing was cut off and placed flat; the head was cut from the thorax and placed face-up with the eye separation, antennae, palpi, and proboscis clearly visible; the posterior portion of the abdomen was cut off and placed to have a ventral view of the genitalia; and the thorax was placed on its side so the still-attached wing was spread out flat against the slide with the wing and legs clearly visible. After placement of a cover-glass (12 mm diameter is large enough), the specimen could be (carefully) microscopically examined; however, the slide had to be kept flat and cured at 50 °C for about two weeks until the medium hardened enough for regular handling or vertical storage.

Micrographs (except Fig. 1, 2, 8, 33, and 293, in alcohol) were taken with a 5MP camera on a Ken-A-Vision® trinocular compound microscope and are not to scale. Figure 8 is a photograph by Carl Olson (with permission) of a *Leptoconops californiensis* Wirth and Atchley specimen he collected. Figures 116 and 195 are taken from Wirth and Blanton (1959: 320, their Fig. 25). Figure 293 is a photograph by Bradley Mullens (with permission) of *C. bottimeri* specimens he collected. Images I took of specimens borrowed from Bradley Mullens are identified by "BM", from the Entomology Research Museum of the University of California at Riverside are identified by "UCRC", and from the Florida State Collection of Arthropods in Gainesville are identified by "FSCA". Those without location data are of specimens from my Utah collections, and those with location data and not otherwise indicated are of specimens I collected or were given to me from out of state.

Data analysis. To compare the responses of different species and sexes to light traps versus CO_2-baited traps, a light-trap response (LTR) number was calculated for each species and sex by dividing the total collected during 1999–2003 by the total number of light traps used, then dividing this average by the sum of this average plus the similarly calculated average per CO_2-baited trap. This results in the fraction (LTR) that would be collected with light traps if equal numbers of light traps and CO_2-baited traps had been used. These LTR numbers are tabulated in Table 4, with LTRs nearer 1.000 suggesting stronger attraction to light-baited traps and LTRs nearer 0.000 suggesting stronger attraction to CO_2-baited traps.

Because CO_2-baited traps were the primary collection method with light traps used only infrequently and irregularly during 2004–2016, data from 2004–2016 were included in Table 4 only for species or sexes infrequently collected during 1999–2003. Data for species collected outside Grand County, where only UVLTs were used, are also included in Table 4 only to document their collection by UVLT and are indicated by shading.

To construct a seasonal distribution for each species, the data from 1999–2004 were compiled by week into a single hypothetical year. Because the weekly numbers and kinds of traps varied widely, and species and sexes respond differently to light-baited and CO_2-baited traps, I decided simple per-trap calculations would not produce good comparative seasonal distributions. Instead, for each week, females of each species were totaled and divided by the sum of the number of light traps multiplied by the female's LTR plus the number of CO_2-baited traps multiplied by one minus the LTR. The same was done with the males collected that week, using the male's LTR. The two results were added and converted to a parts-per-thousand of the total of that species for the year. This produces a seasonal distribution as if equal numbers of each kind of trap were used each week and 1000 specimens of each species were collected during the season.

Some data from Grand County during 2005–2016 were included in the seasonal distribution calculations. However, because collections with CO_2-baited traps were irregular and UVLT collections infrequent after 2004, 2005–2016 data were limited to only add species or broaden or fill gaps in the distributions. In addition, data from the western United States outside Grand County were included for weeks when the species was not collected in Grand County, with such data distinguished by non-numeric symbols in the seasonal distribution Table 5.

Some collections of *C. sonorensis*, *Culicoides luglani* Jones and Wirth, and subgenus *Selfia* from routine trap sites were too large for practical counting; hence, they were estimated by sorting and counting a fractional portion and multiplying for inclusion in the distribution and trap data. Furthermore, extreme numbers from the outlying and irregular Rio Mesa Field Station collections were excluded to avoid biasing the distribution and trap comparisons.

Morphological terms and data. Anatomical terms are those in Downes and Wirth (1981), with modifications to some wing veins and cells as proposed by Szadziewski (1996) and tabulated by Spinelli and Borkent (2004: 362). Capital letters with subscript numerals (M_1, M_2, CuA_1, CuA_2) refer to wing veins; lower-case letters with subscript numerals (r_1, r_2, r_3, m_1, m_2, cua_1) refer to wing cells (Fig. 3, 4, 5).

These measurements and ratios are used:

- Wing length is measured from the basal arculus (anterior branch of media vein) (Fig. 3) to the wing tip.
- Costal ratio is the length of the costa from the basal arculus divided by the wing length.
- Palpal ratio is the length of palpal segment 3 divided by its greatest width.
- Proboscis ratio is the length of the proboscis from the torma to the tip of the labrum-epipharynx divided by the distance from the torma to the interocular hair socket (Fig. 287).
- Antennal ratio is the combined length of the distal five flagellomeres divided by the combined length of the proximal eight, excluding visible intersegmental spaces. However, simplifying the measurements by including the spaces and not measuring each flagellomere individually is unlikely to alter a ratio enough to cause a misidentification.
- Spermathecal ratio compares the fully developed spermathecae (when both are present) by dividing the sum of the larger's width and length including any sclerotized neck by the sum of the smaller's width and length including any sclerotized neck.
- Aedeagal ratio—the ratio of the height of the basal arch of the aedeagus (Fig. 109) to the overall length of the aedeagus—is calculated by measuring along the midline of the aedeagus from an imaginary line between the basal arm tips to the first point of contact with the (sometimes lightly) sclerotized membrane between the arms and dividing this by the overall length of the aedeagus from the center of the imaginary basal line to the distal apex.

Unless otherwise stated, the antennal ratio, palpal ratio, proboscis ratio, eye separation, presence or absence of superior transverse suture (Fig. 287), number of mandibular and lacinial teeth (Fig. 254, 279), and arrangement of antennal sensilla coeloconica (SCo, Fig. 280) apply only to females, whereas color, wing patterns, presence or absence of a palpal sensory pit (Fig. 11, 12, 31, 32, 241–249), interommatidial pubescence (Fig. 18), leg-banding (Fig. 250, 286), number of spines on the hind tibial comb (Fig. 286), and apical fore and hind tarsal spines (Fig. 281–285) apply to both sexes. "SCo on" or "SCo pattern" indicate which antennal flagellomeres 1–13 have SCo, with numbers in parentheses indicating the flagellomeres where SCo may be either present or absent.

Confusion can arise because different terms have been used in the literature for some diagnostically important anatomical structures. I use the last term in the following equalities: in the male genitalia, paraproct = harpe = claspette = paramere, sidepiece = basistyle = basimere = gonocoxite, clasper = dististyle = telomere = gonostylus; on the wing, cell R_5 = r_3, cell Cu_1 = M_4 = cua_1, vannal cell = anal cell, intercalary vein = R_{4+5}, vein Cu_1 = M_{3+4} = CuA_1, vein Cu_2 = Cu_1 = CuA_2; and on the female, galea = maxilla = lacinia, lamellae = cerci. To about 1990, the antennal segments were numbered to include the scape and pedicel, whereas most recent authors (and I) count only the flagellomeres; hence, flagellomeres 1–13 correspond to the "antennal segments" or "antennomeres" 3–15 for reporting sensilla patterns.

When describing the complex bifurcated form of the ventral apodeme (the most meso-posterior basal apodeme when viewed ventrally; often called the "ventral root") of the gonocoxite, authors have reported it variously as footlike, cleatlike, or boat-hook-like. I use "footlike" because it is the most used term. In addition, the term "ventral apodeme" itself can be misleading because the "ventral apodeme" is usually more dorsal than the "dorsal apodeme" in slide preparations that usually and unnaturally flatten the genitalia. This can cause confusion (e.g., Breidenbaugh and Mullens 1999b: 155 description contrasting with their Fig. 4G). However, the term is correct when describing the normal three-dimensional aspect of the genitalia, is consistent with nearly all the literature, and is used here.

Further confusion could arise, especially among workers from outside the Ceratopogonidae, over the term "aedeagus". The aedeagus is actually a membranous structure (Sinclair et al. 2007) often visible as a narrow tonguelike tip or tube extending posteriorly and lying dorsal to the "ventral plate". However, ceratopogonid workers have generally figured and labeled this sclerotized usually Y- or V-shaped "ventral plate" as the aedeagus; and I am continuing this to be consistent with the ceratopogonid literature.

The only internal structures used in the keys and diagnoses are the sclerotized spermathecae and the ring on the spermathecal duct. However, the descriptions and figures of the internal reproductive structures for male and female *C. sonorensis* by Rozo-Lopez et al. (2020) and of the alimentary tract of *Culicoides nubeculosus* Meigen by Megahed (1956) are useful for avoiding confusion distinguishing nematodes and other internal parasites.

Biology and classification. In addition to the species collected, other species reported or likely present in Utah, California, southern Idaho, Nevada, Arizona, western Colorado, and New Mexico are included in the keys and species accounts. Synonymies, Nearctic description references, diagnoses, geographic distributions, and brief summaries of available biological information are provided. When possible, I have provided primary sources, which have much more information; however, some references were likely missed, could not be found, or did not have an English translation, in which cases secondary sources were referenced.

Host, parasite, and plant names are presented as they were reported in the cited literature. Misspellings and other recognized errors were corrected, and scientific names were updated when necessary for consistency; however, to avoid interpretive error, scientific names were not added or expanded when only a common name, genus, or higher taxon was given in the literature.

Leptoconops and *Culicoides* subgeneric and species group placement follow Borkent and Dominiak (2020), with the exceptions of Mirzaeva and Isaev's (1990) placement of the species of the Cockerellii group of *Culicoides* subgenus *Culicoides* Latreille into subgenus *Silvicola* Mirzaeva and Isaev, Vargas's (1960) placement of *Culicoides stellifer* (Coquillett) into *Culicoides* subgenus *Haematomyidium* Goeldi instead of subgenus *Oecacta* Poey, and the proposed status changes for *Culicoides salihi* Khalaf, *Culicoides travisi* Vargas, and *C. luglani* (discussion of these exceptions are in the remarks of their species accounts). All of the named species are in the catalogs of Borkent and Wirth (1997), Borkent and Grogan (2009), and Borkent and Dominiak (2020); so, these references are not listed in the species accounts except to substantiate subgeneric placement when the primary references (specifically Glukhova 1977, 1989, in Russian) were unavailable. To aid comparison of closely related species, species in the accounts and tables are in alphabetical order first by subgenus then, for those not placed to subgenus, by species group.

As suggested by Harrup et al. (2015), the informal term "species group" is for a collection of similar morphologically distinguishable species, whereas "species complex" is for a collection of morphologically indistinguishable cryptic species. To avoid confusion with species names, their names omit genus and author, are capitalized, and are in plain Roman type (such as "Piliferus group" and "Obsoletus complex").

Voucher specimens. Voucher specimens will be deposited in the United States National Museum of Natural History (USNM), Washington; the Canadian National Collection of Insects (CNCI), Ottawa; the Brigham Young University collection (BYUC), Provo, Utah; the Entomology Research Museum (UCRC), University of California, Riverside; the Florida State Collection of Arthropods (FSCA), Gainesville; and my personal collection. Specimens collected by others with previously unpublished new state geographic distribution records and held by the Entomology Department of the California Academy of Sciences collection (CASC) are cited as "Monarch 2021", and those held by the USNM are cited as "USNM" in the species accounts.

Results

Species diversity and geographic records. During 1999–2004, 20 male and 961 female *Leptoconops* and more than 10,500 male and 101,000 female *Culicoides* were collected over 1243 trap-nights with carbon dioxide as the only attractant and 416 trap-nights with light as the only attractant. In addition, *Leptoconops americanus* Carter, *Leptoconops foulki* Clastrier and Wirth, *Leptoconops sublettei* Clastrier and Wirth, *L. torrens*, *Culicoides denningi* Foote and Pratt, and *Culicoides reevesi* Wirth were collected while biting humans.

Considerable diversity was sometimes collected in a single trap. A UVLT collected 14 species of *Culicoides* and a *Leptoconops* on 27 May 2003, and another collected 15 species of *Culicoides* on 24 June 2003 in Grand County. In addition, the Garfield County UVLT collected 15 species of *Culicoides* 7–8 July 2003 (Table 7).

Five species of *Leptoconops* and 46 species of *Culicoides* were collected in Utah (Tables 6–8). Of these, 5 species of *Leptoconops* and 38 species of *Culicoides* were collected in Grand County (Table 8). Collections elsewhere in Utah (Table 7) included these species not collected in Grand County: *Culicoides cacticola* Wirth and Hubert, *Culicoides chewaclae* Glick and Mullen, *Culicoides cockerellii* (Coquillett), *Culicoides copiosus* Root and Hoffman, *Culicoides neomontanus* Wirth, *Culicoides ryckmani* Wirth and Hubert, *C. salihi*, *Culicoides sierrensis* Wirth and Blanton, *Culicoides usingeri* Wirth, and an unnamed *Culicoides* Piliferus group species B.

In addition, *Culicoides* were collected in Idaho, Wyoming, Nevada, Colorado, California, Arizona, and New Mexico (Table 9). These resulted in new state records for Nevada, Idaho, Colorado, and Arizona and included these species not collected in Utah: *Culicoides atchleyi* Wirth and Blanton, *Culicoides bakeri* Vargas, *Culicoides insolatus* Wirth and Hubert, *Culicoides jonesi* Wirth and Hubert, *Culicoides saltonensis* Wirth, *Culicoides torridus* Wirth and Hubert, *C. travisi*, *Culicoides unicolor* (Coquillett), and *Culicoides werneri* Wirth and Blanton.

Of the 5 species of *Leptoconops* and 23 species of *Culicoides* previously reported from Utah, 4 species of *Leptoconops* and 19 species of *Culicoides* were collected. In addition, the following species not previously reported from Utah were collected and reported (Borkent and Grogan 2009): *C. bottimeri*, *Culicoides brookmani* Wirth, *Culicoides byersi* Atchley, *Culicoides californiensis* Wirth and Blanton, *Culicoides erikae* Atchley and Wirth, *Culicoides hinmani* Khalaf, *Culicoides inyoensis* Wirth and Blanton, *C. kibunensis*, *Culicoides lahontan* Wirth and Blanton, *C. luglani*, *Culicoides owyheensis* Jones and Wirth, *C. reevesi*, and *Culicoides sitiens* Wirth and Hubert.

Since then, additional new state records were collected. *Leptoconops sublettei*, *C. cacticola*, *Culicoides calexicanus* Wirth and Rowley, *Culicoides cavaticus* Wirth and Jones, *C. chewaclae*, *C. copiosus*, *Culicoides mortivallis* Wirth and Blanton, *C. occidentalis*, *C. ryckmani*, *C. salihi*, and *C. sierrensis* are **new Utah records**. *Culicoides atchleyi*, *C. bottimeri*, *C. cockerellii*, *C. denningi*, *C. doeringae* Atchley, *C. hieroglyphicus*, *Culicoides jamesi* Fox, *C. kibunensis*, *C. neomontanus*, *C. sierrensis*, and *C. unicolor* are **new Idaho records**. *Culicoides cacticola*, *C. saltonensis*, and *C. torridus* are **new Nevada records**. *Culicoides defoliarti* Atchley and Wirth and

C. neomontanus are **new Colorado records**. *Culicoides jonesi*, *C. mortivallis*, *Culicoides sublettei* Atchley, and *C. torridus* are **new Arizona records**. Furthermore, *C. bakeri* was identified from a collection made by Xinmi Zhang in California and is a **new United States record**, having been previously reported from only its type locality, Mexico City.

Utah records of *C. usingeri* from Salt Lake County in Bullock (1952) and Rees and Bullock (1954) were never incorporated into catalogs or other records—likely because these original records are obscure. Hence, because *C. usingeri* was collected from Garfield County in the present study, it is likely the Salt Lake County records are valid; and ***C. usingeri*** is here **confirmed as a Utah record**.

Additional **new state records** were found in the database of the collection of the California Academy of Sciences (Monarch 2021): **Arizona** for *C. occidentalis*, **California** for *C. kibunensis*, **New Mexico** for *Culicoides neofagineus* Wirth and Blanton, and the Mexico states of **San Luis Potosi**, **Puebla**, and **Oaxaca** for *C. torridus*.

Taxonomic proposals and questions. The previously unknown male of *C. reevesi* was discovered (Grogan et al. 2004), the synonymy of *C. bottimeri* and *Culicoides multidentatus* Atchley and Wirth was proposed (Phillips et al. 2006), and the new species, *Culicoides* (*Monoculicoides*) *grandensis* Grogan and Phillips (2008) and *Culicoides* (*Selfia*) *moabensis* Phillips (2015), were described.

In the present work, six new species of *Culicoides* are diagnosed, but not described: the females of species D and E of subgenus *Silvicola*, a female of species C of the Palmerae group, the male and female of species A (likely species 25) of the Piliferus group, the female of species B of the Piliferus group, and the female of unplaced species F.

The similarity of the male genitalia of *C. salihi* to that of *Culicoides* (*Diphaomyia*) *bergi* Cochrane and *Culicoides* (*Diphaomyia*) *baueri* Hoffman suggests assignment of *C. salihi* to subgenus *Diphaomyia* Vargas; the similarity of *C. stellifer* to *Culicoides* (*Haematomyidium*) *kettlei* Breidenbaugh and Mullens supports Vargas's (1960) assignment of *C. stellifer* to subgenus *Haematomyidium*; the similarity of *C. travisi* to *C.* (*Sensiculicoides*) *kibunensis* suggests assignment of *C. travisi* to subgenus *Sensiculicoides* Shevchenko; and the similarity of *C. luglani* to *Culicoides tenuilobus* Wirth and Blanton (Wirth 1963) suggests the placement of *C. luglani* into the Limai group. Evidence also suggests further study to consider the relationships and possible synonymies of *C. torridus* to the prior *C. cacticola*, of *C. travisi* to the prior *C. kibunensis*, of *Culicoides lophortygis* Atchley and Wirth to the prior *Culicoides doeringae* Atchley, and of *C. owyheensis* to the prior *C. mortivallis*. Specifics on these questions are discussed in the remarks of their species accounts.

Parasite, intersex, and anomalous collections. Four genera of Ceratopogonidae (*Culicoides*, *Dasyhelea* Kieffer, *Forcipomyia* Meigen, and *Stilobezzia* Kieffer) were collected parasitized, including 16 species with mites (Fig. 294, Table 10) and 6 species with mermithid nematodes (Fig. 289, 292, Table 11). The parasite associations, along with those reported by others, are included in the species accounts. Because many of the specimens of the more common species of *Culicoides* were identified without clearing and slide-mounting, and not all mermithid infections cause the host to become an obvious intersex, it is likely some parasitized specimens were missed.

Of note, an otherwise normal-appearing gravid *Forcipomyia tenuichela* Dow and Wirth has four infuscated, apparently dead, eggs (Table 11). Whether these were eggs retained after oviposition or an example of the killing of male embryos by *Wolbachia* Hertig and Wolbach bacteria (Rickettsiales: Anaplasmataceae) would need further study.

Mullens et al. (2008) provide an overview of the reports, taxonomy, and biology of mermithid parasitism in Ceratopogonidae; and Muñoz-Muñoz et al. (2016) propose the feminized antennae and wings often on nematode-parasitized *Culicoides* are adaptive for dispersal of the nematode by enabling the host to find breeding sites where other potential hosts are readily available.

Aberrant females with three developed spermathecae (as opposed to the normal two plus a rudimentary third) were identified in *C. cacticola*, *C. californiensis*, *C. crepuscularis*, *C. butleri*, *C. ryckmani*, *C. lahontan*, *C. saltonensis*, subgenus *Silvicola* species E, and *C. mortivallis* (Table 12). The *C. butleri* specimen also had a vestigial fourth spermatheca. Specifics on the specimens are in their species accounts. Kitaoka (1984), Braverman et al. (1993), Thepparat et al. (2015), and Szadziewski et al. (2016) reported similar aberrant spermathecae in specimens of several Eurasian species.

Seasonal distributions and abundance. Seasonal distributions by week for all the species collected or otherwise included in this study are presented in Table 5. Additional seasonal distribution data for species irregularly collected outside of Moab and Spanish Valleys, Grand County, Utah, are presented in Tables 6, 7, 9. Midge abundance was seasonal in Grand County, with the earliest collection being four female *C. sonorensis* with two CO_2-baited traps on 9 March 2005 in week 10, and the latest collection being three subgenus *Selfia* females with a CO_2-baited trap on 15 November 2002 in week 46. Late May through mid-July had the greatest diversity, with as many as 32 species collected per week in the present study and 56 species collected or reported per week regionally.

Comparison of light-baited and CO_2-baited trap collections. Species differed widely in their proportion collected with light traps (Table 4): from <1% of the *C. reevesi* to >99% of the Piliferus group tabulated. In Grand County, where both light-baited and CO_2-baited traps were used, light traps collected 40 of the 43 species collected, 33 of the 37 identified species of females collected, and 30 of the 31 species of males collected; and CO_2-baited traps collected at least 33 of the 43 species collected, 31 of the 37 identified species of females collected, but only 13 of the 31 species of males collected.

New Jersey traps were the least useful traps for the collection of biting midges, regardless of attractant used. Though used for 20% of the trap-nights in Grand County, they collected <4% of the specimens and only nine species, all of which were more abundant in collections made by the other collection methods. The habitats they could sample were severely limited by dependence on 120V power; their vibration and strong dry airflow damaged many specimens; and smaller species may have escaped through their original-equipment funnel screens.

The unmodified green New Jersey traps may have been made more effective by the simple method of changing their color. Kohler and Fox (1951) collected 4.3× more *Culicoides* with yellow New Jersey traps than with standard green traps over 74 trap-nights during a five-month period in Puerto Rico. They did not report if species diversity was affected.

As expected, light traps collected a greater diversity of biting midges and other insects than CO_2-baited traps. However, CO_2-baited traps regularly collected more female *Leptoconops* and female *Culicoides* and often collected female Culicidae, Simuliidae, Rhagionidae (*Symphoromyia* Frauenfeld), Tabanidae, and Muscidae (*Haematobia* Le Peletier and Serville, *Stomoxys* Geoffroy) when the exclusion screens allowed. Notably, *Corethrella* Coquillett (Chaoboridae), *Lutzomyia* França (Psychodidae), and *Forcipomyia* subgenus *Lasiohelea* Kieffer were not collected, though they also feed on vertebrate blood.

Some Diptera that do not feed on vertebrate blood were also routinely collected in CO_2-baited traps. Mycetophilidae, Psychodidae (non-hematophagous), some Ceratopogonidae (*Atrichopogon* Kieffer, *Bezzia* Kieffer, *Brachypogon* Kieffer, *Dasyhelea*, and *Forcipomyia*), and perhaps a few of the Rhagionidae and Muscidae were likely attracted to the traps because they breed near or on CO_2-emitting habitats such as rotting vegetation, feces, or sewer drains. Indeed, the *Dasyhelea* and *Forcipomyia* were often gravid.

Discussion of Trapping Results

Because five species were absent from light-trap collections and at least seven species were absent from CO_2-baited trap collections in Grand County where both kinds of traps were used, both kinds of traps were needed to collect the greatest diversity (Table 4). Light traps collect only photophilic insects active during crepuscular or nocturnal periods, whereas CO_2-baited traps reliably collect only those insects (such as host-seeking females and males that seek hosts to find females) attracted to the CO_2 bait. However, CO_2-baited traps collect any time of day, provide data on host-seeking and biting-pressure, and can collect species that are strictly diurnal, photoneutral, or photophobic and thus poorly represented in light traps. Nelson and Bellamy (1971), using truck traps, light-baited traps, and CO_2-baited traps at two-hour intervals, showed that light traps greatly under-collect during crepuscular periods, which are peak activity times for many species.

Though these deficiencies of light traps seem obvious now, some authors (Murray 1957; Hair 1966) failed to adequately consider these when reporting flight activity. Furthermore, my commercial 6V UVLT failed to stay lit on colder nights (possibly due to reduced battery voltage or ballast failure), which may partly explain some of the low UVLT collections in early spring and late fall. The homemade 12V UVLT used during 2017–2020 did not have this problem but was not used enough on cold nights to compare its collections with the 6V UVLT collections.

The routine collection of males of *C. sonorensis* in CO_2-baited traps (Table 4) correlates with Nelson's (1965) collections of *C. sonorensis* males in CO_2-baited traps and Gerry and Mullens' (1998) observations of *C. sonorensis* males mating with blood-feeding females. *Culicoides utahensis* males also mate with females on hosts (Wirth and Rowley 1971) and, when abundant, are likely to be easily collected with CO_2-baited traps. Other males readily collected in CO_2-baited traps (such as those of *C. luglani*, Table 4) are also likely to seek hosts or CO_2-emitting habitats for mating.

Trap height placement can significantly influence collections. Southwestern desert areas are often breezy, especially after noon and into or through the crepuscular period; however, effective wind speed drops substantially closer to the ground due to the boundary layer effect. This may allow midges to continue to fly in the calmer air closer to the ground. Bradley Mullens (personal communication) used a CO_2-baited 18-jar rotator trap while recording wind speed, temperature, and relative humidity and found a clear peak of compensatory host-seeking activity when the wind would stop after 2400 hours—much later than the normal crepuscular peak host-seeking period for the species involved. Furthermore, Brenner et al. (1984a), collecting near the Salton Sea in Southern California where the average relatively open maximum vegetation height was 2 m, reported 6–17 times higher collection rates for *L. foulki* and *Leptoconops knowltoni* Clastrier and Wirth when CO_2-baited traps were placed at ground-level instead of at 2 m. No traps were placed at ground-level in the present study; and, nearly all were hung from tree limbs and only rarely from a tripod in an open area.

Host preferences may also influence collection rates for traps placed at different heights. Of the eight species collected with only light traps in Grand County (Table 4), only *C. sitiens* has known hosts: Japanese quail (*Coturnix japonica* Temminck and Schlegel, Odontophoridae) and domestic rabbit (*Oryctolagus cuniculus* [Linnaeus], Leporidae) (Mullens and Dada 1992a). Its apparent preference for ground-dwelling hosts suggests it might have been collected with CO_2-baited traps placed closer to the ground. Alternatively, some *Culicoides* have been more readily collected in the tree canopy (Snow 1955), which suggests a preference for arboreal hosts when CO_2- or host-baited traps are used. Swanson and Adler (2010), using CO_2-baited unlit traps placed 1.5, 5, and 10 m up in the canopy of two forests, collected 97% of their *C. crepuscularis*, 91% of their *C. haematopotus*, and 64% of their *C. hinmani* at 10 m, suggesting that despite mixed host records (Table 20) these species prefer birds or arboreal mammals, whereas only 12% of their *C. stellifer*, which feeds predominantly on ground-dwelling mammals (Table 20), were collected at 10 m. However, McGregor et al. (2018) used light traps and passive traps in a forest canopy to collect *Culicoides* that had deer blood meals, indicating that those midges were using the canopy for harborage instead of for host seeking.

Culicoides doeringae and the other species of the Piliferus group were readily collected in light traps but nearly absent from CO_2-baited traps (Table 4). The hosts of most of these species are not known; however, Piliferus group members are generally considered ornithophilic (Wirth and Hubert 1962). That no traps were placed in tree canopies may explain the paucity of Piliferus group species in my CO_2-baited trap collections; however, CO_2 emission rates can also affect collecting (Mullens 1995; McPhatter and Gerry 2017), and lower emission rates may prove attractive to these species.

Sublimation of CO_2 from dry ice is dependent on the ambient temperature and the surface area of the ice, both of which vary considerably and are difficult to regulate in the field. It may be, for some species, the CO_2 emission rate did not match a preferred host at the same time the females were foraging, the CO_2 emission rate or cold temperature near the dry ice canister was repellent, or the cold CO_2 canister interfered with the proper host heat signature. Furthermore, collections by Tanner and Turner (1974) and Hopken et al. (2017) and experiments by Koch and Axtell (1979) showed that biting preferences of some species of *Culicoides* are influenced more by the amount of CO_2 hosts emanate (a function of size and metabolism) and host availability than by a host's taxonomic class.

Suggestions by Jamnback (1965) and Braverman and Hulley (1979), tentatively confirmed by Isberg et al. (2013), that larger numbers of SCo correlate with ornithophilic behavior can be reinterpreted to be a correlation with preference for smaller animals—whether they are birds or mammals. Detailed studies of *Culicoides* sensilla morphology (Kline and Axtell 1999) have not clarified this. More study is needed to see if the number or location of SCo is related to the CO_2 output or to the taxonomic class of the preferred host.

Braverman et al. (2012) found no correlation of the ratio of the lengths of palpal segments 3 and 4 to ornithophilic behavior of Israeli *Culicoides* but did correlate larger numbers of flagellomeres having SCo with ornithophilic behavior. They also reviewed the literature and found that a shorter proboscis and larger number of lacinial teeth correlated with ornithophilic behavior and postulated that a larger number of lacinial teeth could enable more rapid feeding to help avoid a bird's defensive behavior.

Several studies have compared trapping methods for biting midges. Anderson and Linhares (1989) found significant differences between incandescent light, ultraviolet light, CO_2 alone, and CO_2 with light for collecting different parity states of *C. sonorensis* (as *C. variipennis*). In addition, McDermott et al. (2015) have shown *C. sonorensis* to be more averse to light when infected by bluetongue virus (BTV) (*Orbivirus*, Reoviridae); and Mills et al. (2017) found epizootic hemorrhagic disease virus (EHDV) (*Orbivirus*, Reoviridae) infection in *C. sonorensis* was associated with damaged ommatidia, which likely biases light-trap surveillance for this important vector.

An extensive review of research on the advantages and limitations of light traps and comparison with other collection methods is provided by McDermott and Mullens (2018). Since then, Sloyer et al. (2019b) compared collection efficacy of LED UVLTs and incandescent light traps with and without CO_2 bait for 29 species of Florida *Culicoides*; Walgama and Lysyk (2019) compared collections of 13 species of *Culicoides* in Alberta, Canada, using fluorescent UVLTs with and without CO_2; and McDermott and Lysyk (2020) provided an extensive overview of various sampling strategies and collection methods for adult and immature *Culicoides*.

Keys and Species Accounts

The keys have been constructed to help reduce the need to make microscope slides and allow both sexes of most species to be identified to at least subgenus by characters readily visible in alcohol with a good dissecting microscope. However, clearing and slide-mounting of specimens for study with a compound microscope will be required for identifying species of many groups, notably *Leptoconops* subgenus *Holoconops* Kieffer and the *Culicoides* that lack a distinct wing pattern. After some experience, some species such as the *Culicoides* subgenus *Selfia* and *C. bottimeri* males, both sexes of *C. reevesi*, and species with distinctive wing patterns can be readily identified without slide-making or using the keys.

Though the key characters should be enough for identification, additional characters are included in the diagnoses in the species accounts and in the tables of quantitative characters (Tables 13, 14) and leg-banding (Table 15). The tables should be consulted for interspecies comparison and to confirm identifications made using the keys. All data for species marked (r) and data for mean wing length and costal, antennal, palpal, and proboscis ratios are compiled from the description references in the species accounts, with emphasis on southwestern United States data, and supplemented or modified from borrowed and collected specimens.

The most useful references for identifications and additional biological information are the Manual of Nearctic Diptera Volume 1 (Downes and Wirth 1981) for morphology, definitions, and illustrated keys to the families of Diptera and the genera and subgenera of Ceratopogonidae (available as a free PDF at http://publications.gc.ca/site/eng/9.817747/publication.html as of 1 May 2021), Borkent and Spinelli 2007 for Neotropical Ceratopogonidae (available as a free PDF at https://epdf.pub/neotropical-ceratopogonidae-diptera-insecta-aquatic-biodiversity-in-latin-americ.html as of 1 May 2021), Wirth and Atchley (1973) for *Leptoconops*, Clastrier and Wirth (1978) for the Kerteszi group of *Leptoconops* (available as free PDF at https://naldc.nal.usda.gov/download/CAT78703721/PDF as of 1 May 2021), Atchley (1967) for New Mexico *Culicoides*, Blanton and Wirth (1979) for a wealth of information on eastern and nationwide *Culicoides* (available as a free PDF at https://ufdc.ufl.edu/UF00000090/00001/pdf as of 1 May 2021), Wirth et al. (1985) for female wing photographs and basic quantitative characters for most *Culicoides*, and Atchley (1970) for the subgenus *Selfia*. In addition, Mullen and Hribar (1988) provide a useful summary of Ceratopogonidae larval habitats, food resources, locomotion, development times, and overwintering; and Zimmer et al. (2014) summarize the life cycle and adult and larval ecology of *Culicoides* and review and classify the larval micro-habitats of 135 species.

In some groups—notably the females of the *Leptoconops* Kerteszi group of subgenus *Holoconops* and some members of the *Culicoides* subgenera *Drymodesmyia* Vargas and *Silvicola* and the Piliferus group—few key characters are consistent, and a best-fit determination from a combination of characters is often necessary. Also, SCo patterns, measurements, ratios, and other characters should not be relied upon without considering their variability.

Experiments with *C. sonorensis* (as *C. variipennis*) have shown environmental factors have considerable influence on morphology. Akey et al. (1978) determined wing size can vary as much as 1.9× due to temperature, food availability, and larval population density during development; Mullens (1987) determined average wing length of wild females varied from 1.48 to 2.02 mm inversely with the seasonal 10–30 °C air temperature range during development; Mullens and Rodriguez (1988) found average wing length varied from 1.27 to 1.63 mm with increasing chemical oxygen demand from organic matter enrichment in its larval habitat; and Hensleigh and Atchley (1977) found temperature during the larval stage influences other morphometric traits and discontinuous characters such as the number of spines, SCo, or mandibular teeth. Further studies with *C. occidentalis* in a Southern California coastal salt marsh (Smith and Mullens 2003) found similar inverse variation of wing length to average temperature, varying from 2.1–1.6 mm over temperatures averaging 11–21 °C, with the largest wings in February and the smallest in July. Also, Atchley (1971a) studied three common subgenus *Selfia* species and compared, by regression analysis, 45 female and 36 male adult and pupal size and shape variables with 12 climatic factors of temperature, precipitation, growing season, and geography. Climate correlated with 65% of the morphological variation in *C. denningi*, 41% of the variation in *C. hieroglyphicus*, and 18% of the variation in *C. jamesi*.

Natural variation, specimen preparation, damage, and visual parallax error contribute to variation of measurements, ratios, and some discontinuous numerical characters. Flattening or shrinkage of the head can decrease the apparent eye separation. Apical fore and hind tarsal spines are usually not on all the tarsomeres; so, all tarsomeres should be examined before deciding spines are absent; and when present, they should be as distinct as those always present on the mid tarsomeres (Fig. 281–285). Occasionally, SCo patterns differ between the two antennae on the same specimen; thus, when SCo pattern is critical, both antennae should be examined. Measurements and ratios are expressed as means and used only for approximate comparison, and the other key characters and data in Tables 13–16 should be considered to make a best-fit determination.

Colors are best seen with fresh alcohol specimens because balsam slide-mounting medium can give an artificial yellow, brown, or red tint to the cuticle. Also, specimens that have recently hatched are paler than older specimens, and parous *Culicoides* females often have a distinct dark reddish brown or burgundy coloration to the abdomen (Fig. 288, 293) that nulliparous females lack (Dyce 1969; Akey and Potter 1979). The dramatic difference in abdominal coloration between parous and nulliparous females of the same species is most evident in lighter-colored species (Fig. 293).

Some microscopic diagnostic characters such as SCo, leg spines, and genitalia can often be observed on whole un-cleared specimens in alcohol or glycerin under a coverslip in a concavity slide. This often enables rapid species identification without making a permanent mount. Several specimens can be examined at the same time, and they are not damaged and can be returned to 70% ethanol for storage.

However, lengthy storage in alcohol and some specimen clearing methods, such as KOH, will fade specimens and can make wing patterns hard to discern. Regardless of the cause, faded or naturally faint patterns can often be seen by using a digital microscope camera, and discerning a wing pattern can benefit from experimentation with light intensity and direction (oblique versus more direct light) when using a dissecting microscope. A dark background is sometimes helpful, and the use of dark field for slide-mounted specimens can be beneficial if using a phase-contrast compound microscope. Furthermore, specimens should be stored away from light. I have some alcohol specimens I left out for several months that are nearly unidentifiable because of fading caused by the fluorescent ceiling lights.

Diagnosis to distinguish *Leptoconops* and *Culicoides* from other Diptera. Less than 4 mm long; antenna with 11–13 flagellomeres, combined length much longer than head, hairy, not sculptured with basal longitudinal grooves (Fig. 27, 30, 58–60, 251–253, 280); male flagellomere 1 with setae as long as those on others; palpus 4–5 segmented (Fig. 253); female mandibles and laciniae usually bladelike, toothed (Fig. 279), rarely vestigial and without teeth; ocelli absent; posterior portion of head convex; wings well developed, held horizontally covering abdomen when at rest; costa terminating on midportion of anterior wing margin (Fig. 1–5); M two-branched, reaching distal wing margin (Fig. 1–5); closed discal cell absent; prescutal pits present (Fig. 55), often prominent;

mesonotum without median V-shaped suture; postnotum without median longitudinal groove; fore and hind tibiae with apical spur (Fig. 286); hind tarsomere 1 without row of palisade setae; claws of equal length; empodia vestigial, at most a bristle.

***Leptoconops* Skuse diagnosis.** Crossvein r-m and wing macrotrichia absent; R_1 and R_2 fused into a stigma; R_{4+5} extending to wing tip; wing without pale or dark pattern (Fig. 1, 5); frontal suture absent; eyes of both sexes separated >0.25 head width; palpus four segmented; female antenna with 11–12 flagellomeres, male with 13; female subterminal flagellomeres 2–10 or 2–11 subequal, terminal flagellomere 2–3× longer than others; female cerci usually prominent, usually >3× longer than wide (Fig. 1, 6); gonostylus with subapical socketed tooth (Fig. 14, 15, 19–21, 23).

***Culicoides* Latreille diagnosis.** Crossvein r-m and wing macrotrichia present; r_1 and r_2 well-developed, about equal length; R veins terminating on midportion of anterior wing margin (Fig. 2–4, 50, 51, 56, 57, 117–240); wing often with prominent pale spots (Fig. 2, 50, 51, 56, 57, 117–240); frontal suture present; eyes contiguous to separated <0.2 head width; palpus five segmented; antenna with 13 flagellomeres, 11–13 (and usually 9–10 on female) longer than any of 2–8; cerci small, inconspicuous (Fig. 2, 7); gonostylus without subapical socketed tooth (Fig. 34–43, 61–116).

Key to *Leptoconops* Males

1. Aedeagus a single median rodlike sclerite between basal portion of gonocoxites; thorax blackish, abdomen mostly yellow (as in Fig. 8 female) ..... ***L.* (*Brachyconops*) *californiensis* Wirth and Atchley**

— Aedeagus a pair of elongate sclerites, sometimes fused apically (Fig. 14, 15, 19–21); thorax and abdomen of same basic color, yellowish brown to black, abdomen often lighter (as in Fig. 1 female) **2**

2(1). Tergite 9 evenly tapering to base of widely separated apicolateral processes, which are separated by a distance >0.5 their length (Fig. 14, 19) **3**

— Tergite 9 with distal shoulders abruptly narrowed to base of adjacent apicolateral processes (Fig. 15, 20, 21) .... **(subgenus *Holoconops* Kieffer) 7**

3(2). Hind tibial comb with five spines .... ***L.* (*Leptoconops*) *freeborni* Wirth**

— Hind tibial comb with four spines **4**

4(3). Tergite 9 apicolateral processes thin, ~8× longer than wide, meso-posterior lobes with fine setae; aedeagal sclerites apically fused into shieldlike structure (Fig. 19) **5**

— Tergite 9 apicolateral processes thick, 2–5× longer than wide, meso-posterior lobes with stout setae or spines; aedeagal sclerites separate (Fig. 14) **6**

5(4). Eyes bare; widespread in the southwestern United States ...... ***L.* (*Leptoconops*) *torrens* (Townsend)**

— Eyes with interommatidial pubescence (as in Fig. 18 female); known from only the Central Valley of California .... ***L.* (*Leptoconops*) *carteri* Hoffman**

6(4). Apical flagellomere 13 ~1.4× longer than flagellomere 12; aedeagal sclerites apically expanded blunt (Fig. 14) .... ***L.* (*Proleptoconops*) *werneri* Wirth and Atchley**

— Apical flagellomere 13 ~2.2× longer than flagellomere 12; aedeagal sclerites apically tapered pointed .... ***L.* (*Leptoconops*) *mohavensis* Wirth and Atchley**

7(2). Strongly sclerotized lobe lying dorsal to aedeagus in median portion of tergite 9 (Fig. 15); apical flagellomere 13 ~2.5× longer than flagellomere 12 .... ***L.* (*Holoconops*) *belkini* Wirth and Atchley**

— Without strongly sclerotized lobe in median portion of tergite 9 (Fig. 20, 21); apical flagellomere 13 ~3.0× longer than flagellomere 12 .... **(*L.* [*Holoconops*] Kerteszi group) 8**

8(7). California ocean beach habitats (consult Clastrier and Wirth 1978 for these species) .... ***L. arnaudi* Clastrier and Wirth, *L. asilomar* Clastrier and Wirth, *L. whitseli* Clastrier and Wirth**

— Interior habitats **9**

9(8). Clypeus with median pair of setae <0.5 as far apart from each other as from corresponding lateral setae (as on female Fig. 9); tergite 9 with a short median dorsal posterior-directed process, ventro-posterior setae separated by ~4× as much as separation of apicolateral processes; mid tarsomere 1 with at least one submedian spine (*L.* [*Holoconops*] *andersoni* Clastrier and Wirth likely will key here, but male unknown) .... **L. (*Holoconops*) *americanus* Carter**

— Median clypeal distal setae ≥0.8 as far apart from each other as from corresponding lateral setae (as on female Fig. 10); tergite 9 without dorsal process, ventro-posterior setae separated by ~2× as much as separation of apicolateral processes (Fig. 20); mid tarsomere 1 without submedian spine (except sometimes on *L. atchleyi*) **10**

10(9). Gonostylus with three ventral setae spread over 0.2–0.6 of length (Fig. 22); apical lamelliform expansion often large, broadly covering subapical tooth in dorso-lateral aspect (Fig. 20, 22) **11**

— Gonostylus with three ventral setae all within 0.4–0.6 of length (Fig. 23); apical lamelliform expansion small, not to barely covering subapical tooth (Fig. 21, 23) **12**

11(10). Tarsomere 5 basal seta long and doubly curved, decumbent (Fig. 25); mid tarsomere 1 without median spine; apical lamelliform expansion large, broadly covering subapical tooth in dorso-lateral aspect (Fig. 20, 22); widespread from Montana to California, Texas, and Mexico .... **L. (*Holoconops*) *knowltoni* Clastrier and Wirth**

— Tarsomere 5 basal seta short, erect, curved (as in Fig. 26 *L. foulki*); mid tarsomere 1 often with median spine; apical lamelliform expansion of gonostylus smaller, barely covering subapical tooth; known from only the Central Valley of California ...... **L. (*Holoconops*) *atchleyi* Clastrier and Wirth**

12(10). Apical dilation of paramere with proximal tooth broadly triangular; tarsomere 5 basal seta long and doubly curved, almost decumbent (as in Fig. 25 *L. knowltoni*); entire tibia paler than femur .... **L. (*Holoconops*) *sublettei* Clastrier and Wirth**

— Apical dilation of paramere often with proximal tooth narrow thumblike (Fig. 24); tarsomere 5 basal seta short, erect, curved (Fig. 26); basal portion of tibia same color as femur **13**

13(12). Body blackish brown; femora and tibiae dark brown; mid and hind tarsomeres 1 and all tarsomeres 2 pale brown .... **L. (*Holoconops*) *foulki* Clastrier and Wirth**

— Body, including head, light yellowish brown; femora and tibiae lighter brown, apical portion of tibiae broadly yellowish; all tarsomeres 1, usually 2, yellowish .. **L. (*Holoconops*) *reesi* Clastrier and Wirth**

Key to *Leptoconops* Females

1. Cerci small, wider than long (Fig. 8); thorax blackish, abdomen mostly yellow (Fig. 8)............... .... **L. (*Brachyconops*) *californiensis* Wirth and Atchley**

— Cerci >3× longer than wide (Fig. 1, 6); thorax and abdomen of same basic color, yellowish brown to black, abdomen often lighter (Fig. 1) **2**

2(1). Palpal segment 3 sensilla in superficial excavation wider than deep (Fig. 12); antenna with 12 flagellomeres; hind tarsomeres 3 and 5 subequal (female *L.* (*Leptoconops*) *mohavensis* Wirth and Atchley unknown, but should key here)... **3**

— Palpal segment 3 sensory pit at least as deep as wide (Fig. 11, 31, 32); antenna with 11 flagellomeres; hind tarsomere 3 ≥1.5× longer than 5 .... **(subgenus *Holoconops* Kieffer) 6**

3(2). Clypeus with 2–4 setae; tarsal claw with prominent basal tooth (Fig. 13) **4**

— Clypeus with 10–13 setae; tarsal claw without basal tooth (similar to Fig. 25, 26 males)............ **5**

4(3). Small, wing length <1 mm; two large and one small ovoid spermathecae; hind tibial comb with four spines; mandible with 10–13 teeth ....**L. (*Proleptoconops*) *werneri* Wirth and Atchley**

— Large, wing length >1.5 mm; two subequal ovoid spermathecae, third absent; hind tibial comb with five spines; mandible with 19 teeth ....**L. (*Leptoconops*) *freeborni* Wirth**

5(3). Eyes bare; spermathecae usually ~1.8× longer than wide (as in Fig. 17 *L. carteri*); widespread in the southwestern United States .... **L. (*Leptoconops*) *torrens* (Townsend)**

— Eyes with sparse minute interommatidial pubescence (Fig. 18); spermathecae usually ~1.4× longer than wide (Fig. 16); known from only the Central Valley of California **L. (*Leptoconops*) *carteri* Hoffman**

6(2). Two ovoid spermathecae, third absent; stigma pale, often indistinct .... ***L.* (*Holoconops*) *belkini* Wirth and Atchley**

— Two large and one small ovoid spermathecae (Fig. 28, 29); stigma brown in slide-mounted specimens, often bright red in fresh specimens .... **(*L.* (*Holoconops*) Kerteszi group) 7**

7(6). California ocean beach habitats (consult Clastrier and Wirth 1978 for these species) .... ***L. arnaudi* Clastrier and Wirth, *L. asilomar* Clastrier and Wirth, *L. whitseli* Clastrier and Wirth**

— Interior habitats **8**

8(7). Clypeus with median pair of setae half as far apart from each other as from corresponding lateral setae (Fig. 9); mid tarsomere 1 with at least one submedian spine; posterior margin of stigma convex, distal tip rounded; spermathecae ovoid, without caplike diverticulum (Fig. 29) **9**

— Median distal clypeal setae ≥0.8 as far apart from each other as from corresponding lateral setae (Fig. 10); mid tarsomere 1 without submedian spine; stigma triangular, pointed; flagellomere 11 with one or no submedian black seta; spermathecae somewhat pyriform, often with caplike diverticulum (Fig. 28) **10**

9(8). Flagellomere 11 with two submedian black setae at 0.6–0.7 (these can be difficult to see); widespread .... ***L.* (*Holoconops*) *americanus* Carter**

— Flagellomere 11 without submedian black setae; known from only Mendocino County, California .... ***L.* (*Holoconops*) *andersoni* Clastrier and Wirth**

10(8). Flagellomere 11 with submedian black seta at ~0.7 (Fig. 27) **11**

— Flagellomere 11 without submedian black seta **12**

11(10). Flagellomere 4 hyaline sensory seta laterad of long black seta, in axial alignment with corresponding sensory setae on flagellomeres 5–10; palpal segment 3 sensory pit opening a third the diameter of the interior (Fig. 11) .... ***L.* (*Holoconops*) *knowltoni* Clastrier and Wirth**

— Flagellomere 4 dorsal hyaline sensory seta distal and medial to long black seta, out of axial alignment with corresponding sensory setae on flagellomeres 5–10 (as in Fig. 30 *L. sublettei*); palpal segment 3 sensory pit opening half the diameter of the interior (as in Fig. 31 *L. sublettei*) .... ***L.* (*Holoconops*) *atchleyi* Clastrier and Wirth**

12(10). Clypeus with one to three smaller proximal setae in addition to the four distal setae; median distal clypeal setae out-of-line distad of distal lateral setae by ~0.7 their distance apart **13**

— Clypeus with four (occasionally five) distal setae, without proximal setae; median clypeal setae out-of-line distad of lateral setae by <0.3 their distance apart (as in Fig. 10 *L. knowltoni*) **14**

13(12). Frons bare between eyes, with only a row of supraorbital setae; flagellomere 4 dorsal hyaline sensory seta distal and medial to long black seta, out of axial alignment with corresponding sensory setae on flagellomeres 5–10 (as in Fig. 30 *L. sublettei*); widespread .. ***L.* (*Holoconops*) *reesi* Clastrier and Wirth**

— Frons with pair of black setae between eyes near antennal depressions in addition to row of supraorbital setae; flagellomere 4 hyaline sensory seta laterad of long black seta, in axial alignment with corresponding sensory setae on flagellomeres 5–10; known only from Clark County, Nevada .... ***L.* (*Holoconops*) unnamed species**

14(12). Flagellomere 4 hyaline sensory seta laterad of long black seta, in axial alignment with corresponding sensory setae on flagellomeres 5–10; palpal segment 3 sensory pit opening a third the diameter of the interior (Fig. 32); body blackish brown; fore tibiae slightly pale at tip; mid and hind tarsomeres 1 and all tarsomeres 2 pale brown ....***L.* (*Holoconops*) *foulki* Clastrier and Wirth**

— Flagellomere 4 dorsal hyaline sensory seta distal and medial to long black seta, out of axial alignment with corresponding sensory setae on flagellomeres 5–10 (Fig. 30); palpal segment 3 sensory pit opening half the diameter of the interior (Fig. 31); body light brown; fore tibiae yellowish on apical 0.2; all tarsomeres 1 and 2 yellowish .... ***L.* (*Holoconops*) *sublettei* Clastrier and Wirth**

Systematics of *Leptoconops*

Diptera: Ceratopogonidae
Subfamily Leptoconopinae

Genus *Leptoconops* Skuse, 1889: 288

(Synonyms of genus *Leptoconops* are in Borkent and Dominiak 2020: 36.)

Subgenus *Brachyconops* Wirth and Atchley

Leptoconops (*Brachyconops*) *californiensis* Wirth and Atchley

(Fig. 8)

Leptoconops (*Brachyconops*) *californiensis* Wirth and Atchley, 1973: 16 (subgenus *Brachyconops* Wirth and Atchley; designated *L. californiensis* as type species; key; female, male; fig. female antenna, palpus, hind tarsomere 5, wing, spermathecae, hind tibial comb, fore tarsomeres 1–2, male palpus, antenna, hind tarsomere 5, genitalia; California). Mullens et al. 1997a (biology; discussion of relationship to other *Leptoconops* subgenera; California, Sonora). Turner and Olson 2005 (biology; fig. adult female; Arizona).

Diagnosis. (Table 13) Head and thorax blackish, abdomen mostly yellow with a little brown; femora and tibiae dark brown; tarsomeres pale; eyes bare; palpal segment 3 sensory pit as deep as wide, broadening internally on female (as in Fig. 11 *L. knowltoni*). Female: antenna with 12 flagellomeres; fore tarsomeres 1–2 with stout black ventral spines; claw with basal tooth; two ovoid spermathecae, third absent; cerci short, wider than long. Male: outer tarsal claw with basal process ~0.7 as long as claw; tergite 9 evenly tapering to pair of small submedian lobes and prominent widely separated fingerlike apicolateral processes, which are ~4× longer than wide and separated by a distance ~0.6 their length (as in Fig. 14 *L. werneri*); aedeagus a single median rodlike sclerite between basal portion of gonocoxites; distal sclerite of paramere ~5× longer than wide, apex bifurcate with thin medial point and shorter caudal point.

Distribution. Sandy deserts of Southern California, Arizona, Sonora.

Adult behavior. *Leptoconops californiensis* has been collected feeding on lizards inhabiting desert dune ecosystems during 0900–1200 hours of March, April, May, and October, though humans "in close proximity to the lizards" were not attacked (Mullens et al. 1997a). Hosts were the zebra-tailed lizard (*Callisaurus draconoides* Cope, Phrynosomatidae), Coachella Valley fringe-toed lizard (*Uma inornata* Cope, Phrynosomatidae), Mojave fringe-toed lizard (*U. scoparia* Cope, Phrynosomatidae), flat-tailed horned lizard (*Phrynosoma mcallii* Hallowell, Phrynosomatidae) (Mullens et al. 1997a), Yuman Desert fringe-toed lizard (*U. rufopunctata* Cope, Phrynosomatidae) (Mullens et al. 1997a; Turner and Olson 2005), desert iguana (*Dipsosaurus dorsalis* Baird and Girard, Iguanidae), and desert horned lizard (*Phrynosoma platyrhinos* Girard, Phrynosomatidae) (Turner and Olson 2005).

Symbionts. Wiesenborn (2003) collected eight male and eight female *L. californiensis* from flowers of the rare parasitic dune-inhabiting *Pholisma sonorae* (Torrey ex Gray) Yatskievych (Boraginaceae) during 0600–2000 hours from 18 April to 4 May. Collection period air temperatures were 28–39 °C. No other pollinators were observed before 24 April, and 11 of the 16 specimens had substantial *P. sonorae* pollen loads, suggesting the midge is a critical pollinator for the imperiled plant and should be conserved.

Subgenus *Holoconops* Kieffer

Holoconops Kieffer, 1918: 135 (as genus).
Microconops Kieffer, 1921: 108 (as genus).

Leptoconops (*Holoconops*) *belkini* Wirth and Atchley

(Fig. 15)

Leptoconops (*Holoconops*) *belkini* Wirth and Atchley, 1973: 37 (key; female, male; fig. female head, wing, hind tibial comb, genitalia, hind tarsomere 5, palpus, male genitalia, antenna; California).

Diagnosis. (Table 13) Entirely dark brown to black; stigma pale, often indistinct; eyes bare; palpal segment 3 sensory pit as deep as wide, broadening internally on female (as in Fig. 32 *L. foulki*); hind tibial comb with four spines; claw without basal tooth. Female: antenna with 11 flagellomeres; clypeus with four setae, median pair about as far apart from each other as from corresponding lateral setae; hind tarsomere 3 ~1.5× longer than 5; two ovoid spermathecae, vestigial third absent; cerci >3× longer than wide (as in Fig. 1). Male: tergite 9 with distal shoulders abruptly narrowed to base of adjacent apicolateral processes; aedeagal sclerites longer than any paramere sclerite, >0.3 as long as gonocoxite; strongly sclerotized lobe in median portion of tergite 9 dorsal to aedeagus.

Distribution. California, Arizona.

Adult behavior. Females and males have been collected on the face of and swarming around a human, but not biting (Wirth and Atchley 1973); and Mullens and Dada (1992a) collected *L. belkini* from domestic rabbit (*Oryctolagus cuniculus*), Japanese quail (*Coturnix japonica*), and bighorn sheep (*Ovis canadensis nelsoni* Merriam, Bovidae).

Subgenus *Holoconops***,** Kerteszi group

(Fig. 1)

The definitive reference for the Kerteszi group in North America is Clastrier and Wirth (1978), which should be used if one is to do much work with this group. Few of the characters for distinguishing between the species within this group are consistent, and a best-fit determination involving several characters is often necessary for identification. Indeed, genetic methods would likely be faster and more reliable than morphological methods for identification of the species of this group.

The Kerteszi group of subgenus *Holoconops* is represented in Utah and the inland portions of the southwestern United States by six named and one unnamed species, formerly considered Nearctic representatives of the now strictly Palearctic *L. kerteszi*. Three other species of the Kerteszi group (*L. arnaudi* Clastrier and Wirth, *L. asilomar* Clastrier and Wirth, and *L. whitseli* Clastrier and Wirth) that are likely limited to coastal Central California beach and tideland habitats are not keyed or diagnosed; and Clastrier and Wirth (1978) should be consulted for their identification.

Unless otherwise indicated, all of the literature cited in the following Kerteszi group species accounts prior to 1978 misidentify the species as *L. kerteszi* or *Holoconops kerteszi* (Kieffer). The *L. kerteszi* references that are not otherwise cited in the present work are omitted from the synonymies but can be found in Clastrier and Wirth (1978).

Larval ecology. *Leptoconops americanus*, *L. foulki*, and *L. reesi* Clastrier and Wirth are common in similar habitats around the Great Salt Lake, Utah. Indeterminate immature *L. americanus* or *L. reesi* have been collected from saltgrass (*Distichlis stricta*) soil in North Salt Lake City, Utah (Rees and Smith 1950). Rees and Winget (1970) collected undifferentiated immature *L. americanus*, *L. foulki*, or *L. reesi* from moist alkaline sandy soil and sandy soil with clay and silt, with soil moisture from 5% to saturation with generally high salt content.

Adult behavior. Rees et al. (1969) reported *L. kerteszi* var. *americanus* (which could be *L. americanus*, *L. foulki*, or *L. reesi*) biting can be extremely annoying April–June, with activity into September, and with flight ranges exceeding 16 km in some areas near the Great Salt Lake. Rees and Winget (1970) reported humans and horses attacked by *L. kerteszi* that could be *L. americanus* or *L. reesi*; and Foulk (1969) reported burros as hosts for undifferentiated *Leptoconops*. In addition, Mullens et al. (1997a) collected a female "*L.* (*Holoconops*) near *knowltoni* Clastrier and Wirth" while appearing to feed on the Coachella Valley fringe-toed lizard (*Uma inornata*). Diurnal feeding activity can explain the poor light trap collections in the present study (Table 4). CO_2-baited trap collections show a late March to mid-October active season in southeastern Utah, peaking in August and September (Table 5).

Remarks. All of the male subgenus *Holoconops* collected were identified to species; however, because of the difficulty of slide-mounting and microscopic examination, only those females collected when biting and a small portion of females collected with traps were identified to species (Table 5). Furthermore, female *L.* (*Holoconops*) *foulki*, *L.* (*Holoconops*) *knowltoni* and *L.* (*Holoconops*) *sublettei* are especially challenging to distinguish because important key characters such as the setal arrangement on flagellomeres 4 and 13 are often ambiguous or difficult to see.

***Leptoconops* (*Holoconops*) *americanus* Carter**

(Fig. 9, 29)

Leptoconops kerteszi var. *americanus* Carter, 1921: 22 (key; female; Utah; fig. head, palpus, claw, antenna, wing stigma; Utah). Rees and Smith 1950 (in part; biology). Rees et al. 1969 (in part; biology).

Holoconops kerteszi var. *americana*: Johannsen 1943: 776 (combination; misspelled as feminine "*americana*"; fig. female wing, male genitalia).

Leptoconops (*Holoconops*) *americanus*: Clastrier and Wirth 1978: 16 (status; key; female, male, pupa; fig. female antenna, palpus, spermathecae, fore tarsomere 1, wing, male genitalia, aedeagus, parameres, gonostylus, palpus, pupal cephalothorax, respiratory horn, abdominal segments; Utah).

Leptoconops (*Holoconops*) *kerteszi*, misidentified: Wirth 1952a: 113 (in part; key; female; male genitalia; biology). Fox 1955: 263 (key; taxonomy), Lawyer 1971 (biology; fig. female habitus, egg, larva, pupa; Utah). Wirth and Atchley 1973: 45 (in part; key; female, male; fig. female wing, head, genitalia, spermathecae, hind tibial comb, fore tarsomeres 1 and 2, male genitalia; biology).

Leptoconops kerteszi, misidentified: Rees and Winget 1970 (in part; biology). Rees et al. 1971 (biology; fig. anterior segments of larva).

Tersesthes torrens, misidentified: Pratt 1907: 28 (in part: Salt Lake, Utah, specimens misidentified, according to Carter 1921).

Diagnosis. (Table 13) Body brown, femora and tibiae darker, tarsomeres brownish yellow; palpal segment 3 sensory pit as deep as wide, broadening internally on female (as in Fig. 11 *L. knowltoni*); clypeus with four setae, median pair <0.5 as far apart from each other as from corresponding lateral setae; mid tarsomere 1 with at least one submedian spine. Female: stigma posterior margin convex, distal tip rounded; antenna with 11 flagellomeres; flagellomere 11 with two submedian black setae at 0.6–0.7; flagellomere 4 dorsal hyaline sensory seta distal and medial to long black seta, out of axial alignment with corresponding sensory setae on flagellomeres 5–10 (as in Fig. 30 *L. sublettei*); hyaline sensory setae on flagellomeres 9–10 broadly separated; hind tarsomere 3 ~1.7× longer than 5; spermathecae ovoid, without caplike diverticulum; cerci >3× longer than wide (Fig. 1). Male: tergite 9 with distal shoulders abruptly narrowed to base of adjacent apicolateral processes, with a short dorso-posterior process, ventro-posterior setae separated by ~4× as much as separation of apicolateral processes; gonostylus with three ventral setae spread over 0.2–0.6 of gonostylus length (as in Fig. 22 *L. knowltoni*), apical lamelliform expansion only partly covering apical tooth (as in Fig. 23 *L. foulki*); tarsomere 5 basal seta strictly erect, ~0.2 as long as segment (as in Fig. 26 *L. foulki*).

Distribution. Washington, Idaho, Wyoming, south through Oregon, to California, Nevada, Utah (Box Elder, Grand, Millard, Tooele, Salt Lake, San Juan counties), Colorado.

Larval ecology. Lawyer (1971) collected immatures down to 15 cm in sandy saline soil inhabited by various halophytes, including saltgrass (*Distichlis stricta* [Torrey] Rydberg, Poaceae), red swampfire (*Salicornia rubra* A. Nelson, Amaranthaceae), iodinebush (*Allenrolfea occidentalis* [S. Watson] Kuntze, Amaranthaceae), and foxtail barley (*Hordeum jubatum* Linnaeus, Poaceae) on the shores of the Great Salt Lake, the shores of fresh and brackish water bodies, from sandy marshes and lowlands, and from around the edge of the Kennecott Copper tailings pond.

Life cycle. Rees et al. (1971) colonized *L. americanus* collected from near the Great Salt Lake and found a life cycle of 30–250 d and several generations a year, eggs and larvae overwinter, eggs survive extended drought and high temperatures, and adult females will feed on rabbit, guinea pig, and human, mate singly or in swarms, live ~8 d, and can reproduce autogenously.

Adult behavior. Clastrier and Wirth (1978) reported adults collected from a calf, deer, sheep, rabbits, and a golden eagle nest. Strickman et al. (1995) reported maximum biting rates were in full sun, with no wind, and when the temperature is >15 °C. One female was collected biting me at ~1600 hours on 12 April 2021 in Hunter Canyon, Grand County (38.504°N 109.5828°W).

Symbionts. Lawyer (1971) observed colonized *L. americanus* being predated on by a nematode and others fatally internally parasitized by mermithid nematodes.

Remarks. The *L. americanus* females collected in Grand County lack obvious submedian dark setae on flagellomere 11, have only slightly blunt wing stigma intermediate between figures 2A and 2B of Clastrier and Wirth, and have only the delicate median spines of mid tarsomere 1 as illustrated in figure 4E of Clastrier and Wirth. Brenner et al. (1984a) discuss the difficulty of seeing the flagellomere 11 seta on female *L. knowltoni*; hence, this characteristic may also be inconsistent or difficult to discern on *L. americanus*.

Leptoconops (*Holoconops*) *andersoni* Clastrier and Wirth

Leptoconops (*Holoconops*) *andersoni* Clastrier and Wirth, 1978: 35 (key; female; fig. female antenna, palpus, spermathecae; California).

Diagnosis. (Table 13) Body blackish, femora and tibiae blackish, tarsomeres blackish except paler on ventral surface of fore tarsomere 1; palpal segment 3 sensory pit as deep as wide, broadening internally on female (as in Fig. 11 *L. knowltoni*); clypeus with four setae, median pair <0.5 as far apart from each other as from corresponding lateral setae; mid tarsomere 1 with at least one submedian spine. Female stigma posterior margin convex, distal tip rounded; antenna with 11 flagellomeres; flagellomere 11 without submedian black setae; flagellomere 4 dorsal hyaline sensory seta distal and medial to long black seta, out of axial alignment with corresponding sensory setae on flagellomeres 5–10 (as in Fig. 30 *L. sublettei*); hyaline sensory setae on flagellomeres 9–10 broadly separated; hind tarsomere 3 >1.5× longer than 5; spermathecae ovoid, without caplike diverticulum; cerci >3× longer than wide (Fig. 1). Male unknown.

Distribution. California (Mendocino County).

Adult behavior. Females have been collected from the ears of deer on 17 April and from a calf on 18 May near Hopland, California (Clastrier and Wirth 1978).

Remarks. No *L. andersoni* were examined.

Leptoconops (*Holoconops*) *arnaudi* Clastrier and Wirth

Leptoconops (*Holoconops*) *arnaudi* Clastrier and Wirth, 1978: 29 (key; female, male; fig. female antenna, palpus, spermathecae, male palpus, genitalia; California).

Leptoconops kerteszi Kieffer, misidentified: Freeborn and Zimmerman 1934: 261 (male; fig. male wing, genitalia, female wing; Sonoma County, California).

Holoconops kerteszi (Kieffer), misidentified: Smith and Lowe 1948: 158 (as the Bodega black gnat; distribution, egg, larva, female pupa, male pupa, female adult, male adult, biology; fig.).

Leptoconops (*Holoconops*) *kerteszi*, misidentified: Wirth 1952a: 113 (in part; key; female; male genitalia; biology). Wirth and Atchley 1973: 45 (in part; key; female, male; fig. female wing, head, genitalia, spermathecae, hind tibial comb, fore tarsomeres 1 and 2, male genitalia; biology).

Distribution. Coastal California beaches (Sonoma, Marin, Ventura counties).

Larval ecology. Larvae have been collected from 2–8 cm deep in moist to saturated brackish sandy soil with 640 ppm chloride within a zone occasionally inundated by high tides (Smith and Lowe 1948, as *H. kerteszi*). They found eggs June–August and determined it takes the larvae 8–10 months to mature and then pupate March–August of the following year.

Adult behavior. Males have been collected swarming on the downwind side of objects near shore March–October, and females have been observed to bite humans, dogs, and cats (Smith and Lowe 1948, as *H. kerteszi*).

Remarks. This is the infamous Bodega black gnat. No *L. arnaudi* were examined.

Leptoconops (*Holoconops*) *asilomar* Clastrier and Wirth

Leptoconops (*Holoconops*) *asilomar* Clastrier and Wirth, 1978: 22 (key; female, male, pupa; fig. female fore tarsomere 1, palpus, spermathecae, wing, male genitalia, palpus, pupal respiratory horn, cephalothorax, abdominal segments; California).

Distribution. Coastal Central California (Marin, Monterey, San Luis Obispo counties).

Larval ecology. Immatures have been collected or reared from damp ocean beach sand (Clastrier and Wirth 1978).

Adult behavior. Females have been collected biting humans (Clastrier and Wirth 1978).

Remarks. In addition to the seasonal distribution records included in Table 5, *L. asilomar* adults have been reported in weeks 3, 7–9. No *L. asilomar* were examined.

Leptoconops (*Holoconops*) *atchleyi* Clastrier and Wirth

Leptoconops (*Holoconops*) *atchleyi* Clastrier and Wirth, 1978: 32 (key; female, male; fig. female antenna, palpus, spermathecae, male genitalia, gonostyli, palpus; California).

Diagnosis. (Table 13) Body, femora, tibiae blackish, tarsomeres slightly paler; clypeus with four setae, median pair ≥0.8 as far apart from each other as from corresponding lateral setae and out-of-line distad of lateral setae by <0.3 their distance apart (as in Fig. 10 *L. knowltoni*); palpal segment 3 sensory pit as deep as wide, broadening internally on female (as in Fig. 31 *L. sublettei*); mid tarsomere 1 often with submedian spine. Female: stigma triangular, pointed; antenna with 11 flagellomeres; flagellomere 11 with submedian black seta; flagellomere 4 dorsal hyaline sensory seta distal and medial to long black seta, out of axial alignment with corresponding sensory setae on flagellomeres 5–10 (as in Fig. 30 *L. sublettei*); palpal segment 3 sensory pit opening half the diameter of the interior (as in Fig. 31 *L. sublettei*); hind tarsomere 3 ~1.7× longer than 5; spermathecae slightly pyriform, without caplike diverticulum (as in Fig. 29 *L. americanus*); cerci >3× longer than wide (Fig. 1). Male: tergite 9 with distal shoulders abruptly narrowed to base of adjacent apicolateral processes, without dorsal process, ventro-posterior setae separated by ~2× as much as separation of apicolateral processes (as in Fig. 20 *L. knowltoni*); gonostylus with three ventral setae spread over 0.2–0.6 of gonostylus length (as in Fig. 22 *L. knowltoni*); gonostylus apical lamelliform expansion barely covering apical tooth; tarsomere 5 basal seta short, erect, curved (as in Fig. 26 *L. foulki*).

Distribution. California (San Joaquin, Solano counties).

Adult behavior. Thirteen females were collected by E. T. Schmidtmann from a calf in a creek bed (Clastrier and Wirth 1978).

Remarks. No *L. atchleyi* were examined.

Leptoconops (*Holoconops*) *foulki* Clastrier and Wirth

(Fig. 21, 23, 24, 26, 28, 32)

Leptoconops (*Holoconops*) *foulki* Clastrier and Wirth, 1978: 38 (key; female, male; fig. antenna, palpus, spermathecae, male genitalia, gonostylus, palpus; California).

Leptoconops (*Holoconops*) *kerteszi*, misidentified: Wirth 1952a: 113 (in part; key; female; male genitalia; biology). Fox 1955: 263 (key; taxonomy). Ryckman 1961 (jackrabbit host). Foulk 1967 (blood meal size). Sjogren and Foulk 1967 (biology). Foulk 1968 (biology). Wirth and Atchley 1973: 45 (in part; key; female, male; fig. female wing, head, genitalia, spermathecae, hind tibial comb, fore tarsomeres 1 and 2, male genitalia; biology).

Diagnosis. (Table 13) Body blackish brown, femora and tibiae dark brown, fore tibiae slightly pale at tip, mid and hind tarsomeres 1 and all tarsomeres 2 pale brown; clypeus with four setae, median pair ≥0.8 as far apart from each other as from corresponding lateral setae and out-of-line distad of lateral setae by <0.3 their distance apart (as in Fig. 10 *L. knowltoni*); palpal segment 3 sensory pit as deep as wide, broadening internally on female; mid tarsomere 1 without submedian spine. Female: stigma triangular, pointed; antenna with 11 flagellomeres; flagellomere 11 without submedian black seta; flagellomere 4 hyaline sensory seta laterad of long black seta, in axial alignment with corresponding sensory setae on flagellomeres 5–10; palpal segment 3 sensory pit opening a third the diameter of the interior; hind tarsomere 3 ~1.7× longer than 5; spermathecae with caplike diverticulum; cerci >3× longer than wide (Fig. 1). Male: tergite 9 with distal shoulders abruptly narrowed to base of adjacent apicolateral processes, without dorsal process, ventro-posterior setae separated by ~2× as much as separation of apicolateral processes (as in Fig. 20 *L. knowltoni*); gonostylus with three ventral setae all within 0.4–0.6 of gonostylus length, apical lamelliform expansion only partly covering apical tooth; apical dilation of paramere with proximal tooth narrow, thumblike; tarsomere 5 basal seta short, erect, curved.

Distribution. Oregon, Montana, south to California, Nevada, Utah (Carbon, Garfield, Juab, Kane, Salt Lake, San Juan, Tooele, Uintah, Washington, Wayne, Weber counties).

Larval ecology. A larval habitat near the Salton Sea in Southern California was characterized by alkali or saline soil dominated by iodinebush (*Allenrolfea occidentalis*) and desert holly (*Atriplex hymenelytra* Torrey ex S. Watson, Amaranthaceae) (Foulk 1969). Brenner et al. (1984a) clarified that the habitat also produced *L. knowltoni*.

Life cycle. Sjogren and Foulk (1967) found that, in the laboratory, undisturbed blood-feeding lasted 7–8 minutes; oviposition began ~88 h later; 70–75 eggs were usually laid, which hatched in 2.5 d at ~32°C; and first generation adults emerged in ~24 d; and, in the wild, a generation was completed in <8 weeks in March–May in Southern California.

Adult behavior and vector potential. Known wild hosts are human (Clastrier and Wirth 1978) and jackrabbit (*Lepus californicus* Gray, Leporidae) (Ryckman 1961). Laboratory hosts include rabbits, mice, chicks, and humans (Sjogren and Foulk 1967). Mullens and Dada (1992a) collected *L. foulki* from domestic rabbit (*Oryctolagus cuniculus*), Japanese quail (*Coturnix japonica*), and bighorn sheep (*Ovis canadensis nelsoni*), Furthermore, Foulk (1967) found the average replete blood meal to be 0.21 mg (0.20 µl).

Adults have been observed to alight on sunlit sand when its temperature drops to ~41 °C in late afternoon, rest within the top 4 mm of dry sand through the night and return to the surface when the temperature rises to ~18 °C in the morning (Foulk 1968). I collected a female biting my ear midday on 23 April 2000 in Spanish Valley, Grand County (38.5274°N 109.4997°W), 7 km southeast of Moab.

Brenner et al. (1984a) reported host-seeking activity March–June, and females CO_2-trapped in the same area in May had high parity rates (up to ~90%), suggesting a high vector potential. It is worth noting, however, that parity profiles are best interpreted along with knowledge of how prevalent autogeny is in the study population. We know little about the details of autogeny in biting midges, but it is quite possible that certain species have obligate autogeny, while others (or even populations within a species) express it at varying levels, based on aspects such as larval nutrition.

Symbionts. *Leptoconops foulki*'s propensity to alight on and harbor within the top layer of sandy soil can explain Foulk's (1968) observation of adults being preyed upon by *Myrmeleon immaculatus* De Geer antlions (Neuroptera: Myrmeleontidae) and parasitized by larval *Microtrombidium* mites (Prostigmata: Microtrombidiidae).

Remarks. Brenner et al. (1984a) discussed the difficulty distinguishing *L. knowltoni* from *L. foulki* because the color of the submedian black seta on flagellomere 11 of female *L. knowltoni* is often difficult to discern.

Leptoconops (*Holoconops*) *knowltoni* Clastrier and Wirth

(Fig. 10, 11, 20, 22, 25, 27)

Leptoconops (*Holoconops*) *knowltoni* Clastrier and Wirth, 1978: 26 (key; female, male; fig. female palpus, spermathecae, antenna, male genitalia, gonostylus, palpus; California). Ronderos and Spinelli 1992: 45 (key; female, male diagnoses; Brazil). Borkent and Spinelli 2000: 9 (in Neotropical catalog).

Leptoconops (*Holoconops*) *kerteszi*, misidentified: Wirth 1952a: 113 (in part; key; female; male genitalia; biology). Fox 1955: 263 (key; taxonomy). Foulk 1966 (biology). Foulk 1969 (biology). Jones et al. 1972 (Texas, horse). Wirth and Atchley 1973: 45 (in part; key; female, male; fig. female wing, head, genitalia, spermathecae, hind tibial comb, fore tarsomeres 1 and 2, male genitalia; biology).

Leptoconops bequaerti (Kieffer), misidentified: Wirth and Atchley 1973: 39 (misidentified record from Padre Island, Texas [Ronderos and Spinelli 1992]).

Diagnosis. (Table 13) Body brown, femora and tibiae pale brown, fore tibia yellowish apically, tarsomeres 1, 2 yellowish; clypeus with four setae, median pair ≥0.8 as far apart from each other as from corresponding lateral setae and out-of-line distad of lateral setae by <0.3 their distance apart; palpal segment 3 sensory pit as deep as wide, broadening internally on female; mid tarsomere 1 without submedian spine. Female: stigma triangular, pointed; antenna with 11 flagellomeres; flagellomere 11 with submedian black seta at ~0.7; flagellomere 4 hyaline sensory seta laterad of long black seta, in axial alignment with corresponding sensory setae on flagellomeres 5–10; hyaline sensory setae on flagellomeres 9–10 usually fused into a single hypertrophied seta; palpal segment 3 sensory pit opening a third the diameter of the interior; hind tarsomere 3 ~1.7× longer than 5; spermathecae somewhat pyriform, with caplike diverticulum (as in Fig. 28 *L. foulki*); cerci >3× longer than wide (Fig. 1). Male: tergite 9 with distal shoulders abruptly narrowed to base of adjacent apicolateral processes, without dorsal process, ventro-posterior setae separated by ~2× as much as separation of apicolateral processes; gonostylus with three ventral setae spread over 0.2–0.6 of gonostylus length, apical lamelliform expansion broadly covering subapical tooth; tarsomere 5 basal seta curved, as long as ~0.4 length of segment, decumbent.

Distribution. Idaho, Montana, south through California, Nevada, Utah (Box Elder, Grand, Millard, San Juan, Tooele, Utah, Washington counties), Arizona, Texas, Sinaloa, to Santa Catarina (Brazil).

Larval ecology. A habitat adjacent to a small creek near the Salton Sea in Southern California characterized by scattered iodinebush (*Allenrolfea occidentalis*) and desert holly (*Atriplex hymenelytra*) and sandy alkali or saline soil with 10–13% moisture produced abundant *L. knowltoni* larvae along with larval *Culicoides mohave* Wirth and *Dasyhelea festiva* Wirth (Foulk 1966). A similar habitat near the Salton Sea also produced *L. foulki* (Brenner et al. 1984a). Of the 19 males collected in the present study, 13 were collected at 38.54606°N 109.59159°E, and four were collected 0.3 km south at 38.54458°N 109.59424°E, suggesting the traps were placed near the larval habitat. The other two specimens were collected 9 and 42 km from those sites.

Adult behavior and vector potential. *Leptoconops knowltoni* has diurnal early to midmorning and late afternoon biting activity peaks with a midday lull (Foulk 1969; Brenner et al. 1984a). Foulk (1969) also noted that attack rates markedly declined when the human host stopped moving. Furthermore, Brenner et al. (1984a) reported host-seeking activity near the Salton Sea June–October and CO_2-trapped female parity rates up to 58% in the same area, suggesting high vector potential (however, see *L. foulki* adult behavior and vector potential section). Known hosts are human, brush rabbit (*Brachylagus idahoensis* [Merriam], Leporidae) (Foulk 1969), horse (Foulk 1969; Jones et al. 1972), and sheep (Clastrier and Wirth 1978).

Symbionts. Foulk (1969) reported that >143 of 26,951 female *L. knowltoni* were parasitized by *Microtrombidium* mite larvae. That no males were parasitized suggests that the mites use female midges to disperse to other habitats when the females oviposit.

Remarks. See *L. foulki* remarks.

Leptoconops (*Holoconops*) *reesi* Clastrier and Wirth

Leptoconops (*Holoconops*) *reesi* Clastrier and Wirth, 1978: 42 (key; female, male; fig. female antenna, palpus, spermathecae; Utah).

Leptoconops kerteszi, misidentified: Rees and Smith 1950 (in part; biology).

Leptoconops (*Holoconops*) *kerteszi*, misidentified: Wirth 1952a: 113 (in part; key; female; male genitalia; biology). Fox 1955: 263 (key; taxonomy). Wirth and Atchley 1973: 45 (in part; key; female, male; fig. female wing, head, genitalia, spermathecae, hind tibial comb, fore tarsomeres 1 and 2, male genitalia; biology).

Diagnosis. (Table 13) Body, including head capsule, light yellowish brown, femora and basal portion of tibiae brown, apical portion yellowish, all tarsomeres 1, usually 2, yellowish; median pair of distal clypeal setae ≥0.8 as far apart from each other as from corresponding lateral setae (as in Fig. 10 *L. knowltoni*); palpal segment 3 sensory pit as deep as wide, broadening internally on female (as in Fig. 32 *L. foulki*); mid tarsomere 1 without submedian spine. Female: stigma triangular, pointed; clypeus with one to three smaller proximal setae in addition to the four distal setae, distomedian pair out-of-line distad of lateral setae by ~0.7 their distance apart; antenna with 11 flagellomeres; flagellomere 11 without submedian black seta; flagellomere 4 dorsal hyaline sensory seta distal and medial to long black seta, out of axial alignment with corresponding sensory setae on flagellomeres 5–10 (as in Fig. 30 *L. sublettei*); hind tarsomere 3 ~1.7× longer than 5; spermathecae somewhat pyriform, with caplike diverticulum (as in Fig. 28 *L. foulki*); cerci >3× longer than wide (Fig. 1). Male: tergite 9 with distal shoulders abruptly narrowed to base of adjacent apicolateral processes, without dorsal process, ventro-posterior setae separated by ~2× as much as separation of apicolateral processes (as in Fig. 20 *L. knowltoni*); gonostylus with three ventral setae within 0.4–0.6 of gonostylus length, apical lamelliform expansion barely covering apical tooth (as in Fig. 23 *L. foulki*); tarsomere 5 basal seta short, erect, curved (as in Fig. 26 *L. foulki*).

Distribution. British Columbia, Saskatchewan, south through Idaho, Wyoming, Utah (Box Elder, Juab, Millard, Salt Lake, Toole counties), Colorado, to New Mexico.

Adult behavior. Known hosts are human and sheep (Clastrier and Wirth 1978).

Remarks. No *L. reesi* were examined.

***Leptoconops* (*Holoconops*) *sublettei* Clastrier and Wirth**

(Fig. 30, 31)

Leptoconops (*Holoconops*) *sublettei* Clastrier and Wirth, 1978: 36 (key; female, male; fig. female antenna, palpus, spermathecae, male genitalia, gonostyli, palpus; Texas).

Leptoconops (*Holoconops*) *kerteszi*, misidentified: Wirth 1952a: 113 (in part; key; female; male genitalia; biology; Montana, Wyoming, Nebraska, Colorado, Utah, New Mexico, Colorado). Fox 1955: 263 (key; taxonomy). Jones 1965 (collection from sheep).

Diagnosis. (Table 13) Body light brown, femora brown, tibiae paler, fore tibiae broadly yellowish apically, all tarsomeres 1–2 yellowish; clypeus with four setae, median pair ≥0.8 as far apart from each other as from corresponding lateral setae and out-of-line distad of lateral setae by <0.3 their distance apart (as in Fig. 10 *L. knowltoni*); palpal segment 3 sensory pit as deep as wide, broadening internally on female; mid tarsomere 1 without submedian spine. Female: stigma triangular, pointed; antenna with 11 flagellomeres; flagellomere 11 without submedian black seta; flagellomere 4 dorsal hyaline sensory seta distal and medial to long black seta, out of axial alignment with corresponding sensory setae on flagellomeres 5–10; palpal segment 3 sensory pit opening half the diameter of the interior; hind tarsomere 3 ~1.7× longer than 5; spermathecae somewhat pyriform, with caplike diverticulum (as in Fig. 28 *L. foulki*); cerci >3× longer than wide (Fig. 1). Male: tergite 9 with distal shoulders abruptly narrowed to base of adjacent apicolateral processes, without dorsal process, ventro-posterior setae separated by ~2× as much as separation of apicolateral processes (as in Fig. 20 *L. knowltoni*); gonostylus with three ventral setae within 0.4–0.6 of gonostylus length, apical lamelliform expansion barely covering apical tooth (as in Fig. 23 *L. foulki*); apical dilation of paramere with proximal tooth broadly triangular; tarsomere 5 basal seta long and doubly curved, almost decumbent (as in Fig. 25 *L. knowltoni*).

Distribution. Wyoming, Montana, North Dakota, south through Utah (Grand, San Juan, Washington (Monarch 2021) counties, **new state record**), Colorado, Nebraska, and Oklahoma, to California, Arizona, New Mexico, Texas.

Adult behavior. Clastrier and Wirth (1978) reported specimens collected from a magpie nest, and while biting humans, sheep, and deer. I collected six female *L. sublettei* biting midday on 30 March 2003 in Hunter Canyon, 9 km south-southwest of Moab, San Juan County (38.4990°N 109.5843°W), and one female biting my ear midday on 23 April 2000 in Spanish Valley, Grand County (38.5274°N 109.4997°W), 7 km southeast of Moab.

Leptoconops sublettei has the longest season of any *Leptoconops* species in Grand County (Table 5), and its bimodal distribution suggests it is bivoltine or has a summer diapause. The abundance of *L. sublettei* females and the absence of males in the collections indicates that traps were not near their larval habitats.

Remarks. *Leptoconops sublettei* is most similar to *L. foulki*. Primary morphological distinctions for the females are flagellomere 4 sensory seta alignment, palpal segment 3 sensory pit opening diameter, and body and leg color. Based on these characters—principally the flagellar sensory setae alignment—20 females from Utah were identified as *L. sublettei*.

***Leptoconops* (*Holoconops*) *whitseli* Clastrier and Wirth**

Leptoconops (*Holoconops*) *whitseli* Clastrier and Wirth, 1978: 20 (key; female, male, pupa; fig. female antenna, palpus, spermathecae, male fore tarsomere 1, genitalia, palpus, pupal respiratory horn, abdominal segments; California).

Leptoconops kerteszi, misidentified: Whitsel and Schoeppner 1965 (attractant study).

Distribution. Coastal California beaches (Monterey and Santa Barbara counties).

Larval ecology. Immatures have been reared from ocean beach sand (Clastrier and Wirth 1978).

Adult behavior. Males have been collected from Umbelliferae flowers (Clastrier and Wirth 1978). Little else is known about the biology of this species other than that the mandibular and lacinial teeth on the female and attraction to CO_2 indicate it feeds on vertebrate blood.

Remarks. No *L. whitseli* were examined.

Leptoconops (*Holoconops*) unnamed species

Diagnosis. Female essentially the same as *L. foulki* except for having these additional setae: two between the eyes on the lower portion of frons and two on the basal portion of clypeus. Male unknown.

Distribution. Known from only one female collected at Rogers Spring, 23 April 1971 at 460 m elevation in Clarke County, Nevada, and designated as "species C" by Clastrier and Wirth (1978).

Adult behavior. The mandibular and lacinial teeth indicate it feeds on vertebrate blood; however, its hosts are unknown.

Subgenus *Leptoconops* Skuse

Leptoconops (*Leptoconops*) *carteri* Hoffman

(Fig. 12, 16–19)

Leptoconops carteri Hoffman, 1926: 133 (female; fig. antenna, palpus, spermathecae, abdomen; California).

Leptoconops (*Leptoconops*) *carteri*: Wirth and Atchley 1973: 22 (resurrected from *L. torrens* synonymy; key; female, male; fig. female head, wing, palpus, abdomen, subgenital plate, spermathecae, eye, male genitalia, antenna; larva comparison to Kerteszi group [as *L. kerteszi*, p. 9]; biology). Atchley 1974: 467 (female; distinction from *L. torrens* [Townsend]).

Leptoconops torrens, misidentified: Freeborn and Zimmerman 1934: 258 (demoted *L. carteri* to junior synonym; male; fig. male wing, genitalia, female wing; Yolo County, California). Smith and Lowe 1948: 167 (egg, larva, female, male; biology; fig. larva habitus, last segment, internal head morphology; Sacramento, Santa Clara, and San Joaquin Valleys, California). Wirth 1952a: 110 (in part; key; female; male genitalia; fig. female wing, abdomen, palpus, male genitalia). Fox 1955: 263 (in part; key; taxonomy). Fontaine et al. 1957 (biology). Whitsel and Schoeppner 1965 (biology). Whitsel and Schoeppner 1966 (biology). Whitsel and Schoeppner 1970 (in part; biology).

Diagnosis. (Table 13) Entirely dark brown to black; stigma brown (as in Fig. 5 *L. torrens*); eyes with sparse minute interommatidial pubescence on lower portion; clypeus with eight or more setae; palpal segment 3 sensilla in superficial excavation wider than deep; hind tibial comb with four spines; claw with basal bristle, without basal tooth. Female: antenna with 12 flagellomeres; mandible with 16–18 prominent teeth; hind tarsomeres 3 and 5 subequal; two ovoid spermathecae usually ~1.4× longer than wide, third absent; cerci >3× longer than wide (as in Fig. 6 *L. torrens*). Male: flagellomere 13 ~1.5× longer than 12; tergite 9 evenly tapering to base of thin widely separated apicolateral processes, which are ~8× longer than wide and separated by a distance about equal to their length; aedeagal sclerites apically fused, blunt; distal sclerite of paramere ~2× longer than wide, apical portion flat, not bent.

Distribution. Central Valley of California.

Biology. Northern and central California references to *L. torrens* from 1934 to 1973 refer wholly or in part to *L. carteri*.

Larval ecology. *Leptoconops carteri* (as *L. torrens*) larvae have been found 0.4–1.0 m deep in alkaline soils with >40% expanding clay that crack on drying, which allow adult egress for dispersal and access for oviposition (Smith and Lowe 1948; Fontaine et al. 1957, as *L. torrens*). Normal larval development time was 2 years, but could be 1–5 years, depending on precipitation; inadequate soil moisture-initiated diapause; and pupal development took <5 d (Whitsel and Schoeppner 1966, as *L. torrens*).

Experiments have shown that inter-ommatidial pubescence helps protect insect eyes by reducing impact and deposition of airborne particles onto ommatidia (Amador et al. 2015). Similarly, *L. carteri*'s eye hairs may prevent soil particles from lodging between or damaging ommatidia and facilitate adult egress from the soil larval habitat.

Life cycle. Unlike *L. torrens*, *L. carteri* does not form mating swarms (Smith and Lowe 1948, as *L. torrens*). In the laboratory at 24 °C, Whitsel and Schoeppner (1970, as *L. torrens*) found females laid an average of 19 eggs, of which 43% were viable. Furthermore, Schmidtmann and Washino (1982) found that Sacramento Valley, California, populations had high rates of autogeny and that some of the anautogenous females survived in the wild long enough to take a second blood meal, contrary to previous studies (Smith and Lowe 1948, Whitsel and Schoeppner 1970) that suggested this species was extremely short-lived.

Adult behavior. *Leptoconops carteri* is a locally seasonal severe biting pest of humans, other mammals, and birds (Smith and Lowe 1948; Fontaine et al. 1957, as *L. torrens*). Whitsel and Schoeppner (1965, as *L. torrens*) found it a strictly diurnal biter, peaking between 1100 and 1500, when air temperature was 21–38 °C, relative humidity was 18% to 62%, and wind speed was <13 km/h. Laboratory observations (Whitsel and Schoeppner 1970, as, *L. torrens*) found *L. carteri* took from 2 minutes 20 seconds to 8 minutes 15 seconds, averaging 3 minutes 45 seconds, to blood-engorge on humans. In contrast with *L. torrens*, *L. carteri* tend to bite humans on the lower extremities rather than around the head and arms (Wirth and Atchley 1973).

Incandescent light traps have been ineffective at collecting this species (Fontaine et al. 1957, as *L. torrens*), likely because it is diurnal. However, CO_2-baited sticky traps were highly effective (Whitsel and Schoeppner 1965, as *L. torrens*), and males comprised nearly 2% of the collections, suggesting that males mate with females near their hosts (Wirth and Atchley 1973).

Remarks. Of the eight specimens selected and slide-mounted from a Yolo County, California, collection from Dave Woodward, one female, identified as *L. carteri* based on having pubescent eyes, had spermathecae (Fig. 17) like those described and illustrated by Wirth and Atchley (1973) for *L. torrens*. In addition, of seven *L. torrens* specimens examined from Utah and Arizona identified by having bare eyes, four had the elongate spermathecae normal for *L. torrens* (as in Fig. 17), two had an elongate and an ovoid spermatheca, and one had two ovoid spermathecae like those described for *L. carteri* (as in Fig. 16), further suggesting that spermathecal shape is not a reliable diagnostic characteristic for distinguishing these species. However, statistical comparison of spermathecal length in combination with the lengths of palpal segments 3 and 4 and flagellomeres 10 and 11 and ventral head width reliably distinguished the species consistent with their eye pubescence and biological differences (Atchley 1974).

Leptoconops (*Leptoconops*) *freeborni* Wirth

Leptoconops (*Styloconops*) *freeborni* Wirth, 1952a: 115 (assignment to subgenus *Styloconops* Kieffer; key; female, male; fig. female antenna, wing, genitalia, fore and hind tarsomeres, palpus, male genitalia; California).

Leptoconops (*Leptoconops*) *freeborni*: Wirth and Atchley 1973: 24 (assignment to subgenus *Leptoconops*; key; female, male; fig. female wing, head, antenna, hind tarsomere 5, genitalia, fore tarsomeres 1–2, male, genitalia, antenna, genitalia, hind tarsomere 5). Borkent and Spinelli 2000: 9 (in Neotropical catalog).

Diagnosis. (Table 13) Entirely dark brown to black; stigma indistinct; eyes bare; palpal segment 3 sensilla in superficial excavation wider than deep (female as in Fig. 12 *L. carteri*); clypeus with two setae; hind tibial comb with five spines. Female: antenna with 12 flagellomeres; mandible with 19 teeth; hind tarsomeres 3 and 5 subequal; claw with prominent basal tooth; two ovoid spermathecae, third absent; cerci >3× longer than wide (as in Fig. 6 *L. torrens*). Male: flagellomere 13 ~2.4× longer than 12; tergite 9 evenly tapering to base of fingerlike widely separated apicolateral processes, which are ~4× longer than wide and separated by a distance about equal to their length; aedeagal sclerites separate, apically expanded, blunt; distal sclerite of paramere slightly sinuate ~3× longer than wide, apical half not greatly expanded.

Distribution. Coastal Southern California, Baja California.

Adult behavior. The holotype male was collected by sweeping at a salt marsh in Ventura County, California, in week 24; and, in addition to the collections indicated in Table 5, *L. freeborni* has been collected 28 December in Orange County, California. However, little else is known about the biology of this species other than that the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Remarks. No *L. freeborni* were examined.

Leptoconops (*Leptoconops*) *mohavensis* Wirth and Atchley

Leptoconops (*Leptoconops*) *mohavensis* Wirth and Atchley, 1973: 29 (male; fig. male genitalia, hind tibial comb, tarsomere 5, antenna; California).

Diagnosis. (Table 13) Female unknown. Male brownish black, legs dark brown; eyes bare; palpal segment 3 sensilla in superficial excavation wider than deep; hind tibial comb with four spines; flagellomere 13 ~2.2× longer than 12; tergite 9 evenly tapering to base of stout widely separated apicolateral processes, which are 2–3× longer than wide and separated by a distance about equal to their length; aedeagal sclerites separate, apically pointed; distal sclerite of paramere ~6× longer than wide, apical portion bent ~90° meso-ventrally.

Distribution. The only record of this species is of three males collected with "suction trap" at Needles, San Bernardino County, California, 19 May 1965 by M. S. Mulla. Its collection in the Mojave Desert along the Colorado River at 150 m elevation indicates it may also occur in the lower and warmer areas of Arizona and Utah.

Biology. No other data are available.

Remarks. No *L. mohavensis* were examined; see *L. torrens* remarks.

Leptoconops (*Leptoconops*) *torrens* (Townsend)

(Fig. 5, 6)

Tersesthes torrens Townsend, 1893: 371 (female; fig. female head, wing, abdomen, legs; New Mexico).

Leptoconops torrens: Kieffer 1908: 577 (combination; key; male, female; fig. female palpus, antenna male antenna, claw, gonocoxite). Carter 1921: 15 (key; female, male; fig. male gonostylus, claw, antenna, female palpus, antenna, wing stigma). Wirth 1952a: 110 (in part; key; female; male genitalia; fig. female wing, abdomen, palpus, male genitalia). Fox 1955: 263 (in part; key; taxonomy). Whitsel and Schoeppner 1970 (in part; biology).

Leptoconops (*Leptoconops*) *torrens*: Wirth and Atchley 1973: 30 (key; female, male; fig. female antenna, palpus, tarsomere 5, spermathecae, head, genitalia, male antenna, genitalia; biology). Atchley 1974: 467 (female; distinction from *L. carteri* Hoffman). Downes and Wirth 1981: 397 (fig. male genitalia). Borkent and Spinelli 2000: 9 (in Neotropical catalog).

Diagnosis. (Table 13) Dark brown to black, tarsomeres often paler; stigma brown; eyes bare; clypeus with eight or more setae; palpal segment 3 sensilla in superficial excavation wider than deep (female as in Fig. 12 *L. carteri*); hind tibial comb with four spines; claw with basal bristle, without basal tooth. Female: antenna with 12 flagellomeres; mandible with 16–18 prominent teeth; hind tarsomeres 3 and 5 subequal; two elongate spermathecae usually ~1.8× longer than wide (as in Fig. 17 *L. carteri*), third absent; cerci >3× longer than wide. Male: flagellomere 13 ~1.6× longer than 12; tergite 9 evenly tapering to base of thin widely separated apicolateral processes, which are ~8× longer than wide and separated by a distance about equal to their length; aedeagal sclerites apically fused, blunt; distal sclerite of paramere ~2× longer than wide, apical portion flat, not bent. (Male genitalia nearly indistinguishable from that of *L. carteri* Fig. 19.)

Distribution. California, Nevada, Utah (Grand, Kane, Washington counties), and Colorado, south through Arizona, New Mexico and Texas to Baja California and Sonora. A report of *L. torrens* at Salt Lake, Utah (Pratt 1907) was a misidentification of *L. americanus* (Carter 1921).

Larval ecology and life cycle. Immatures have been collected from coarse, damp sand and moss in areas protected from floods in washes of mountain canyons (Brenner and Wargo 1984). Also, they and Mullens and Dada (1992b) noted outbreaks occurred several days after major rainfall and lasted 1–3 weeks. Unlike *L. carteri*, *L. torrens* males form mating swarms (Atchley 1973). In the laboratory at 24 °C, Whitsel and Schoeppner (1970) found females laid an average of 42 eggs, of which 42% were viable.

Adult behavior. Known hosts are horse (Townsend 1893; Wirth and Atchley 1973), human (Wirth 1952a; Wirth and Atchley 1973), and sheep (Jones 1965). In contrast with *L. carteri*, *L. torrens* tend to bite humans around the head and arms more than on the lower body (Wirth and Atchley 1973).

In the present study, 53 of the 56 females collected in Utah were while biting humans: two on my ears 8 May 2017, nine on 8 June 1999, and one on 4 June 2001 in Grand County, one by T. Graham on 4 June 2001 in Kane County, and forty on 2–6 June 2019 in Washington County. Two of the other three were CO_2-trapped in Grand County, and one was collected with UVLT in Washington County where diurnal biting pressure was high—suggesting its capture with UVLT was accidental. Low dispersal from larval habitats may explain why it was rarely CO_2-trapped; and strictly diurnal activity would explain its near absence from light traps.

Vector potential. Low parity rates, low dispersal, and short life span were reported for *L. torrens*, suggesting it has low vector potential (Brenner and Wargo 1984).

Remarks. The Kane and Grand County specimens have uniformly dark brown legs as described by Wirth and Atchley (1973) for California specimens; but the Washington County specimens all have at least their mid and hind tarsomeres paler yellowish brown as they described for other states. Because the females of the low-desert inhabiting *L. mohavensis* are unknown, it is uncertain if all the *L. torrens* females collected in Washington County are actually *L. torrens*. See also *L. carteri* remarks.

Subgenus *Proleptoconops* Clastrier

***Leptoconops* (*Proleptoconops*) *werneri* Wirth and Atchley**

(Fig. 13, 14)

Leptoconops (*Leptoconops*) *werneri* Wirth and Atchley, 1973: 34 (key; female, male; fig. female head, wing, genitalia, hind tibial comb, antenna, spermathecae, palpus, hind tarsomere 5, male genitalia, antenna; California).

Leptoconops (*Proleptoconops*) *werneri*: Clastrier 1974: 231 (assignment to subgenus *Proleptoconops*). Borkent and Spinelli 2000: 10 (in Neotropical catalog).

Diagnosis. (Table 13) Entirely dark brown to black; stigma indistinct; eyes bare; palpal segment 3 sensilla in superficial excavation wider than deep (female as in Fig. 12 *L. carteri*); clypeus with four setae, median pair farther apart from each other than from corresponding lateral setae; hind tibial comb with four spines. Female: antenna with 12 flagellomeres; mandible with 10–13 teeth; hind tarsomeres 3 and 5 subequal; claw with prominent basal tooth; two large and one small elongate ovoid spermathecae; cerci >3× longer than wide (as in Fig. 6 *L. torrens*). Male: flagellomere 13 ~1.4× longer than 12; tergite 9 evenly tapering to base of fingerlike widely separated apicolateral processes, which are ~4× longer than wide and separated by a distance about equal to their length; aedeagal sclerites separate, apically expanded, blunt; distal sclerite of paramere ~2× longer than wide, apical half greatly expanded quadrate with blunt ventromedian tooth.

Distribution. California, Arizona, New Mexico, Kansas, Missouri, Texas, Baja California, Baja California Sur, Sonora, Zacatecas, Morelos.

Adult behavior. Females have been collected in a quail-baited trap and while biting a human (Wirth and Atchley 1973). In addition, Weinmann et al. (1979) collected blood-engorged *L. werneri* from California quail (*Callipepla californica* [Shaw], Odontophoridae)-baited traps; however, they found no *L. werneri* infected with quail heartworm (*Splendidofilaria californiensis* [Wehr and Herman] [Nematoda: Filarioidea]) or other evidence it can transmit the parasite.

Key to *Culicoides* Males

(Measurement and ratio definitions are in the “Morphological terms and data” section of Materials and Methods)

1. Wing without pattern of pale spots (often false pale areas caused by paucity of macrotrichia in base of wing and from r-m crossvein posterior along r_1 and r_2 to around end of costa, but veins not pale) (as in Fig. 3, 4) **2**

— Wing with pale spots at least at tip of costa and on r-m crossvein (Fig. 50, 51, 57, 117–169) **14**

2(1). Distal portion of parameres fused (Fig. 34–40); SCo absent from flagellomeres 9–13 . . . . **C. (*Selfia* Khalaf) 3**

— Parameres separate (Fig. 41–43) or rarely fused only at base by a narrow bridge (*C. saundersi* Wirth and Blanton); SCo often on some of flagellomeres 9–13 . . . . **9**

3(2). Brown or yellowish to reddish yellow (Fig. 33 female); scutellum with four setae; hind tarsomeres without apical spines; posterior margin of sternite 9 convex over basal portion of aedeagus, without median lobes; aedeagus apically trifurcate (Fig. 34, 35) **4**

— Variously medium to dark brown or gray (Fig. 33 female); scutellum with six to eight setae; hind tarsomeres with apical spines (Fig. 281); posterior margin of sternite 9 variously lobular, cleft, concave, or straight, not simply convex; apical portion of aedeagus entire, if appearing trifurcate, then not into separate lobes (Fig. 36–40) **5**

4(3). Brown; aedeagus about as long as wide, lateral arms in the form of boomerang-shaped sclerites (Fig. 34) . . . . **C. (*Selfia*) *brookmani* Wirth**

— Yellowish to reddish yellow (Fig. 33 female); aedeagus ~2× longer than wide, lateral arms not boomerang-shaped sclerites (Fig. 35) . . . . **C. (*Selfia*) *moabensis* Phillips**

5(3). Sternite 9 with pair of prominent caudomedial lobes (Fig. 36, 37); gonocoxal apodeme without a basal process **6**

— Sternite 9 without caudomedial lobes; gonocoxal apodeme with a small posterior hooklike or pointed toothlike basal process (Fig. 38–40) **7**

6(5). Caudomedial lobes of sternite 9 not much longer than wide, apex of gonostylus rounded clublike (Fig. 36) . . . . **C. (*Selfia*) *denningi* Foote and Pratt**

— Caudomedial lobes of sternite 9 ~4× longer than wide; apex of gonostylus expanded foot-shaped (Fig. 37) . . . . **C. (*Selfia*) *hieroglyphicus* Malloch**

7(5). Apex of gonostylus markedly expanded and foot-shaped; aedeagus elongate, almost parallel-sided except on basal 0.1 (Fig. 38) . . . . **C. (*Selfia*) *jamesi* Fox**

— Apex of gonostylus at most only slightly expanded, blunt; aedeagus Y-shaped (Fig. 39, 40) **8**

8(7). Posterior margin of sternite 9 concave or cleft; parameres with heavily sclerotized knoblike shoulders at ~0.5, posterior median process elongate parallel-sided, fingerlike (Fig. 39) . . . . **C. (*Selfia*) *jacksoni* Atchley**

— Posterior margin of sternite 9 nearly straight; parameres without distinct shoulders, posterior median portion tapering blunt triangular (Fig. 40) . . . . **C. (*Selfia*) *tenuistylus* Wirth**

9(2). Head black, thorax mostly shiny black; aedeagus V-shaped, apex bifurcate; paramere with conspicuous submedian blunt triangular process and truncate tip . . . . **(unplaced) *C. monoensis* Wirth**

— Light to dark brown; aedeagus Y-shaped, apex entire; paramere without submedian process, apex either a simple straight, slightly curved, or strongly hooked point (Fig. 41, 42) or a long curved serrated saberform blade (Fig. 43) **10**

10(9). Distal portion of paramere conspicuous as a long curved heavily sclerotized serrated saberform blade (Fig. 43) . . . . **C. (*Wirthomyia*) *bottimeri* Wirth**

— Paramere relatively discreet, distal portion simple, pointed, straight to hooklike (Fig. 41, 42) **11**

11(10). Eyes with interommatidial pubescence (as in Fig. 18 *L. carteri*, but more distinct); ventro-posterior membrane of sternite 9 bare; distal portion of paramere slender, straight to slightly curved; hind tibial comb with five or six (occasionally 4) spines **12**

— Eyes bare; ventro-posterior membrane of sternite 9 spiculate; distal portion of paramere a stout hook (Fig. 41, 42); hind tibial comb with four spines **13**

12(11). Parameres separate, distal tip not extending beyond tip of aedeagus . . . . **(Saundersi group) *C. atchleyi* Wirth and Blanton**

— Parameres fused at base by a narrow bridge, distal tip extending beyond tip of aedeagus . . . . **(Saundersi group) *C. saundersi* Wirth and Blanton**

13(11). Dark to medium brown, including legs; median process of aedeagus truncate (Fig. 42) . . . . **(Stonei group) *C. werneri* Wirth and Blanton**

— Variously brown to yellowish brown, legs yellow to straw-colored; median process of aedeagus blunt (Fig. 41) . . . . **(Stonei group) *C. stonei* James, *C. mortivallis* Wirth and Blanton, *C. owyheensis* Jones and Wirth**

14(1). Flagellomeres 9–10 each only half as large as 8 (Fig. 59); SCo absent from flagellomeres 2–13; eyes with interommatidial pubescence (as in Fig. 18 *L. carteri*); minute, wing length 0.7 mm . . . . **(Leoni group) *C. reevesi* Wirth**

— Flagellomeres 9–10 normal, each larger than 8 (Fig. 251, 252); SCo on some of flagellomeres 2–13; eyes bare (except sometimes on *C. boydi* Wirth and Mullens and *C. chiopterus* [Meigen], which have normal antennae and SCo on flagellomeres 11–13); wing length usually >1 mm **15**

15(14). At least distal portion of cell r_2 within a pale spot (Fig. 117–125); tergite 9 posterior margin either convex with or without tiny apicolateral processes not extending beyond median portion (Fig.

65–72) or broadly concave with square shoulders (Fig. 63) or with short apicolateral processes (Fig. 64); hind tibial comb with 5–7 spines; SCo absent from 2–9, often 10 . . . . **16**

— Cell r_2 entirely dark (Fig. 50, 51, 126–169); tergite 9 posterior margin concave, with distinct apicolateral processes extending beyond medial portion (Fig. 73–116); hind tibial comb often with four spines; SCo often present on some of 2–9 . . . . **27**

16(15). Mesal surface of gonocoxite clothed with short pale inconspicuous setae (Fig. 63–65); ventral apodeme of gonocoxite ~2× longer than dorsal apodeme, slender, 5–7× longer than basal width (Fig. 63–65); tergite 9 broadly convex without apicolateral processes (Fig. 65), or broadly concave with square corners (Fig. 63) or short triangular apicolateral processes (Fig. 64); wing pattern of pale spots faint to absent from distal third (Fig. 117, 118); hind tibial comb with five spines . . . . **C. (*Avaritia* Fox) 17**

— Mesal surface of gonocoxite clothed with short dark conspicuous setae or spinules (Fig. 66–72); ventral apodeme of gonocoxite not longer than dorsal apodeme, strongly tapered, pointed, 1–2× as long as basal width; tergite 9 tapering convex with tiny apicolateral processes (rarely absent) not extending past mesal portion of tergite (Fig. 66–72); wing pattern of pale spots extensive into distal portion of wing (Fig. 119–125); hind tibial comb with six or seven spines (Fig. 286) . . . . **C. (*Silvicola* Mirzaeva and Isaev) 20**

17(16). Sternite 9 posterior margin with broad caudomedian excavation; tergite 9 posterior margin concave, with blunt apicolateral processes (Fig. 64) or square lateral corners (Fig. 63); aedeagus with sclerotized membrane between arms and sclerotized anterior-directed point at base of median process; aedeagal ratio <0.5 (Fig. 63, 64) **18**

— Sternite 9 posterior margin notched; tergite 9 posterior margin convex, without apicolateral processes; aedeagus without sclerotized membrane between basal arms and without sclerotized anterior-directed point at base of median process; aedeagal ratio >0.5 (Fig. 65) **19**

18(17). Basal arms of aedeagus forming pointed lateral shoulders adjacent to median process; tergite 9 with square apicolateral corners (Fig. 63) . . . . **C. (*Avaritia*) *boydi* Wirth and Mullens**

— Aedeagus without lateral shoulders; tergite 9 with short broad apicolateral processes (Fig. 64) . . . . **C. (*Avaritia*) *chiopterus* (Meigen)**

19(17). Aedeagal ratio >0.7; tip of aedeagus convex, sides bare (Fig. 56); paramere tip with minute hairs, which may require an oil-immersion lens to see . . . . **C. (*Avaritia*) *obsoletus* (Meigen)**

— Aedeagal ratio <0.7; tip of aedeagus concave, sides usually spinulose; paramere tip simple . . . . **C. (*Avaritia*) *sanguisuga* (Coquillett)**

20(16). Major bend of paramere near its middle; aedeagal ratio ~0.3; coastal tidelands . . . . **C. (*Silvicola*) *tristriatulus* Hoffman**

— Major bend of paramere at a fifth to a third of length from basal end (Fig. 66–72); aedeagal ratio often 0.4–0.6; inland **21**

21(20). Hind tarsomeres with apical spines (Fig. 282) (species D and E likely key this path, but males unknown) **22**

— Hind tarsomeres without apical spines **24**

22(21). Hind tibiae with distinct basal pale band ~2× longer than wide (Fig. 286) . . . . **C. (*Silvicola*) *sierrensis* Wirth and Blanton**

— Hind tibiae without pale band, or sometimes with indistinct band not longer than wide **23**

23(22). Distal wing pattern indistinct, hourglass-shaped distal dark spot in r_3 usually not darker than other distal dark patches (Fig. 123); gonocoxite with moderately strong black setae on mesal surface; aedeagal ratio <0.4 (Fig. 70) . . . . **C. (*Silvicola*) *neomontanus* Wirth**

— Distal wing pattern distinct, hourglass-shaped distal dark spot in r_3 darker than other distal dark patches (Fig. 119); gonocoxite with fine brown setae on mesal surface; aedeagal ratio >0.4 (Fig. 66) . . . . **C. (*Silvicola*) *cockerellii* (Coquillett)**

24(21). Fore tarsomeres 1 or 2 with apical spines (as in Fig. 285 *C. calexicanus*); dark spot over portions of r_1 and r_2 not broadly connected to dark spot over M fork (Fig. 120) . . . . . . ***C.* (*Silvicola*) *freeborni* Wirth and Blanton**

— Fore tarsomeres without apical spines; dark spot over r_1 and r_2 broadly connected to dark spot over M fork (Fig. 121, 122, 124) **25**

25(24). Median process of aedeagus broadly triangular, tapering to broad blunt tip (Fig. 71); tergite 9 often without apicolateral processes; palpal segment 3 with patch of scattered sensilla instead of pit; known only from the low southern deserts of California and Nevada . . . ***C.* (*Silvicola*) *saltonensis* Wirth**

— Median process of aedeagus more abruptly narrowing on distal half to slender fingerlike tip (Fig. 68, 69); tergite 9 with apicolateral processes; palpal segment 3 with distinct sensory pit (Fig. 241); widespread **26**

26(25). Hind tibiae with distinct basal pale band as in Fig. 286 *C. sierrensis*; distal pale wing spots with distinct borders (Fig. 122) . . . . . . ***C.* (*Silvicola*) *neofagineus* Wirth and Blanton**

— Hind tibiae without pale band; distal pale wing spots with indistinct borders (Fig. 121) . . . . . . ***C.* (*Silvicola*) *lahontan* Wirth and Blanton**

27(15). Parameres fused at base (Fig. 46, 48); hind tibial comb with six or seven spines; fore and hind tarsomeres 1, 2 with apical spines . . . . . . ***C.* (*Monoculicoides* Khalaf) 28**

— Parameres separate (Fig. 73–116); hind tibial comb with four or five spines (rarely six on *C. californiensis* and *C. kettlei*); fore and hind tarsomeres without apical spines (except on *C. usingeri*, Palmerae group species, and unplaced species F) **30**

28(27). Aedeagus apex entire; wing with faint pattern (as in Fig. 173 female); scutum yellowish brown without dark spots; legs pale brown without apparent banding . . . . . . ***C.* (*Monoculicoides*) *grandensis* Grogan and Phillips**

— Aedeagus apex deeply bifurcate (Fig. 47, 49); wing with distinct pattern (Fig. 50, 51); scutum brown with dark spots at setal bases (as in Fig. 55); legs brown with distinct pale banding **29**

29(28). Ventral surface of aedeagus spiculate (Fig. 47) . . . . ***C.* (*Monoculicoides*) *sonorensis* Wirth and Jones**

— Aedeagus bare (Fig. 49) . . . . . . ***C.* (*Monoculicoides*) *occidentalis* Wirth and Jones**

30(27). Aedeagal arms each with sclerotized spurlike process on posterior margin (Fig. 73–78) . . . . . . ***C.* (*Diphaomyia* Vargas) 31**

— Aedeagal arms simple (Fig. 79–116) **35**

31(30). Paramere without submedian lobe (Fig. 77); posterior process of footlike ventral apodeme of gonocoxite difficult to see, often unapparent (Fig. 78) **32**

— Paramere with submedian lobe; posterior process of footlike ventral apodeme of gonocoxite distinct (Fig. 73–76) **33**

32(31). Wing pattern extensive with distinct distal pale spots in r_3, m_1, m_2 (as in Fig. 194 female) . . . . . . ***C.* (*Diphaomyia*) *bergi* Cochrane**

— Wing pattern without distal pale spots in r_3, m_1, m_2 (Fig. 130) . . . . ***C.* (*Diphaomyia*) *salihi* Khalaf**

33(31). Distal half of r_3 mostly dark, with small distinct pale spot entirely within distal 0.2 of cell (Fig. 126, 127) . . . . . ***C.* (*Diphaomyia*) *defoliarti* Atchley and Wirth, *C.* (*Diphaomyia*) *haematopotus* Malloch**

— Distal pale spot in r_3 central in distal half or filling most of distal third of cell, but may be faint or absent (Fig. 128, 129) **34**

34(33). Wing pattern extensive with diffuse pale spots in r_3, m_1, m_2 (Fig. 128); SCo pattern 1, (6), (7), 8, 9 . . . . . . ***C.* (*Diphaomyia*) *inyoensis* Wirth and Blanton**

— Distal pales spots absent from r_3, m_1, m_2 (Fig. 129); SCo pattern 1, (10), 11–13 . . . . . . ***C.* (*Diphaomyia*) *erikae* Atchley and Wirth**

35(30). Ventral apodeme of gonocoxite complex, with two widely divergent processes, footlike (Fig. 79–87) **36**

— Ventral apodeme of gonocoxite simple (Fig. 88–116) **45**

36(35). Parameres with submedian lobe (Fig. 79, 80); SCo absent from flagellomeres 11–13 .... **37**
— Parameres without submedian lobe (Fig. 81–87); SCo present on 12–13 .... **40**

37(36). Hind tibial comb with four spines **38**
— Hind tibial comb with five or six spines .... **_C._ (_Haematomyidium_ Goeldi) 39**

38(37). Aedeagus tip truncate, spinose (Fig. 79); inland .... **(Mohave group) _C. mohave_ Wirth**
— Aedeagus tip rounded, without spines; coastal .... **(Mohave group) _C. hoguei_ Wirth and Moraes**

39(37). Two separate pale spots in m_1 (Fig. 133) . . **_C._ (_Haematomyidium_) _kettlei_ Breidenbaugh and Mullens**
— Three separate pale spots in m_1 (Fig. 134, 135) .... **_C._ (_Haematomyidium_) _stellifer_ (Coquillett)**

40(36). Distal pale spots distinct in r_3, m_1, m_2 (Fig. 136–139) **41**
— Distal pale spots faint or absent from r_3, m_1, m_2 (Fig. 140, or as in Fig. 233, 234 females) **42**

41(40). Pale band or patch along posteromedian margin of anal cell (Fig. 136, 137); sternite 9 caudomedian excavation ~0.3 as deep as wide, about evenly curved; heavily sclerotized basal arms of aedeagus with basal ends sharply bent laterally, posteromedial ends connected only by unsclerotized or barely sclerotized membrane, aedeagal ratio ~0.7 (Fig. 81–83) .... **(Piliferus group) _C. cavaticus_ Wirth and Jones**

— No pale band or patch on posteromedian margin of anal cell (Fig. 138, 139); sternite 9 caudomedian excavation ~0.5 as deep as wide, about three-sided; heavily sclerotized basal arms of aedeagus with basal ends bent more ventrally, posteromedial ends fused by moderate sclerotization, aedeagal ratio 0.45–0.6 (Fig. 84, 85) (*C. lophortygis* Atchley and Wirth may key here too, but male unknown) .... **(Piliferus group) _C. doeringae_ Atchley**

42(40). Hind tibial comb with five spines .... **(Piliferus group) _C. unicolor_ (Coquillett)**
— Hind tibial comb with four spines **43**

43(42). Pale yellowish-brown .... **(Piliferus group) species A**
— Dark brown **44**

44(43). Faint distal pale spots in r_3, m_1, m_2, straddling midportions of M_1 and M_2 (as in Fig. 233 female) ...... **(Piliferus group) likely species B (male unknown)**

— Distal pale spots absent from r_3, m_1, m_2, sometimes from midportions of M_1 and M_2 (as in Fig. 234 female) **(Piliferus group) likely _C. chewaclae_ Glick and Mullen (male unknown)**

45(35). Distal half of paramere with elongate curved pointed thornlike process and distal fringe of spines (Fig. 88); SCo pattern 1, (7), 8–10 .... **(Limai group) _C. luglani_ Jones and Wirth**

— Distal half of paramere simple or with only apical spines (Fig. 89–116); SCo pattern 1, (2), (3), (4), (5), (11), 12, (13) **46**

46(45). Ventral apodeme of gonocoxite inconspicuous as an obtuse antero-medially directed toothlike bump (Fig. 89); distal pale wing spots ovoid, no isolated pale spots straddling M_1 or M_2 (Fig. 142, 143) .... **_C._ (_Beltranmyia_) _crepuscularis_ Malloch**

— Ventral apodeme of gonocoxite slender elongate, 3–10× longer than median width, >0.5 as long as dorsal apodeme (Fig. 90–116); distal pale wing spots often irregular or absent, isolated pale spots often straddling M_1 or M_2 (Fig. 144–169) **47**

47(46). Antennae, palpi, and wings feminized (Fig. 147, 251); genitalia normal (Fig. 93) **48**
— Antennae, palpi, and wings normal (Fig. 252) **49**

48(47). Wing pattern extensive with distal pale spots (Fig. 147); tergite 9 apicolateral processes long and slender, ~5× longer than wide, projecting nearly parallel caudally (Fig. 93) .... **(Palmerae group) _C. utahensis_ Fox**

— Wing pattern greatly reduced, with pale spots only at tip of costa and on r-m crossvein; tergite 9 apicolateral processes stout, ~2× longer than wide, broadly flaring laterally ~30° .... **(Palmerae group) _C. leechi_ Wirth**

49(47). Hind tibial comb with five spines; distal pale spots present in cua_1 and anal cell, absent from or barely discernable in r_3, m_1, m_2; no pale spots straddling M_1 or M_2; basal arms of aedeagus slightly curved, slender, each ~10× longer than wide, distal process simple, tapering to narrow blunt tip; parameres without apical spines .... **(unplaced) *C. nanellus* Wirth and Blanton**

— Hind tibial comb often with four spines; distal pale spots sometimes absent from or often present and distinct in in r$_3$, m$_1$, m$_2$, cua$_1$, anal cells; pale spots often straddling M$_1$ or M$_2$; basal arms of aedeagus often more robust (Fig. 90–92, 94–116), distal process often broad or truncate (Fig. 90–92, 104–116); parameres sometimes with apical spines (Fig. 90, 94–96) **50**

50(49). Fore tarsomeres with apical spines (Fig. 285) (uncertain for *C. novamexicanus* and *C. oregonensis*); mid and hind femora without pale bands; no pale spot straddling midportion of M$_1$ (Fig. 144–146); SCo often absent from flagellomere 13; gonostylus often abruptly bent medially ~90° at ~0.2, L-shaped (Fig. 92) **51**

— Fore tarsomeres without apical spines; mid or hind femora often with basal or subapical pale band; pale spot often straddling at ~0.5 on M$_1$ (Fig. 154–167); SCo on flagellomere 13; gonostylus more or less evenly curved, not L-shaped **55**

51(50). Median process of aedeagus with wide, usually sharp, shoulders abruptly constricting to a narrow tip (Fig. 92) .... **(Palmerae group) *C. palmerae* James**

— Median process of aedeagus simple, without shoulders (Fig. 90, 91) **52**

52(51). Aedeagus broadly Y-shaped; median process slender, nearly parallel-sided, <0.1 as wide as basal arm spread, ~5× longer than median width .... **(Palmerae group) *C. oregonensis* Wirth and Rowley**

— Aedeagus tapering with almost a V-shape; median process of aedeagus broad, tapering to narrow or broad tip (Fig. 90, 91) **53**

53(52). Aedeagus tapering to broad tip ~0.4 as wide as basal arm spread (Fig. 91); distal pale wing spots faint or absent (Fig. 145) .... **(Palmerae group) *C. hawsi* Wirth and Rowley**

— Aedeagus tapering to narrow tip ~0.2 as wide as basal arm spread (Fig. 90); wing with extensive distal pale spots, but may be diffuse (Fig. 144) **54**

54(53). Gonostylus abruptly bent medially ~90° at ~0.2, L-shaped (as in Fig. 92 *C. palmerae*); scutellum about same brown as scutum (as in Fig. 221 *C. utahensis*) .... **(Palmerae group) *C. novamexicanus* Atchley**

— Gonostylus evenly curved, not abruptly bent (Fig. 90); scutellum more yellowish than scutum (Fig. 221) .... **(Palmerae group) *C. calexicanus* Wirth and Rowley**

55(50). Distal portion of paramere with 3–6 spines (Fig. 94–96) **56**

— Distal portion of paramere simple, tapering to filamentous tip (Fig. 97–116) **59**

56(55). Wing pattern extensive (as in Fig. 158, 159, 161, 162) .... ***C.* (*Drymodesmyia*) *bakeri* Vargas**

— Wing pattern reduced, distal pale spots absent from r$_3$, m$_1$, often from m$_2$, cua$_1$, anal cell (Fig. 148–150) .... ***C.* (*Silvaticulicoides* Glukhova) 57**

57(56). Distal pale spots present in cua$_1$, anal cell, often m$_2$ (Fig. 148); paramere apex with 3–4 spines (Fig. 94) .... ***C.* (*Silvaticulicoides*) *sublettei* Atchley**

— Distal pale spots absent (Fig. 149, 150); paramere apex with 4–6 spines (Fig. 95, 96) **58**

58(57). Hind tarsomeres with apical spines (as in Fig. 283 *C. palmerae*); ventral apodeme of gonocoxite slender, 2× longer than dorsal apodeme; paramere apex with five or six spines (Fig. 95) .... ***C.* (*Silvaticulicoides*) *usingeri* Wirth**

— Hind tarsomeres without apical spines; ventral apodeme of gonocoxite triangular tapering, about as long as dorsal apodeme; paramere apex with four spines (Fig. 96) .... ***C.* (*Silvaticulicoides*) *vetustus* Breidenbaugh and Mullens**

59(55). Distal pale spots absent from r$_3$, m$_1$, m$_2$, or small, faint, and only in apices of cells; pale spots not straddling M$_1$ or M$_2$ (Fig. 151–153) **60**

— Distal pale spots extensive, often prominent, in r$_3$, m$_1$, m$_2$; pale spots straddling M$_2$, often M$_1$ (Fig. 154–169) **62**

60(59). Pale spots absent from above CuA fork, distally from r$_3$, m$_1$, m$_2$ (Fig. 151) .... **(unplaced) *C. posoensis* Wirth and Blanton**

— Distinct pale spot anterior to CuA fork, sometimes faint distally in r_3, m_1, m_2 (Fig. 152, 153) . . . . **C. (*Sensiculicoides* Shevchenko) 61**

61(60). Aedeagal ratio ~0.5; median process stout at base, tapering to blunt tip (Fig. 98) . . . . **C. (*Sensiculicoides*) *kibunensis* Tokunaga**

— Aedeagal ratio ~0.4; median process narrow, parallel-sided on distal half (Fig. 99) . . . . **C. (*Sensiculicoides*) *travisi* Vargas**

62(59). Hind tibial comb with five, occasionally six, spines; hind tibiae with prominent subapical pale band; distinct pale spots straddling at ~0.3 on M_1; distal pale spot in r_3 double, bilobed about C- or 8-shaped, oriented perpendicular to M_1, central in distal half of cell (Fig. 154–156) . . . . **C. (*Amossovia* Glukhova) 63**

— Hind tibial comb with four spines; subapical pale band often absent from or indistinct on hind tibiae, but if distinct then no pale spot straddling M_1; distal pale spot in r_3 often single or U-shaped extending into apex of cell (Fig. 157–169) **66**

63(62). Yellowish coppery-brown; fore and mid tibiae with subapical pale band; aedeagus nearly V-shaped, median process broad triangular with lateral caudally directed spines on midsection, tapering to small simple blunt tip (Fig. 100) . . . . **C. (*Amossovia*) *californiensis* Wirth and Blanton**

— Dark brown; fore and mid tibiae without subapical pale band; aedeagus Y-shaped, median process slender with truncate or pointed tip or with lateral filaments (Fig. 101, 102) **64**

64(63). Hind femora with prominent subapical pale band; median process of aedeagus narrow parallel-sided with truncate tip . . . . **C. (*Amossovia*) *pecosensis* Wirth**

— Hind femora entirely dark or with only faint pale band; median process of aedeagus with pointed tip (Fig. 101, 102) **65**

65(64). Hind femora unbanded; median process of aedeagus simple (Fig. 101) . . . . **C. (*Amossovia*) *cochisensis* Wirth and Blanton**

— Hind femora with faint basal and subapical pale bands; median process of aedeagus with lateral pair of subapical filaments (Fig. 102) . . . . **C. (*Amossovia*) *oklahomensis* Khalaf**

66(62). Ventro-posterior membrane of sternite 9 spiculate (Fig. 110–112); distal pale spot in r_3 simple (Fig. 165) or if irregular then not U- or distinctly 8-shaped (Fig. 164, 166) . . . . **C. (*Drymodesmyia* Vargas) (part) 67**

— Ventro-posterior membrane of sternite 9 bare (Fig. 103–109, 113–116); distal pale spot in r_3 irregular (Fig. 157–163) or simple (Fig. 167–169) **69**

67(66). SCo pattern 1, 11–13; tip of median process of aedeagus papilliform, <0.1 as wide as arm spread (Fig. 110) . . . . **C. (*Drymodesmyia*) *insolatus* Wirth and Hubert**

— SCo pattern 1, 12–13; tip of median process of aedeagus rounded blunt or truncate, >0.1 as wide as arm spread (Fig. 111, 112) **68**

68(67). Ventro-posterior membrane of sternite 9 densely spiculate; ventral apodeme of gonocoxite ~0.5 as long as dorsal apodeme; aedeagal ratio ~0.6 (Fig. 111) . . . . **C. (*Drymodesmyia*) *arizonensis* Wirth and Hubert**

— Ventro-posterior membrane of sternite 9 with a few spicules; ventral apodeme of gonocoxite about as long as dorsal apodeme; aedeagal ratio 0.3–0.4 (Fig. 112) . . . . **C. (*Drymodesmyia*) *copiosus* Root and Hoffman**

69(66). Distal pale spot in r_3 distinctly double, bilobed, or mushroom-shaped, oriented perpendicular to M_1, extending to anterior margin of wing, not extending into distal 0.2 of cell; apices of M_1, M_2 pale, forming small pale spots at wing margin; distinct isolated pale spot straddling at ~0.3 on M_1 (Fig. 158–163) . . . . **C. (*Drymodesmyia* Vargas) (part) 70**

— Distal pale spot in r_3 single, ovoid, or quadrate (Fig. 167–169) to irregular U-shaped extending into distal 0.3 of cell (Fig. 157); apices of M_1, M_2 dark or no more pale than interior portions of veins and not forming apical spots; distinct isolated pale spot often absent from M_1 (Fig. 167–169) **74**

70(69). Aedeagus V-shaped, straight-sided until broad flaring truncate tip ~0.25 width of arm spread; aedeagal ratio ~0.3 (Fig. 107, 108) **71**

— Aedeagus more Y-shaped, constricting at base of median process, tapering to truncate or rounded tip <0.2 width of arm spread; aedeagal ratio 0.4–0.5 (Fig. 104–106, 109) **72**

71(70). Smaller, mean wing length 0.86 mm; pale wing markings more extensive (Fig. 161); Chihuahuan Desert from southeastern Arizona to Texas and probably Mexico . . . . ***C.* (*Drymodesmyia*) *jonesi* Wirth and Hubert**

— Larger, mean wing length 0.98 mm; pale wing markings less extensive (Fig. 162); Sonoran Desert and Colorado Plateau from Baja California to California, Utah, Arizona, and New Mexico . . . . ***C.* (*Drymodesmyia*) *sitiens* Wirth and Hubert**

72(70). Two pale spots of about same intensity in distal half of anal cell, often merged with broad pale area along wing margin; pale apices of M$_1$ and M$_2$ broadly flaring (Fig. 158, 159); aedeagal ratio >0.43; narrowest diameter of paramere before first ~90° bend in apical half >0.0027 mm (Fig. 104, 105) . . . . ***C.* (*Drymodesmyia*) *butleri* Wirth and Hubert**

— Only one distinct pale spot in distal half of anal cell, usually not merging with fainter pale area along wing margin; pale apices of M$_1$ and M$_2$ not flaring (Fig. 160, 163); either aedeagal ratio <0.42 or narrowest diameter of paramere before first ~90° bend in apical half <0.0026 mm (Fig. 106, 109) . . **73**

73(72). Aedeagal ratio >0.43; narrowest diameter of paramere before first ~90° bend in apical half <0.0026 mm (Fig. 106) . . . . ***C.* (*Drymodesmyia*) *cacticola* Wirth and Hubert**

— Aedeagal ratio <0.42; narrowest diameter of paramere before first ~90° bend in apical half >0.0027 mm (Fig. 109) . . . . ***C.* (*Drymodesmyia*) *torridus* Wirth and Hubert**

74(69). Median process of aedeagus broad, tapering abruptly at ~0.6 to slender blunt finger-like tip (Fig. 103); pale spot in distal half of r$_3$ broadly U-shaped, extending from near anterior wing margin through midportion of distal half of cell along M$_1$ to apex of cell (Fig. 157) . . . . **(Daedalus group) *C. pampoikilus* Macfie**

— Median process of aedeagus evenly narrowing to broad truncate or blunt tip (Fig. 113–116); distal pale spot in r$_3$ simple, ovoid or quadrate to slightly C-shaped, not broadly U-shaped or extending to apex of cell (Fig. 167–169, or as in Fig. 195 female) **75**

75(74). Ventral apodeme of gonocoxite much more slender and often shorter than the broad, pointed dorsal apodeme (Fig. 113); distal pale spot in r$_3$ elongate ovoid, tapering distally, oriented parallel with M$_1$ (Fig. 167) . . . . ***C.* (*Drymodesmyia*) *ryckmani* Wirth and Hubert**

— Ventral apodeme of gonocoxite as long as or longer and only a little more slender than dorsal apodeme (Fig. 114–116); distal pale spot in r$_3$ ovoid or quadrate to slightly C-shaped, oriented oblique or perpendicular to M$_1$ (Fig. 168, 169, or as in Fig. 195 female) **76**

76(75). Aedeagus Y-shaped, aedeagal ratio ~0.6, median process narrow, nearly parallel-sided (Fig. 116); southern, rare . . . . **(Daedalus group) *C. daedalus* Macfie**

— Aedeagus more V-shaped, aedeagal ratio 0.3–0.4, median process more tapered (Fig. 114, 115); widespread treehole species **77**

77(76). Ventral apodeme of gonocoxite about as long as dorsal apodeme (Fig. 115); yellow (in alcohol); distal spot in r$_3$ oriented perpendicular to M$_1$; pale spot at tip of costa bent back beneath r$_2$ (Fig. 169); pale leg-banding subapical on mid femora, basal and subapical on hind femora, subapical on hind tibiae (Fig. 250) . . . . ***C.* (*Drymodesmyia*) *hinmani* Khalaf**

— Ventral apodeme of gonocoxite up to 2× longer than dorsal apodeme (Fig. 114); brown (in alcohol); distal spot in r$_3$ oriented oblique to M$_1$; pale spot at tip of costa not bent back beneath r$_2$ (Fig. 168); pale leg-banding reduced: absent subapically from mid femora, basally and subapically from hind femora, subapically from hind tibiae (Fig. 250) . . . . ***C.* (*Drymodesmyia*) *byersi* Atchley**

Key to *Culicoides* Females

(Measurement and ratio definitions are in the "Morphological terms and data" section of Materials and Methods)

1. Wing without pattern of pale spots (often false pale areas caused by paucity of macrotrichia in base of wing and from r-m crossvein posterior along r_1 and r_2 to around end of costa, but veins not pale) (Fig. 3, 4) **2**

— Wing with pale spots at least at tip of costa and on r-m crossvein (Fig. 2, 56, 170–240) **14**

2(1). Three long unsclerotized or lightly sclerotized fingerlike spermathecae, usually unrecognizable even in slide preparations . . . . ***C.* (*Selfia* Khalaf) 3**

— Two distinctly sclerotized ovoid or pyriform spermathecae, with vestigial third (Fig. 44, 45) **7**

3(2). Brown or yellowish to reddish yellow (Fig. 33); scutellum with four setae if brown, eight setae if yellow; hind tarsomeres without apical spines **4**

— Variously medium to dark brown or gray (Fig. 33); scutellum with 8–14 setae; hind tarsomeres with apical spines (Fig. 281) **5**

4(3). Brown; scutellum with four setae . . . . ***C.* (*Selfia*) *brookmani* Wirth**

— Yellowish to reddish yellow (Fig. 33); scutellum with eight setae . . . . ***C.* (*Selfia*) *moabensis* Phillips**

5(3). SCo pattern 1, 5–8 . . . . ***C.* (*Selfia*) *denningi* Foote and Pratt**

— SCo pattern 1, (2), (3), 4–8 . . . . **6**

6(5). SCo pattern 1, 4–8 . . . . ***C.* (*Selfia*) *hieroglyphicus* Malloch (part)**

— SCo pattern 1, (2), 3–8 . . . . . . ***C.* (*Selfia*) *hieroglyphicus* Malloch (part), *C.* (*Selfia*) *jacksoni* Atchley, *C.* (*Selfia*) *jamesi* Fox, *C.* (*Selfia*) *tenuistylus* Wirth**

7(2). Head black, thorax mostly shiny black; SCo pattern 1, 12–13 . . . . . . **(unplaced) *C. monoensis* Wirth**

— Light to dark brown; SCo on some of flagellomeres 2–11. . . . . **8**

8(7). Eyes with prominent interommatidial pubescence (as in Fig. 18 *L. carteri*, but more distinct); mandible either with 14–20 teeth or without teeth; anterior wing veins dark and thick (Fig. 4) **9**

— Eyes bare; 9–13 mandibular teeth; anterior wing veins more normal (Fig. 3) **10**

9(8). Eyes separated by <1 ommatidium diameter; mandibular teeth vestigial . . . . **(Saundersi group) *C. atchleyi* Wirth and Blanton**

— Eyes separated by ~2 ommatidium diameters; mandible with 14–20 teeth . . . . **(Saundersi group) *C. saundersi* Wirth and Blanton**

10(8). Hind tibial comb with five or six spines; eyes separated by <1 ommatidium diameter; SCo pattern 1, (2), 3, (4), 5–8; posterior portion of sternite 8 medially concave but not cleft, with pair of pointed submedian posterior projections (Fig. 44) . . . . ***C.* (*Wirthomyia*) *bottimeri* Wirth**

— Hind tibial comb with four spines; eyes separated by >1 ommatidium diameter; SCo on at least 8–12; posterior portion of sternite 8 medially cleft, with blunt submedian posterior projections (Fig. 45) **11**

11(10). SCo pattern 1, 8–12, sometimes also on flagellomere 5 or 7 . . . . **(Stonei group) *C. werneri* Wirth and Blanton**

— SCo pattern 1, 5–12 or 1, (2), 3–12 . . . . **12**

12(11). SCo pattern 1, (2), 3–12 . . . . **(Stonei group) *C. stonei* James**

— SCo pattern 1, 5–12 . . . . **13**

13(12). Wing length <1.06 mm; length of flagellomeres 7+8 divided by length of flagellomere 9 <1.50; length of palpal segment 3 divided by length of flagellomere 9 <1.90; length of proboscis divided by length of flagellomere 9 <3.95 . . . . **(Stonei group) *C. mortivallis* Wirth and Blanton**

— Wing length >1.06 mm; length of flagellomeres 7+8 divided by length of flagellomere 9 >1.50; length of palpal segment 3 divided by length of flagellomere 9 >1.90; length of proboscis divided by length of flagellomere 9 >3.95 . . . . **(Stonei group) *C. owyheensis* Jones and Wirth**

14(1). Flagellomeres 9–10 much shorter and narrower than any others (Fig. 58); eyes with interommatidial pubescence (as in Fig. 18 *L. carteri*); one fully developed spermatheca with vestigial second; minute, wing length ≤0.8 mm .... **(Leoni group) *C. reevesi* Wirth**

— Flagellomeres 9–10 normal, each as large as or larger than any of 2–8 (Fig. 253); eyes bare (except sometimes on *C. boydi* and *C. chiopterus*, which have normal antennae and two fully developed spermathecae); either one developed spermatheca rarely with vestigial second (Fig. 52–54) or two developed spermathecae with vestigial third (Fig. 255–278); wing length usually >1 mm **15**

15(14). One fully developed spermatheca (Fig. 52–54), sometimes with vestigial second; r_2 entirely dark; distal wing pattern extensive and either with one isolated ovoid distal pale spot in r_3 and two isolated ovoid pale spots in m_1 and no spots straddling M_1 or M_2 (Fig. 170–172) or of dark irregular curves, extensively interconnected pale streaks, and zigzags (Fig. 173, 174) **16**

— Two fully developed spermathecae with vestigial third (Fig. 255–278); r_2 often in a pale spot (Fig. 175–186); only one or no isolated ovoid pale spot within m_1 not straddling a vein (Fig. 175–186, 190–215, 217–240) or isolated distal spots in r_3 irregular, not ovoid (Fig. 187–203, 207–210, 216) **19**

16(15). Distal wing pattern of ovoid pale spots (Fig. 170–172); eyes separated by ~1 ommatidium diameter; hind tarsomeres without apical spines; spermatheca ovoid, opening ~0.1 the diameter of the spermatheca (Fig. 52) .... ***C.* (*Beltranmyia*) *crepuscularis* Malloch**

— Distal wing pattern more of dark irregular curves, pale streaks, and zigzags than ovoid spots (Fig. 173, 174); eyes widely separated by >2 ommatidium diameters; hind tarsomeres with apical spines (as in Fig. 281–284); spermatheca with opening >0.5 the diameter of the spermatheca, often U-shaped (Fig. 53, 54) .... ***C.* (*Monoculicoides* Khalaf) 17**

17(16). Spermatheca ovoid (Fig. 53); wing with faint pattern (Fig. 173); scutum yellowish brown without dark spots; legs pale brown without apparent banding; mandibular teeth vestigial .... ***C.* (*Monoculicoides*) *grandensis* Grogan and Phillips**

— Spermatheca U-shaped (Fig. 54); wing with prominent pattern (Fig. 174); scutum brown with dark spots at seta bases (Fig. 55); legs brown with prominent pale banding; mandibular teeth well-developed **18**

18(17). Immatures in aquatic alkaline or highly organic soils (females morphologically indistinguishable) .... ***C.* (*Monoculicoides*) *sonorensis* Wirth and Jones**

— Immatures in aquatic highly saline soils (females morphologically indistinguishable) .... ***C.* (*Monoculicoides*) *occidentalis* Wirth and Jones**

19(15). At least distal portion of cell r_2 within a pale spot (Fig. 175–186); hind tibial comb with 5–7 spines (Fig. 286); eyes contiguous (except for *C. tristriatulus*); SCo on at least 1, 10–13 .... **20**

— Cell r_2 entirely dark or with only the vein at distal tip of r_2 in a pale spot (Fig. 187–240); hind tibial comb often with four spines; if with five spines, then: eyes separated, or SCo absent from 11–13, or pale wing spots distinct and extensive (Fig. 187–193) or greatly reduced (Fig. 227) **33**

20(19). Wing pattern of pale spots faint to absent from distal third (Fig. 175–177); palpal segment 3 with distinct round sensory pit ≤0.5 width of segment; hind tibial comb with five spines .. ***C.* (*Avaritia* Fox) 21**

— Wing pattern of pale spots extensive into apex (Fig. 178–186); palpal segment 3 with scattered sensilla or broad shallow pit >0.5 width of segment; hind tibial comb with six or seven spines (Fig. 286) .... ***C.* (*Silvicola* Mirzaeva and Isaev) 24**

21(20). Wing length usually <0.9 mm; pale spot overlapping only distal tip of r_2 (Fig. 175); five or six scutellar setae; SCo pattern 1, (9), 10–13; known from deserts of Southern California and Baja California .... ***C.* (*Avaritia*) *boydi* Wirth and Mullens**

— Wing length usually >0.9 mm; pale spot overlapping distal half of r_2 (Fig. 176, 177); four scutellar setae; SCo pattern 1, 9–13; rare or absent from arid warm areas of southwestern North America ... **22**

22(21). Length of palpal segment 3 <1.5× that of palpal segment 5; mandible with 6–10 teeth; proboscis ratio <0.75 .... ***C.* (*Avaritia*) *chiopterus* (Meigen)**

— Length of palpal segment 3 >1.5× that of palpal segment 5; mandible with 11–17 teeth; proboscis ratio >0.75 . . . . . . **23**

23(22). Vein CuA$_1$ with 7–14 macrotrichia; cell cua$_1$ with >4 macrotrichia, including those near the margin . . . . . . ***C.*** **(*Avaritia*) *obsoletus* (Meigen)**

— Vein CuA$_1$ with 1–6 macrotrichia; cell cua$_1$ with <4 macrotrichia, including those near the margin . . . . . . ***C.*** **(*Avaritia*) *sanguisuga* (Coquillett)**

24(20). Eyes separated by >1 ommatidium diameter; palpal ratio >3.5; coastal tidelands . . . . . . ***C.*** **(*Silvicola*) *tristriatulus* Hoffman**

— Eyes contiguous; palpal ratio <3.5; inland **25**

25(24). Hind tarsomeres with apical spines (Fig. 282) **26**

— Hind tarsomeres without apical spines **30**

26(25). Palpal segment 3 with scattered sensilla instead of pit (Fig. 245) **27**

— Palpal segment 3 with regular roundish pit (as in Fig. 242 *C. lahontan*) or irregular subdivided pit (Fig. 246) **29**

27(26). Distal wing pattern faint (Fig. 182); eyes contiguous for >0.3 ommatidium diameter; SCo on some of flagellomeres 2–8 . . . . . . ***C.*** **(*Silvicola*) *neomontanus* Wirth**

— Distal wing pattern relatively distinct (Fig. 178, 184); eyes contiguous for <0.3 ommatidium diameter (Fig. 287); SCo rarely on any of flagellomeres 2–8 . . . . . . **28**

28(27). Hind tibiae with distinct basal pale band ~2× longer than wide (Fig. 286) . . . . . . ***C.*** **(*Silvicola*) *sierrensis* Wirth and Blanton**

— Hind tibiae without basal pale band, sometimes with indistinctly pale base . . . . . . ***C.*** **(*Silvicola*) *cockerellii* (Coquillett)**

29(26). SCo pattern 1, (5), (6), 7, (8), 9–13; sensory pit on palpal segment 3 irregular, subdivided (Fig. 246) . . . . . . ***C.*** **(*Silvicola*) species D**

— SCo pattern 1, 9–13; sensory pit on palpal segment 3 regular roundish (as in Fig. 242 *C. lahontan*) . . . . . . ***C.*** **(*Silvicola*) species E**

30(25). Fore tarsomeres 1 or 2 with apical spines (as in Fig. 285 *C. calexicanus*); distal hourglass-shaped dark spot in r$_3$ with narrow waist (Fig. 179) . . . . . . ***C.*** **(*Silvicola*) *freeborni* Wirth and Blanton**

— Fore tarsomeres without apical spines; distal hourglass-shaped dark spot in r$_3$ with wider waist (Fig. 180, 181, 183) **31**

31(30). Palpal segment 3 with patch of scattered sensilla instead of pit; known only from the low southern deserts of California and Nevada . . . . . . ***C.*** **(*Silvicola*) *saltonensis* Wirth**

— Palpal segment 3 with distinct wide sensory pit, sometimes irregular with scattered sensilla (Fig. 242, 244); more widespread **32**

32(31). Hind tibiae with basal pale band; distal pale wing spots with sharply defined borders (Fig. 181); palpal segment 3 ratio ~2.8, with irregular pit and sometimes scattered sensilla (Fig. 244) . . . . . . ***C.*** **(*Silvicola*) *neofagineus* Wirth and Blanton**

— Hind tibiae without pale band; distal pale wing spots with indistinct borders (Fig. 180); palpal segment 3 ratio ~2.1, with distinct wide sensory pit (Fig. 242) . . ***C.*** **(*Silvicola*) *lahontan* Wirth and Blanton**

33(19). Hind tibial comb with five or six spines; hind tibia with prominent subapical pale band; wing pattern prominent with distal pale spots in r$_3$, m$_1$, m$_2$; distal spot in r$_3$ irregular C-shaped or 8-shaped centered in distal half of cell, sometimes extending along wing margin into apex of cell to form an arch (Fig. 187–193); pit in palpal segment 3 not broadening internally (Fig. 247) **34**

— Hind tibial comb with four (occasionally five) spines; if comb with five spines, then distal pale spot in r$_3$ regular ovoid (Fig. 211, 212, 225, 228) or absent (Fig. 227, 231–239) or hind tibia without prominent subapical pale band; if hind tibia with pale band or distal pale spot in r$_3$ irregular (Fig. 197, 202), then comb with four spines or pit in palpal segment 3 broadening internally to ~2× diameter of pore (Fig. 248) **39**

34(33). SCo pattern 1, (3), (4), (5), 6–8; M_1 and M_2 dark, not straddled by distinct pale spots (Fig. 187–189) . . . . **C. (*Haematomyidium* Goeldi) 35**

— SCo pattern 1, (2), 3, (4), 5, (6), 7, 9–13; isolated pale spots straddling at 0.2–0.3 on M_1, 0.4–0.5 on M_2 (Fig. 190–193) . . . . **C. (*Amossovia* Glukhova) 36**

35(34). Two pale spots in m_1, distal-most not at wing margin (Fig. 187, 188); SCo pattern 1, (4), 5–8 . . . . **C. (*Haematomyidium*) *kettlei* Breidenbaugh and Mullens**

— Three pale spots in m_1, distal-most at wing margin, sometimes conjoined narrowly with second back along posterior margin of cell to form a U (Fig. 189); SCo pattern 1, (3), (4), (5), 6–8 . . . . **C. (*Haematomyidium*) *stellifer* (Coquillett)**

36(34). Yellowish coppery-brown; fore and mid tibiae with subapical pale band . . . . **C. (*Amossovia*) *californiensis* Wirth and Blanton**

— Dark brown; fore and mid tibiae without subapical pale bands **37**

37(36). M_1, M_2 barely pale at wing margin (Fig. 191); SCo pattern 1–7, 9–13; hind femora without pale bands . . . . **C. (*Amossovia*) *cochisensis* Wirth and Blanton**

— M_1, M_2 broadly pale at wing margin (Fig. 192, 193); SCo often absent from flagellomeres 2, 4, 6; hind femora with pale bands **38**

38(37). SCo pattern 1, (2), 3, (4), 5, (6), 7, 9–13; proboscis ratio ~1.0; 14–20 mandibular teeth; ~22 scutellar setae . . . . **C. (*Amossovia*) *pecosensis* Wirth**

— SCo pattern 1, 3, 5, 7, 9–13; proboscis ratio ~0.8; 11–14 mandibular teeth; ~16 scutellar setae . . . . **C. (*Amossovia*) *oklahomensis* Khalaf**

39(33). Distal pale spot in r_3 irregular: bilobed, 8-shaped, C-shaped, or quadrate, centered in distal half of cell, sometimes with additional tiny pale spot in apex of cell; pale spot straddling at ~0.5 on M_2 (Fig. 194–203, 208–210) **40**

— Distal pale spot in r_3 simple, single, convex, ovoid, diffuse, faint, or absent; not bilobed, medially constricted, or divided (Fig. 204–207, 211–240); pale spot often absent from M_2 . . . . **50**

40(39). SCo absent from 10–13; at least midportion of CuA_1 within pale area (Fig. 194, 208–210), often entire CuA_2 within pale stripe (Fig. 194); pit in palpal segment 3 not broadening internally **41**

— SCo present on 10–13; CuA_1 and CuA_2 nearly to entirely dark (Fig. 195–203); pit in palpal segment 3 broadening internally to ~2× diameter of pore (Fig. 248) **42**

41(40). CuA_2 entirely within a pale stripe; pale spots relatively small and isolated (Fig. 194); 11–13 scutellar setae . . . . **C. (*Diphaomyia*) *bergi* Cochrane**

— CuA_2 entirely dark; pale spots relatively large and somewhat interconnected (Fig. 208–210); 6–8 scutellar setae . . . . **(Mohave group) *C. mohave* Wirth (part)**

42(40). Sclerotized ring absent from spermathecal duct; either SCo absent from flagellomeres 2–8 or small third distal pale spot in apex of r_3 (Fig. 196) **43**

— Sclerotized ring present on spermathecal duct; SCo on some of flagellomeres 2–8; no pale spot in apex of r_3 (Fig. 197–203) . . . . **C. (*Drymodesmyia* Vargas) (part) 44**

43(42). Distal pale spot in m_1 not extending to wing margin (Fig. 195); SCo pattern 1, 9–13 . . . . **(Daedalus group) *C. daedalus* Macfie**

— Distal pale spot in m_1 at wing margin (Fig. 196); SCo pattern 1, (2), 3, (4), 5, (6), 7, 9–13 . . . . **(Daedalus group) *C. pampoikilus* Macfie**

44(42). Two distinct pale spots in distal half of anal cell (Fig. 197, 198, 201, 202); spermathecae saclike with broad neckless opening ~0.3 width of spermatheca (Fig. 255–257) or subspherical with narrow sclerotized neck as long as wide (Fig. 259) **45**

— One distinct pale spot in distal half of anal cell, not reaching wing margin (Fig. 199, 200, 203); spermathecae subspherical with narrow neckless opening <0.2 width of spermatheca (Fig. 258) **48**

45(44). Spermathecae subspherical to slightly pyriform, with sclerotized necks reducing to <0.2 width of spermatheca (Fig. 259) . . . . **C. (*Drymodesmyia*) *bakeri* Vargas**

— Spermathecae pyriform to elongate saclike, opening ~0.3 width of spermatheca, without sclerotized necks (Fig. 255–257) **46**

46(45). Spermathecae <1.5× longer than wide (Fig. 255); antennal ratio >1.1, combined distal five flagellomeres (including intersegmental spaces) longer than combined proximal eight; wing length >1.3 mm . . . . ***C.* (*Drymodesmyia*) *sitiens* Wirth and Hubert**

— Spermathecae >1.5× longer than wide (Fig. 256, 257); antennal ratio ~1.0, combined distal five flagellomeres (including intersegmental spaces) shorter than combined proximal eight; wing length <1.3 mm **47**

47(46). Spermathecae <2× longer than wide (Fig. 256) . . . . ***C.* (*Drymodesmyia*) *jonesi* Wirth and Hubert**

— Spermathecae >2× longer than wide (Fig. 257) . . . . . . ***C.* (*Drymodesmyia*) *butleri* Wirth and Hubert**

48(44). Apices of M_1, M_2, CuA_1 dark; anterior distal pale spot in r_3 usually attenuated; pale spot at ~0.3 of M_1 sometimes reduced to only touching anterior side of (not straddling) vein (Fig. 200); pale bands absent from mid femora apically, hind femora entirely . . . . ***C.* (*Drymodesmyia*) *insolatus* Wirth and Hubert (part)**

— Apices of M_1, M_2, sometimes CuA_1 pale; anterior distal pale spot in r_3 distinct and separate from or conjoined with posterior spot; pale spot at ~0.3 of M_1 straddling vein (Fig. 199, 203); faint pale bands apical on mid femora, basal on hind femora **49**

49(48). Distal pale spot in r_3 not divided into two separate spots (Fig. 199) . . . . ***C.* (*Drymodesmyia*) *cacticola* Wirth and Hubert**

— Distal pale spot in r_3 distinctly divided into two separate spots (Fig. 203) . . . . ***C.* (*Drymodesmyia*) *torridus* Wirth and Hubert**

50(39). Distal half of r_3 dark except for small distinct pale spot entirely within distal 0.2 of cell; distinct isolated pale spots straddling at ~0.3 on M_1 and ~0.5 on M_2 (Fig. 204, 205) **51**

— Distal pale spot in r_3 central in distal half or filling most of distal third, but may be faint or absent (Fig. 206–240); pale spots often absent from M_1 or M_2 . . . . **52**

51(50). SCo pattern 1, (5), (7), (8), 9–13; antennal ratio <1.4; distal pale spots in r_3, m_1 usually not touching wing margin (Fig. 204) . . . . ***C.* (*Diphaomyia*) *defoliarti* Atchley and Wirth**

— SCo pattern 1, 3, (4), 5, (6), 7–13; antennal ratio >1.4; distal pale spots in r_3, m_1 usually at wing margin (Fig. 205) . . . . ***C.* (*Diphaomyia*) *haematopotus* Malloch**

52(50). SCo absent from at least 10–13; sclerotized spermathecal necks 2–3× longer than wide (Fig. 269, or as in Fig. 268 *C. haematopotus*) **53**

— SCo present on at least 11–13; sclerotized spermathecal necks absent to about as long as wide (Fig. 260–266, 270–278) **57**

53(52). Prominent subapical pale band on all femora; distal pale spot pattern distinct (Fig. 206) . . . . **(Limai group) *C. luglani* Jones and Wirth**

— Subapical pale bands absent from mid and hind femora, at most faint on fore femora; distal pale spot pattern more diffuse or absent (Fig. 207, 211–213) **54**

54(53). Distal pale spot in r_3 present but not filling into apical 0.2 of cell (Fig. 207); eyes separated >0.4 ommatidium diameter; SCo pattern 1, (4), (5), 6–8 . . . . **55**

— Either distal pale spot in r_3 extending into apex of cell (Fig. 211, 212) or absent (Fig. 213); eyes contiguous to separated <0.4 ommatidium diameter; SCo pattern 1, (2), 3–8, (9) **56**

55(54). Eyes narrowly separated ~0.5 ommatidium diameter; palpal ratio 2.1; inland . . . . **(Mohave group) *C. mohave* Wirth (part)**

— Eyes widely separated ~2 ommatidium diameters; palpal ratio 2.5; coastal . . . . **(Mohave group) *C. hoguei* Wirth and Moraes**

56(54). Indistinct distal pale spots extensive into r_3, m_1, m_2 (Fig. 211, 212) . . . . ***C.* (*Diphaomyia*) *inyoensis* Wirth and Blanton**

— Distal pale spots absent from r_3, m_1, m_2 (Fig. 213) . . . . ***C.* (*Diphaomyia*) *salihi* Khalaf**

57(52). Hind tibial comb with five spines; SCo pattern 1–5, 7, 9–13; distal pale spots faint or absent from r_3, m_1, m_2; pale spots absent from M_1, M_2; palpal segment 3 fusiform, with a deep sensory pit 0.4 as wide as segment (similar to pit in Fig. 249 *C. hinmani*) ...... **(unplaced) *C. nanellus* Wirth and Blanton**

— Hind tibial comb often with four spines; SCo patterns from 1, 11–13 to 1–13, not 1–5, 7, 9–13; distal pale spots often distinct in r_3, m_1, m_2; pale spots often straddling M_1, M_2; palpal sensory pit often more broad than deep, wider than 0.5 diameter of segment (as in Fig. 242, 247, 251) **58**

58(57). Palpal segment 3 sensory pit widening internally, distinctly wider and deeper than pore diameter; pore diameter <0.4 the diameter of segment (Fig. 249, or similar to 248 *C. sitiens*); distal pale spots present in r_3, m_1, m_2 (Fig. 200, 214–220); hind tibial comb with four spines; SCo often absent from flagellomeres 2–8; pale spot at tip of costa bi-lobed, often extending back beneath r_2 (Fig. 200, 215–220); if distal pale spot in anal cell double then no pale spots straddling M_1 or M_2 (Fig. 214, 216) .... **C. (*Drymodesmyia* Vargas) (part) 59**

— Palpal segment 3 sensory pit not or slightly widening internally; pore diameter >0.5 the diameter of segment (as in Fig. 242, 244, 251); distal pale spots often absent from r_3, m_1, m_2; hind tibial comb sometimes with five spines; if SCo absent from flagellomeres 2–8, then no distal pale spots in r_3, m_1, m_2; pale spot at tip of costa often ovoid, not distinctly extending back beneath r_2; if distal pale spot in anal cell double, then distinct pale spots straddling M_1 and M_2 (Fig. 229, 230) **64**

59(58). SCo on some of flagellomeres 2–7 .... **60**

— SCo absent from flagellomeres 2–7 .... **62**

60(59). Pale spot at tip of costa not bent back under r_2 (Fig. 214); SCo pattern 1, 3, 5, 7, 9–13 .... ***C.* (*Drymodesmyia*) *byersi* Atchley**

— Pale spot at tip of costa bent back under entire r_2 (Fig. 200, 215); SCo pattern 1–3, (4), (5), (6), (7), 9–13 .... **61**

61(60). Spermathecal ratio ~1.5; SCo pattern 1–3, (4), (5), 9–13; pale spot at ~0.3 of M_1 straddling vein (Fig. 215) .... ***C.* (*Drymodesmyia*) *arizonensis* Wirth and Hubert**

— Spermathecal ratio ~1.2; SCo pattern 1–5, (6), (7), 9–13; pale spot at ~0.3 of M_1 sometimes reduced to only touching anterior side of (not straddling) vein (Fig. 200) ....***C.* (*Drymodesmyia*) *insolatus* Wirth and Hubert (part)**

62(59). Yellow (in alcohol); distal pale spot in anal cell double, reaching wing margin; no pale spots straddling M_1 or M_2 (Fig. 216); eyes contiguous; sensory pit on palpal segment 3 little widening internally (Fig. 249); pale leg-banding basal and subapical on mid and hind femora, subapical on hind tibiae (Fig. 250); dendrophilic .... ***C.* (*Drymodesmyia*) *hinmani* Khalaf**

— Pale brown (in alcohol); distal pale spot in anal cell single, not reaching wing margin; pale spots straddling M_2, often M_1 (Fig. 217–220); eyes separated; sensory pit on palpal segment 3 greatly widening internally (as in Fig. 248 *C. sitiens*); pale leg-banding reduced: absent from mid and hind femora, subapically from hind tibiae (as in Fig. 250 *C. byersi*); cactiphilic **63**

63(62). Spermathecae unequal by ~1.2×, pyriform, largest is larger than flagellomere 1 (Fig. 260, 261); distal pale spot in r_3 circular to ovoid, 1–1.5× longer than wide (Fig. 217, 218); SCo on flagellomeres 9–10 .... ***C.* (*Drymodesmyia*) *copiosus* Root and Hoffman**

— Spermathecae subequal, subspherical, smaller than flagellomere 1 (Fig. 262); distal pale spot in r_3 elongate parallel with M_1, ~2× longer than wide (Fig. 219, 220); SCo often absent from flagellomeres 9–10 .... ***C.* (*Drymodesmyia*) *ryckmani* Wirth and Hubert**

64(58). Fore tarsomeres and often hind tarsomeres with apical spines (Fig. 283–285) (uncertain for *C. novamexicanus* and *C. oregonensis*); eyes separated >1 ommatidium diameter (except for species F); no pale spot straddling midportion of M_1 (except for species F); SCo on at least flagellomeres 1, 3, 5, 7, 9, 11–13 .... **65**

— Fore tarsomeres and hind tarsomeres without apical spines (except for hind tarsomere spines on *C. usingeri*); eyes contiguous to separated <1 ommatidium diameter (except for *C. cavaticus* and *C. posoensis*);

pale spot often straddling at ~0.5 on M$_1$; SCo often absent from some of flagellomeres 3, 5, 7, or 9 ... **73**

65(64). Eyes separated ~0.5 ommatidium diameter; isolated pale spots straddling at ~0.3 on M$_1$ and ~0.5 on M$_2$ (Fig. 226) ... **(unplaced) species F**

— Eyes widely separated >1 ommatidium diameter; no isolated pale spots straddling M$_1$; if pale spot apparently straddling M$_2$, then contiguous with larger proximal pale area in m$_2$ (Fig. 222–225) ... **66**

66(65). Mandible with eight teeth (Fig. 254); hind tarsomeres without apical spines ... **(Palmerae group) species C**

— Mandible with 13–16 teeth; hind tarsomeres often with apical spines (as in Fig. 283 male) ... **67**

67(66). Spermathecal ratio ≥1.3; sclerotized ring on spermathecal duct (Fig. 276); antennal ratio >1.4; distal pale spots faint in r$_3$, m$_1$, m$_2$, or absent (Fig. 224) ... **(Palmerae group) *C. hawsi* Wirth and Rowley**

— Spermathecae subequal (Fig. 275, 277); sclerotized ring often absent; antennal ratio <1.4; distal pale spots often more distinct in r$_3$, m$_1$, m$_2$ (Fig. 223, 225, or as in Fig. 147 male) ... **68**

68(67). SCo pattern 1–13; spermathecae without sclerotized necks (Fig. 277) ... **69**

— SCo often absent from some of flagellomeres 2, 4, 6, 8, 10; spermathecae with short, sclerotized necks (Fig. 275) ... **70**

69(68). Wing with distal pale spots in r$_3$, m$_1$, m$_2$, cua$_1$ ... **(Palmerae group) *C. palmerae* James**

— Wing without distal pale spots ... **(Palmerae group) *C. oregonensis* Wirth and Rowley**

70(68). SCo pattern 1–5, (6), 7, (8), 9–13; scutellum about same brown as scutum (Fig. 221) ... **71**

— SCo pattern 1, (2), 3, (4), 5, 7, 9, (10), 11–13; scutellum often lighter and more yellowish than scutum (Fig. 221) ... **72**

71(70). Wing with extensive pale spots, but often faint on distal half (as in Fig. 147 male); SCo often absent from 6, 8, 10 ... **(Palmerae group) *C. utahensis* Fox**

— Wing pattern greatly reduced to pale spots only at tip of costa and on r-m crossvein; SCo pattern 1–13 ... **(Palmerae group) *C. leechi* Wirth**

72(70). Proboscis ratio <0.8; SCo pattern 1, 3, 5, 7, 9, 11–13 ... **(Palmerae group) *C. calexicanus* Wirth and Rowley**

— Proboscis ratio >0.9; SCo pattern 1, (2), 3, (4), 5, 7, 9, (10), 11–13 ... **(Palmerae group) *C. novamexicanus* Atchley**

73(64). Eyes contiguous; SCo pattern 1, 11–13; apex of labrum with small distinct median lightly sclerotized grayish tonguelike projection (Fig. 279); 11 or fewer mandibular teeth; hind tibial comb with five spines; pale bands absent from all tibiae, apically from all femora; wing with only proximal pale spots (Fig. 227), no distal pale spots in r$_3$, m$_1$, m$_2$, cua$_1$, or anal cell ... **(Piliferus group) *C. unicolor* (Coquillett)**

— Eyes separated; SCo usually on at least some of flagellomeres 2–10; labral projection absent; 11 or more mandibular teeth; hind tibial comb often with four spines; pale bands on at least fore femora or basally on tibiae; distal pale spots distinct to faint in cua$_1$, anal cell, often in r$_3$, m$_1$, m$_2$ (Fig. 228–240) ... **74**

74(73). Distinct pale spots distal in r$_3$, m$_1$, m$_2$, straddling at ~0.3 on M$_1$ and ~0.5 on M$_2$ (Fig. 228–230) ... **75**

— Distal pale spots faint or absent from r$_3$, m$_1$, m$_2$; spots faint or absent from M$_1$, M$_2$ (Fig. 231–240) ... **77**

75(74). SCo pattern 1–13; antennal ratio 1.0; scutellum with 26–30 setae; spermathecal ratio ~1.1 (Fig. 263) ... **(Piliferus group) *C. cavaticus* Wirth and Jones**

— SCo pattern 1, 3, (5), (7), (9), (10), 11–13; antennal ratio >1.2; scutellum with 8–12 setae; spermathecal ratio 1.3–1.4 (Fig. 264) ... **76**

76(75). Eyes separated <1.0 ommatidium diameter; SCo pattern 1, 3, 5, 7, (9), (10), 11–13 ... **(Piliferus group) *C. doeringae* Atchley**

— Eyes separated >1.0 ommatidium diameter; SCo pattern 1, 3, (5), (7), 11–13 . . . . **(Piliferus group) *C. lophortygis* Atchley and Wirth**

77(74). SCo always absent from some of flagellomeres 2–10 from both antennae, never forming a 1, 3, 5, 7 SCo pattern; antennal ratio <1.3; spermathecae subequal, necks as long as wide (Fig. 270, 271); sclerotized ring often absent from spermathecal duct; pale spots never straddling M_1 or M_2 (Fig. 236–240) **78**

— SCo pattern 1–13 or 1, 3, 5, 7, (8), (9), (10), 11–13, rarely also with SCo also on 2, 4, or 6 of one antenna; antennal ratio >1.2; spermathecae subequal to unequal by 1.6×, necks absent to half as long as wide (Fig. 265, 266, 273, 274); sclerotized ring on spermathecal duct; faint pale spots often straddling at ~0.3 on M_1 and ~0.5 on M_2 (Fig. 233–235) **82**

78(77). Eyes widely separated ~2 ommatidium diameters; SCo pattern 1, 9–13; pale spots only at tip of costa and over r-m crossvein (Fig. 236); sclerotized ring on spermathecal duct (Fig. 272) . . . . **(unplaced) *C. posoensis* Wirth and Blanton**

— Eyes separated ≤1 ommatidium diameter; SCo often on some of flagellomeres 2–8; pale spots often distally in cua_1 and anal cell, basally in m_1, m_2, anal cell (Fig. 237–240); ring often absent **79**

79(78). Distal pale spots present in cua_1, anal cell, often m_2 (Fig. 237); eyes narrowly separated ~0.2 ommatidium diameter . . . . **C. (*Silvaticulicoides*) *sublettei* Atchley**

— Distal pale spots absent (Fig. 238–240); eyes moderately separated ≥0.4 ommatidium diameter . . . **80**

80(79). SCo on 1, 6, 8–13, often others; antennal ratio >1.15; pale bands basal on all tibiae, apical on fore tibiae; sclerotized ring on spermathecal duct (Fig. 271) . . . . **C. (*Diphaomyia*) *erikae* Atchley and Wirth**

— SCo absent from some or all of 2–10; antennal ratio <1.15; pale bands often absent from tibiae; sclerotized ring often absent from spermathecal duct (Fig. 270) **81**

81(80). SCo pattern 1, (5), (6), (7), (8), 9–13; proboscis ratio <0.9; hind tarsomeres with apical spines on the specimen examined (as in Fig. 283 *C. palmerae*) . . . . **C. (*Silvaticulicoides*) *usingeri* Wirth**

— SCo pattern 1, (9), (10), 11–13; proboscis ratio >0.9; hind tarsomeres without apical spines . . . . **C. (*Silvaticulicoides*) *vetustus* Breidenbaugh and Mullens**

82(77). SCo pattern 1–13; no pale spots straddling M_1 or M_2 (Fig. 231, 232); spermathecal ratio <1.2 (Fig. 273, 274) . . . . **C. (*Sensiculicoides* Shevchenko) 83**

— SCo pattern 1, 3, 5, 7, (9), (10), 11–13, rarely also with SCo on 2, 4, or 6 of one antenna; faint pale spots straddling at ~0.3 on M_1 and ~0.5 on M_2 (Fig. 233–235); spermathecal ratio >1.2 (Fig. 265, 266) **84**

83(82). Spermathecae subequal (Fig. 273) . . . . **C. (*Sensiculicoides*) *kibunensis* Tokunaga**

— Spermathecal ratio ~1.2 (Fig. 274) . . . . **C. (*Sensiculicoides*) *travisi* Vargas**

84(82). SCo pattern 1, 3, 5, 7–13, occasionally also with SCo on 2, 4, or 6 of one antenna; eyes separated <0.2 ommatidium diameter . . . . **(Piliferus group) species B**

— SCo pattern 1, 3, 5, 7, (9), (10), 11–13; eyes separated ≥0.5 ommatidium diameter **85**

85(84). Dark brown; combined length of flagellomeres 7+8 greater than 9, antennal ratio <1.45; proboscis ratio <0.70 . . . . **(Piliferus group) C. chewaclae Glick and Mullen**

— Pale yellowish brown; combined length of flagellomeres 7+8 less than 9, antennal ratio >1.45; proboscis ratio >0.70 . . . . **(Piliferus group) species A**

Systematics of *Culicoides*

Diptera: Ceratopogonidae
Subfamily Ceratopogoninae
Tribe Culicoidini

Genus *Culicoides* Latreille, 1809: 251 (p. 232 in translation)

(Synonyms of genus *Culicoides* are in Borkent and Dominiak 2020: 102.)

Subgenus *Amossovia* Glukhova

Culicoides (*Amossovia*) *californiensis* Wirth and Blanton

(Fig. 100. 154, 190, 247, 291)

Culicoides californiensis Wirth and Blanton, 1967: 215 (key; female, male, pupa; fig. female wing, antenna, palpus, eye separation, spermathecae, leg, pupal respiratory trumpet, male genitalia, parameres; California). Wirth et al. 1985: 20 (numerical characters; fig. female wing). Murphree and Mullen 1991: 329 (key; larva; numerical characters; fig. mandible, epipharynx).

Culicoides (*Amossovia*) *californiensis*: Borkent and Grogan 2009: 12 (in Nearctic catalog).

Diagnosis. (Tables 14, 15) Yellowish coppery-brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 medially constricted and roughly 8-shaped; pale spots straddling at ~0.25 on M_1 and ~0.4 on M_2; CuA_1 and CuA_2 within dark areas except at tip of CuA_1; pore of sensory pit on palpal segment 3 >0.5 the diameter of segment; prominent pale bands basal and subapical on all femora and tibiae; ventral apodeme of gonocoxite simple; aedeagus nearly V-shaped, median process broad triangular with lateral caudally directed spines on midsection, tapering to small blunt tip; parameres separate, apices simple, thick bladelike, pointed.

Distribution. California, Arizona, Utah (Grand County).

Larval ecology and adult behavior. *Culicoides californiensis* has been reared from cottonwood treeholes (Wirth and Blanton 1967), and the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood. Furthermore, though its larval habitat is arboreal, its frequent collection in low-level CO_2-baited traps (Table 4) suggests it is a mammalophilic, ground-dwelling bird, or generalist feeder.

Atypical biology. Of thirteen females and seven males that were slide-mounted, one male has an irregularly disseminated granular infuscation through the thorax and abdomen—possibly by an infection (Fig. 291, Table 11); and two have a third ovoid spermatheca, 0.4 as large as the others, instead of a shriveled vestigial third (Table 12).

Culicoides (*Amossovia*) *cochisensis* Wirth and Blanton

(Fig. 101, 155, 191)

Culicoides cochisensis Wirth and Blanton, 1967: 218 (key; female, male, pupa; fig. female antenna, wing, eye separation, spermathecae, leg, palpus, male genitalia, parameres; Arizona; paratype records show *Culicoides villosipennis* Root and Hoffman record for Utah was a misidentification). Wirth et al. 1985: 20 (numerical characters; fig. female wing). Wirth et al. 1988: 30 (numerical characters; fig. female wing). Murphree and Mullen 1991: 330 (key; larva; numerical characters; fig. epipharynx, mandible, hypostoma, caudal segment).

Culicoides (*Amossovia*) *cochisensis*: Borkent and Spinelli 2000: 27 (in Neotropical catalog).

Culicoides villosipennis Root and Hoffman, misidentified: Bullock 1952: 24 (misspelled as "villosopennis"; key; female [male description invalid]; Utah: Salt Lake County). Rees and Bullock 1954 (misspelled as "villosopennis"; Utah: Salt Lake County).

Diagnosis. (Tables 14, 15) Dark brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 medially constricted and roughly C-shaped; pale spots straddling at ~0.2 on M_1 and ~0.4 on M_2; CuA_1 and CuA_2 within dark areas except at tip of CuA_1; pore of sensory pit on palpal segment 3 >0.5 the diameter of segment (as in Fig. 247 *C. californiensis*); pale band subapical on hind tibiae, absent from hind femora and subapically from fore and mid tibiae; ventral apodeme of gonocoxite simple; aedeagus Y-shaped, median process slender to pointed tip; parameres separate, apices simple, pointed.

Distribution. California, Utah (Salt Lake City), Arizona, Baja California. The only Utah record is of a female collected at a window in Salt Lake City 14 September 1952 (Bullock 1952). The other collection records are from the Sonoran Desert; hence, it is likely not resident in Utah, and the record is of a transient.

Larval ecology and adult behavior. *Culicoides cochisensis* larvae have been collected from water in a pocket of a saguaro cactus (*Carnegiea gigantea* [Engelmann] Britton and Rose, Cactaceae) (Wirth and Blanton 1967). However, its adult hosts are unknown, though the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Culicoides (*Amossovia*) *oklahomensis* Khalaf

(Fig. 102, 156, 192)

Culicoides villosipennis oklahomensis Khalaf, 1952a: 355 (male; Oklahoma).

Culicoides (*Oecacta*) *villosipennis oklahomensis*: Khalaf 1954: 37 (assignment to subgenus *Oecacta* Poey). Fox 1955: 260 (key and diagnoses of subgenera; species key; taxonomy). Khalaf 1957: 212 (diagnosis; key; biology).

Culicoides (*Oecacta*) *oklahomensis*: Jones and Wirth 1958: 82 (status; diagnosis; key). Atchley 1967: 1006 (key; female; male genitalia; fig. female wing, palpus, male genitalia, parameres).

Culicoides oklahomensis: Wirth and Blanton 1967: 223 (rejection of placement in subgenus *Oecacta*; key; female, male; fig. female antenna, wing, palpus, leg, eye separation, spermathecae, male genitalia, parameres). Childers and Wingo 1968: 16 (key; fig. female wing, spermathecae). Khalaf 1969: 1160 (diagnosis). Wirth et al. 1985: 20 (numerical characters; fig. female wing). Wirth et al. 1988: 30 (numerical characters; fig. female wing). Murphree and Mullen 1991: 334 (key; larva; numerical characters; fig. epipharynx, hypostoma, mandible, caudal segment). Lamberson et al. 1992: 116 (key; pupa; fig. respiratory trumpet, operculum, abdominal segment 9, dorsal tubercles, abdominal chaetotaxy).

Culicoides (*Amossovia*) *oklahomensis*: Borkent and Spinelli 2000: 27 (in Neotropical catalog).

Culicoides arboricola Root and Hoffman, misidentified: Wirth and Bottimer 1956: 261 (in part; biology).

Diagnosis. (Tables 14, 15) Brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 medially constricted and roughly 8-shaped; pale spots straddling at ~0.25 on M_1 and ~0.4 on M_2; CuA fork and CuA_1 and CuA_2 dark except at tips; pore of sensory pit on palpal segment 3 >0.5 the diameter of segment (as in Fig. 247 *C. californiensis*); pale band subapical on hind tibiae, absent subapically from fore and mid tibiae; ventral apodeme of gonocoxite simple; aedeagus Y-shaped, median process narrow, pointed, with lateral pair of subapical filaments; parameres separate, apices simple, thick bladelike, pointed.

Distribution. California, Arizona, New Mexico, Texas, Oklahoma, Missouri (Childers and Wingo 1968), Arkansas, Louisiana, Mississippi, Alabama (Vigil et al. 2014), Baja California, Sonora, Guatemala.

Larval ecology and adult behavior. Wirth and Bottimer (1956, misidentified as *C. arboricola*) and Jones (1961b) collected immatures from oak stump holes in Texas, and Lamberson et al. (1992) collected pupae from treeholes in Texas. However, its adult hosts are unknown, though the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Culicoides (*Amossovia*) *pecosensis* Wirth

(Fig. 193)

Culicoides pecosensis Wirth, 1955: 358 (female; male genitalia; fig. female wing, mesonotum, palpus, male genitalia, parameres; Texas). Jones and Wirth 1958: 84 (key; diagnosis). Wirth and Blanton 1967: 228 (key; female; male genitalia; fig. female antenna, wing, palpus, eye separation, spermathecae, leg, male genitalia, parameres; rejection of placement in subgenus *Oecacta*). Wirth et al. 1985: 20 (numerical characters; fig. female wing).

Culicoides (*Glaphiromyia*) *pecosensis*: Vargas 1960: 41 (assignment to subgenus *Glaphiromyia* Vargas).

Culicoides (*Oecacta*) *pecosensis*: Wirth 1965: 130 (placement in subgenus *Oecacta*). Atchley 1967: 1004 (key; female; male genitalia; fig. female wing, palpus, tibial comb, spermathecae, male genitalia, parameres).

Culicoides (*Amossovia*) *pecosensis*: Borkent and Grogan 2009: 12 (in Nearctic catalog).

Diagnosis. (Tables 14, 15) Brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 medially constricted and roughly 8-shaped; pale spots straddling at ~0.3 on M_1 and ~0.5 on M_2; CuA fork and CuA_1 and CuA_2 dark except at tips; pore of sensory pit on palpal segment 3 >0.5 the diameter of segment (as in Fig. 247 *C. californiensis*); pale band subapical on hind tibiae; ventral apodeme of gonocoxite simple; aedeagus Y-shaped, median process narrow, parallel-sided, truncate; parameres separate, apices simple, thick bladelike, pointed.

Distribution. New Mexico, Texas.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; however, its hosts are unknown.

Subgenus *Avaritia* Fox

***Culicoides* (*Avaritia*) *boydi* Wirth and Mullens**

(Fig. 63, 117, 175)

Culicoides (*Avaritia*) *boydi* Wirth and Mullens, 1992: 1006 (female, male; fig. female antenna, palpus, eye separation, spermathecae, male genitalia, parameres; California). Breidenbaugh and Mullens 1999a: 851 (egg, larva, pupa; fig. egg, larval head, mouthparts, thorax, caudal segment, pupal respiratory trumpet, operculum, caudal segment, chaetotaxy). Borkent and Spinelli 2000: 28 (in Neotropical catalog).

Diagnosis. (Tables 14, 15) Wing pattern faint on distal third; pale spot over distal half of r_2; eyes contiguous, with sparse interommatidial pubescence on dorsal portions; superior transverse suture absent; palpal segment 3 with sensory pit; two ovoid subequal spermathecae, with necks and vestigial spermatheca (Wirth and Mullens [1992] describe *C. boydi* with "vestigial third spermatheca absent"; however, five of five specimens provided to me by Bradley Mullens had a fingerlike vestigial third spermatheca); posterior margin of male sternite 9 with broad caudomedian excavation; posterior margin of male tergite 9 concave with square lateral corners; ventral apodeme of gonocoxite simple, ~2× longer than dorsal apodeme, slender, 5–7× longer than basal width (original description says ventral apodeme "short and pointed" and illustrates it as about as long as basal width; however, two of two specimens from original series show otherwise); aedeagus with sclerotized membrane between arms, aedeagal ratio ~0.3, basal arms forming pointed lateral shoulders and a median sclerotized anterior-directed point at base of triangular median process; parameres separate, apices simple curved pointed.

Distribution. California, Baja California.

Adult behavior. *Culicoides boydi* has been collected biting desert bighorn sheep (*Ovis canadensis nelsoni*) and human ears (Wirth and Mullens 1992), and Mullens and Dada (1992b) found activity peaks April–June and October.

Life cycle. Parity rates of females collected in CO_2-baited traps averaged 13% (Wirth and Mullens 1992); and laboratory studies by Breidenbaugh and Mullens (1999a) found that a single wild-caught female laid 95 eggs, which hatched in 5 d at 21–25 °C. The larvae fed on the bacterial-feeding nematode *Pelodera* Schneider (Rhabditidae), and started pupating 24 d after hatch.

Symbionts. Mullens et al. (1997b) experimented with the potential biocontrol parasitic nematode, *Heleidomermis magnapapula* Poinar and Mullens (Stichosomida: Mermithidae) in the laboratory and found it readily entered, infected, developed, and emerged from and killed *C. boydi* larvae.

Remarks. Willis Wirth referred to this species as new species number 63 (Bradley Mullens, personal communication).

***Culicoides* (*Avaritia*) *chiopterus* (Meigen)**

(Fig. 64, 176)

Because the conspecificity of the Palearctic *C. chiopterus* with Nearctic *C. chiopterus* is in question (Meiswinkel et al. 2004), only the Nearctic and limited Palearctic data and references are presented.

Ceratopogon chiopterus Meigen, 1830: 263 (Europe).

Culicoides chiopterus (Meigen): Root and Hoffman 1937: 156 (key; male wing; fig. male genitalia; Maryland). Edwards et al. 1939: 45, 143 (biology; male genitalia, fig.; Britain). Foote and Pratt 1954: 18 (key; diagnosis; fig. male genitalia).

Culicoides (*Culicoides*) *chiopterus*: Khalaf 1954: 39 (assignment to subgenus *Culicoides*).

Culicoides (*Avaritia*) *chiopterus*: Fox 1955: 231 (assignment to subgenus *Avaritia*; key and diagnoses of subgenera; species diagnosis; taxonomy). Jamnback and Wirth 1963: 187 (key; female, male, pupa, larva; fig. female head, mandibular teeth, palpus, eye separation, male genitalia, male pupa, female pupa, larva). Jamnback 1965: 50 (key; female; male genitalia; pupa, larva; biology; fig. male genitalia, female wing, antenna, palpus, eye, pupa, larva). Khalaf 1969: 1160 (female, male). Jorgensen 1969: 13 (key; male genitalia; fig. male genitalia, parameres). Battle and Turner 1971: 32 (female; male genitalia; larval habitats; feeding habits; seasonal distribution; fig. female eye separation, palpus, wing, spermathecae, male genitalia, parameres). Blanton and Wirth 1979: 72 (key; numerical characters; female; male genitalia; pupa, larva; fig. female antenna, palpus, wing, eye separation, spermathecae, leg, male genitalia, parameres; larval habitat; feeding habits; seasonal distribution). Wirth et al. 1985: 12 (numerical characters; fig. female wing). Murphree and Mullen 1991: 317 (key; larva; numerical characters; fig. thorax, epipharynx, hypostoma, mandible). Borkent 2014: 24 (key to genera of pupae of Ceratopogonidae; fig. pupal dorsal apotome, respiratory organ). Mathieu et al. 2020: 10 (phylogenetic analysis of subgenus *Avaritia* showing *C. chiopterus* in Obsoletus group).

Ceratopogon amoenus Winnertz, 1852: 35 (male; fig. wing; Germany).

Culicoides dobyi Callot and Kremer, 1969: 610 (France).

Diagnosis. (Tables 14, 15) Wing pattern faint on distal third; pale spot over distal half of r_2; eyes contiguous, often with interommatidial pubescence; superior transverse suture absent; palpal segment 3 with sensory pit; two ovoid subequal spermathecae with necks and vestigial spermatheca; posterior margin of male sternite 9 with broad concave caudomedian excavation; posterior margin of male tergite 9 concave with short blunt apicolateral processes; ventral apodeme of gonocoxite simple, ~2× longer than dorsal apodeme, slender, ~7× longer than basal width; aedeagus V-shaped, with sclerotized membrane between arms and a sclerotized anterior-directed point at base of median process; aedeagal ratio ~0.4; parameres separate, apices simple curved pointed hooks.

Distribution. Holarctic, temperate North America, Eurasia. *Culicoides chiopterus* was not collected. Distribution and habitat records indicate it prefers cooler and more humid forested and agricultural environments than were sampled (Sprygin 2014). Blanton and Wirth (1979: 74) on their *C. chiopterus* distribution map show it present in every state and province north of the Mexico border, but nowhere south—a distribution I think unlikely. Furthermore, the only collection record I have found for *C. chiopterus* from western North America is a female collected 11 July 1960 in Ocean Falls, British Columbia, and misidentified as *C. obsoletus*; thus, it may not be present in the western United States.

Larval ecology. *Culicoides chiopterus* has been reared from humus polluted with chicken or horse manure (Jamnback and Wirth 1963), moist straw, and moist soil mixed with chicken manure (Jamnback 1965).

Adult behavior. Known Nearctic hosts are poultry (Humphreys and Turner 1973) and human (Blanton and Wirth 1979). Palearctic hosts include cattle (*Bos taurus* Linnaeus, Bovidae) (Ninio et al. 2011; Garros et al. 2011; Lassen et al. 2012; Elbers and Meiswinkel 2015), roe deer (*Capreolus capreolus* [Linnaeus], Cervidae) (Lassen et al. 2012), horses, and sheep (Elbers and Meiswinkel 2015). Its proclivity for bovid hosts, along with the molecular detection of bluetongue virus (BTV) in *C. chiopterus*, has implicated it as a probable vector of bluetongue virus (BTV) in Europe (Dijkstra et al. 2008; Foxi et al. 2016).

Symbionts. Möhlmann (2019) found wild-collected *C. chiopterus* in Europe to be infected with *Wolbachia*, an endosymbiont that can alter dipteran reproduction by killing male embryos, inducing gamete incompatibility, or feminizing genetic males (Stouthamer 1999).

Culicoides (*Avaritia*) *obsoletus* (Meigen)

(Fig. 65, 118, 177)

Because *C. obsoletus* (Meigen) has been recognized as a species complex and because the conspecificity of the Palearctic with the Nearctic *C. obsoletus* is in question (Meiswinkel et al. 2004), only the Nearctic and limited Palearctic data and references are presented. (However, Mathieu et al. [2020] has cast doubt on Holarctic *C. obsoletus* having cryptic species diversity.) Twenty-seven Eurasian taxonomic, descriptive, distributional, and biological references for *C. obsoletus* are listed in Arnaud 1956: 116.

Ceratopogon obsoletus Meigen, 1818: 76 (Europe). (Twelve Eurasian and African synonyms are listed in Borkent and Dominiak 2020: 105.)

Culicoides obsoletus (Meigen): Root and Hoffman 1937: 155 (in part; key; female; male genitalia; fig. male genitalia is that of *C. sanguisuga*). James 1943: 148 (seasonal distribution; Colorado). Wirth 1951: 77 (key; female; fig. wing, palpus, spermathecae). Wirth 1952a: 169 (key; female; male genitalia; fig. female wing, palpus). Rees and Bullock 1954 (Utah: Salt Lake County). Foote and Pratt 1954: 29 (in part; key; diagnoses of female, male, pupa, larva, egg; bionomics; fig. wing, mesonotum, spermathecae [fig. female palpus, male genitalia represent *C. sanguisuga*]).

Culicoides (*Culicoides*) *obsoletus*: Khalaf 1954: 39 (assignment to subgenus *Culicoides*).

Culicoides (*Avaritia*) *obsoletus*: Fox 1955: 218, 248 (subgenus *Avaritia* Fox; designated *C. obsoletus* as type species; key and diagnoses of subgenera; species diagnosis; taxonomy). Jamnback and Wirth 1963: 188 (key; female, male, pupa, larva; fig. female palpus, antenna, male genitalia, male pupa, female pupa, larva). Jamnback 1965: 84 (key; female; male genitalia; larva; biology; fig. male genitalia, female wing, antenna, palpus, eye, pupa). Atchley 1967: 969 (key; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres; biology). Childers and Wingo 1968: 16 (key; biology; fig. female wing, spermathecae). Jorgensen 1969: 20 (quantitative characters; key; female, male; seasonal distribution; fig. female antenna, palpus, spermathecae, wing, male genitalia, parameres). Battle and Turner 1971: 64 (female; male genitalia; larval habitats; feeding habits; seasonal distribution; fig. female eye separation, palpus, wing, spermathecae, male genitalia, parameres). Downes and Wirth 1981: 407 (fig. female palpus). Wirth et al. 1985: 14 (numerical characters; fig. female wing). Murphree and Mullen 1991: 318 (key; larva; numerical characters; fig. epipharynx, hypostoma, caudal segment). Mathieu et al. 2020: 10 (phylogenetic analysis of subgenus *Avaritia* found no evidence of cryptic species diversity within *C. obsoletus*).

Culicoides sp. near *obsoletus*: Bullock 1952: 16 (key; female; male genitalia; August, September; Utah: Salt Lake County). Jones 1961a: 730 (key; pupa; fig. chaetotaxy, operculum, respiratory trumpet; Wisconsin).

Diagnosis. (Tables 14, 15) Wing pattern faint on distal third; pale spot over distal half of r_2; eyes contiguous, bare; superior transverse suture absent; palpal segment 3 with sensory pit; two ovoid subequal spermathecae with necks and vestigial spermatheca; posterior margin of male sternite 9 cleft, without broad excavation; posterior margin of male tergite 9 convex, without apicolateral processes; ventral apodeme of gonocoxite simple, ~2× longer than dorsal apodeme, slender, ~7× longer than basal width; aedeagus broadly U-shaped, without sclerotized membrane between basal arms or sclerotized anterior-directed point at base of short median process; median process with bare convex tip; aedeagal ratio ~0.8; parameres separate, curved, pointed, tipped with tiny spines.

Distribution. Holarctic, Eurasia, North Africa, North America from Alaska, British Columbia, Alberta, Ontario, Quebec, south to Northern California (and into Southern California along the cooler Pacific coast), Utah (Salt Lake County), Colorado (Monarch 2021), New Mexico, Oklahoma, Tennessee, Georgia. Habitat records indicate it prefers mountain coniferous forests (Wirth 1952a; Atchley 1967; Sprygin 2014). *Culicoides obsoletus* was not collected, though seemingly suitable habitats were sampled several times in Utah, Idaho, Wyoming, Colorado, and Arizona (Tables 2, 3), suggesting it is relatively rare or in only scattered populations south of the northern coniferous forests of western North America. However, Bullock (1952) collected adults during August and September in Salt Lake County, Utah.

Larval ecology. It is likely that some of the biological accounts for Nearctic *C. obsoletus* prior to 1963 apply to *C. sanguisuga*. Reports that immatures have been collected or reared from a flowing water spring (Wirth 1952a), treeholes with decaying matter, and sandy stream banks, but mostly shaded piles of composting leaves (Murray 1957), damp terrestrial habitats, manure piles, and a mound of decomposing cornstalks (Jones 1961b) are thus suspect. Reliable records of collections or rearings of immatures include manure-polluted soil, decaying organic matter (Jamnback and Wirth 1963; Jamnback 1965), a pile of used chicken litter (Hair et al. 1966), and leaf litter in a drainage ditch (Childers and Wingo 1968). Zimmer et al. (2013) characterized its larval habitats in Belgium and found that higher lignin and insoluble fiber favored larval presence, whereas higher magnesium and calcium negatively correlated with larval presence, which might explain the absence of *C. obsoletus* from the seemingly suitable, but calcic, agricultural areas of the southwestern United States.

Adult behavior. *Culicoides obsoletus* is mammalophilic. Reported Nearctic hosts are turkey (Humphreys and Turner 1973), sheep (Zimmerman and Turner 1983), horse (Jamnback 1965), cow (Jamnback 1965; Schmidtmann et al. 1981; Zimmerman and Turner 1983), domestic rabbit, gray squirrel (Wright and DeFoliart 1970), elk (*Cervus elaphus* Linnaeus, Cervidae) (Reeves et al. 2004), and human (Jamnback and Wirth 1963; Jamnback 1965). Atchley (1967) reported it to be a crepuscular biting pest in the mountains of southern New Mexico. Schmidtmann et al. (1981) reported *C. obsoletus* strongly preferred biting calves on the belly instead of on the head, back, or legs.

Palearctic hosts include cow (*Bos taurus*), horse (*Equus ferus* Linnaeus, Equidae), sheep (*Ovis aries* Linnaeus, Bovidae) (Lassen et al. 2012; Martínez-de la Puente et al. 2012; Elbers and Meiswinkel 2015), goat (*Capra aegagrus* [Linnaeus], Bovidae) (Lassen et al. 2012; Martínez-de la Puente et al. 2012), roe deer (*Capreolus

capreolus), red deer (*Cervus elaphus* Linnaeus, Cervidae), house mouse (*Mus musculus* Linnaeus, Muridae), and human (Lassen et al. 2012).

Vector potential. *Culicoides obsoletus* is a vector of bluetongue virus (BTV) in Europe (Meiswinkel et al. 2004; Mehlhorn et al. 2007; Foxi et al. 2016). Hence, its Nearctic host preferences indicate it may also be a vector of BTV or epizootic hemorrhagic disease virus (EHDV) in North America.

Symbionts. Pagès et al. (2017) found wild-collected *C. obsoletus* in Spain to be infected with *Wolbachia* and "*Candidatus* Cardinium" (Sphingobacteriales: Flexibacteraceae) endosymbionts. *Wolbachia* can alter dipteran reproduction by killing male embryos, inducing gamete incompatibility, or feminizing genetic males (Stouthamer 1999); and "*Candidatus* Cardinium" has been found to alter reproduction in parasitoid wasps and is being investigated for its effect on *Culicoides* (Pilgrim et al. 2020).

***Culicoides* (*Avaritia*) *sanguisuga* (Coquillett)**

Ceratopogon sanguisuga Coquillett, 1901: 604 (key; female; Maryland).

Culicoides sanguisuga (Coquillett): Kieffer 1906: 55 (combination). Malloch 1915: 301 (misspelled as *sanguisugum*; key; male, female; fig. female flagellomere, palpus, wing, male flagellomeres, genitalia).

Culicoides (*Avaritia*) *sanguisuga*. Jamnback and Wirth 1963: 189 (key; female, male, pupa, larva; biology; fig. female head palpus, mandibular teeth, hind tibial spines, spermathecae, male genitalia, male pupa, female pupa, larva). Jamnback 1965: 91 (key; female; male genitalia; pupa; biology; fig. male genitalia, female wing, antenna, palpus, eye, pupa, larva). Childers and Wingo 1968: 16 (key; biology; fig. female wing, spermathecae). Battle and Turner 1971: 74 (female; male genitalia; larval habitats; feeding habits; seasonal distribution; fig. female eye separation, palpus, wing, spermathecae, male genitalia). Wirth et al. 1985: 14 (numerical characters; fig. female wing). Murphree and Mullen 1991: 319 (key; larva; numerical characters; fig. thoracic pigmentation, head, epipharynx, hypostoma, mandible).

Culicoides obsoletus, misidentified in part: Root and Hoffman 1937: 155 (key; female; male genitalia; fig. male genitalia is that of *C. sanguisuga*). Foote and Pratt 1954: 29 (key; fig. female palpus, male genitalia represent *C. sanguisuga*).

Culicoides (*Culicoides*) *obsoletus*, misidentified in part: Khalaf 1954: 39 (assignment to subgenus *Culicoides*).

Culicoides (*Avaritia*) *obsoletus*, misidentified in part: Fox 1955: 218, 248 (subgenus *Avaritia* Fox; key and diagnoses of subgenera; species diagnosis; taxonomy). Murray 1957 (biology).

Diagnosis. (Tables 14, 15) Wing pattern faint on distal third; pale spot over distal half of r_2 (as in Fig. 118, 177 *C. obsoletus*); eyes contiguous, bare; superior transverse suture absent; palpal segment 3 with sensory pit; two ovoid subequal spermathecae, with necks and vestigial spermatheca; posterior margin of male sternite 9 cleft, without broad excavation; posterior margin of male tergite 9 convex, apicolateral processes absent; ventral apodeme of gonocoxite simple, ~2× longer than dorsal apodeme, slender, ~7× longer than basal width; aedeagus broadly U-shaped, without sclerotized membrane between basal arms or sclerotized anterior-directed point at base of median process (similar to Fig. 65 *C. obsoletus*, but with shallower arch and longer median process); median process with concave often spinulose tip; aedeagal ratio ~0.6; parameres separate, curved, apical portion simple pointed.

Distribution. Forested areas of Alaska east to Nova Scotia, south to Northern California and east to Georgia. Its period of synonymy with *C. obsoletus* has caused records prior to 1963 to be confused.

Larval ecology and life cycle. It is likely that some of the biological accounts for Nearctic *C. obsoletus* prior to 1963 apply to *C. sanguisuga*. Jamnback and Wirth (1963) report collecting immatures from piled leaves, forest litter, small piles of straw, a pile of spruce needles, twigs, and wood chips—all characterized by being dry on the surface and moist internally. *Culicoides sanguisuga* is univoltine in New York, with the larvae overwintering; the pupal stage lasts 3–6 d; there is some evidence the first generation is autogenous; females that engorged lay eggs 6–7 d later; and larvae hatch in ~5 d (Jamnback and Watthews 1963).

Adult behavior. Murray's (1957) report of *C. obsoletus* adults as most active on the edge of and in forested areas with peak nighttime activity during 0200–0500 hours, with season peaks mid-June to mid-July and late July to mid-August in Virginia and Hearle's (1938) report of horse, cow, and human hosts for *C. obsoletus* are likely for *C. sanguisuga* (Jamnback and Wirth 1963).

Culicoides sanguisuga is a generalist feeder with a preference for larger mammals and birds (Tanner and Turner 1974). It is a severe biting pest of humans (Jamnback and Wirth 1963; Jamnback 1965; Battle and Turner 1971). Jamnback and Watthews (1963) described in detail its behavior while feeding on human hosts and found that diurnal biting activity was highest at dawn and dusk, though they did not attempt to determine nocturnal activity, which could have been higher.

Other reported hosts are cow (Jamnback 1965; Schmidtmann et al. 1981; Zimmerman and Turner 1983), sheep (Zimmerman and Turner 1983), goat, rabbit (Humphreys and Turner 1973), cotton-tail rabbit (*Sylvilagus* Gray, Leporidae), guinea pig (*Cavia* Pallas, Caviidae), opossum (*Didelphis* Linnaeus, Didelphidae), rat (*Rattus* Fischer de Waldheim, Muridae), quail (*Colinus* Goldfuss, Odontophoridae), mourning dove (*Zenaida* Bonaparte, Columbidae), mallard (*Anas* Linnaeus, Anatidae) (Hair and Turner 1968), chicken (*Gallus* Brisson, Phasianidae) (Hair and Turner 1968; Humphreys and Turner 1973), turkey (*Meleagris* Linnaeus, Phasianidae) (Hair and Turner 1968; Humphreys and Turner 1973; Tanner and Turner 1974), grouse, blue jay, white-throated sparrow, horse (Jamnback 1965), and little brown bat (*Myotis lucifugus* [Le Conte], Chiroptera) (Reeves et al. 2004).

Remarks. No specimens of *C. sanguisuga* were examined, and its seasonal distribution in Table 5 is entirely from eastern North American records.

Subgenus *Beltranmyia* Vargas

Culicoides (*Beltranmyia*) *crepuscularis* Malloch

(Fig. 52, 89, 142, 143, 170–172)

Culicoides crepuscularis Malloch, 1915: 303 (male, female; fig. male genitalia, female wing; thoracic dorsum; Illinois). Hoffman 1925: 298 (key; female; fig. wing, mesonotum). Root and Hoffman 1937: 159 (key; female; male genitalia; fig. male genitalia). Thomsen 1937: 69 (key; larva, pupa; fig. respiratory trumpet). Fox 1942: 415 (pupa; fig. respiratory trumpet, female anal segment). James 1943: 149 (seasonal distribution: Colorado). Knowlton and Fronk 1950: 114 (Utah: Cache, Garfield counties). Knowlton and Kardos 1951: 163 (Utah: Washington County). Wirth 1952a: 188 (key; female; male genitalia; fig. female wing, dorsal thoracic pattern, palpus). Bullock 1952: 13 (female; male genitalia; habitat and biotic associations; seasonal distribution; Utah: Salt Lake County). Rees and Bullock 1954 (Utah: Salt Lake County). Foote and Pratt 1954: 19 (key; diagnoses of female, male, pupa; fig. female wing, mesonotum, spermatheca, palpus, male genitalia).

Culicoides (*Beltranmyia*) *crepuscularis*: Vargas 1953: 33 (subgenus *Beltranmyia* Vargas; designated *C. crepuscularis* as type species). Fox 1955: 233 (key and diagnoses of subgenera; species key; taxonomy). Williams 1956: 299 (key; Bermuda). Wirth and Bottimer 1956: 263 (Texas ecology). Wirth and Williams 1957: 13 (key; diagnosis). Vargas 1960: 47 (fig. female wing, male genitalia). Jamnback 1965: 52 (key; female; male genitalia; pupa, larva; biology; fig. male genitalia, female wing, antenna, palpus, eye separation, pupa, larva). Atchley 1967: 972 (key; numerical characters; female; male genitalia; variation; fig. female wing, palpus, tibial comb, spermatheca, male genitalia, parameres; biology). Childers and Wingo 1968: 11 (key; biology; fig. female wing, spermathecae). Jorgensen 1969: 13 (quantitative characters; key; female, male; seasonal distribution; fig. female wings, palpus, spermatheca, antenna, head, male genitalia, parameres, head, intersex head). Battle and Turner 1971: 34 (female; male genitalia; larval habitats; feeding habits; seasonal distribution; fig. female eye separation, palpus, wing, spermathecae, male genitalia, parameres). Blanton and Wirth 1979: 75 (key; numerical characters; female; male genitalia; pupa, larva; fig. female antenna, palpus, wing, eye separation, spermatheca, leg, male genitalia, parameres; larval habitat; feeding habits; seasonal distribution). Downes and Wirth 1981: 415 (fig. male genitalia). Wirth et al. 1985: 30 (numerical characters; fig. female wing). Wirth et al. 1988: 56 (numerical characters; fig. female wing). Murphree and Mullen 1991: 356 (key; larva; numerical characters; fig. mandible, hypostoma, head, epipharynx, thorax). Brickle and Hagan 1999: (key; numerical characters; biology; Belize). Borkent and Spinelli 2000: 29 (in Neotropical catalog).

Culicoides (*Monoculicoides*) *crepuscularis*: Khalaf 1954: 40 (assignment to subgenus *Monoculicoides* Khalaf).

Diagnosis. (Tables 14, 15) Wing pattern distinct; r_2 dark; M_1 and M_2 dark except at fork; r_3, m_1, m_2 each with medial and distal ovoid pale spots, though the medial pale spot in m_1 or m_2 may be absent (see remarks); one sclerotized fully developed ovoid spermatheca with neck shorter than wide; ventral apodeme of gonocoxite lacking or merely an inconspicuous obtuse bump; aedeagus V-shaped, median process tapered blunt; parameres separate, apices simple pointed. (See remarks.)

Distribution. North America from southern Alaska and Canada (British Columbia to Nova Scotia), through the United States, Bermuda, Mexico, Belize, El Salvador, Honduras, Nicaragua, to Costa Rica. Utah: Grand, Salt Lake, Uintah, Washington counties.

Larval ecology. Bullock (1952) collected and reared immatures from spikerush (*Eleocharis acicularis* [Linnaeus] Roemer and Schultes, Cyperaceae) mats in Salt Lake County. Jones (1961b) collected pupae from an organic boggy area in direct sunlight in Garfield County, Utah, and from the nonvegetated sunlit margin of an alkaline stream near Cisco (47 km north-northeast of Moab), Grand County, along with immatures of a Stonei group species (as *Culicoides stonei* James), *C. occidentalis* or *C. sonorensis* (as *C. variipennis australis*), *C. haematopotus* (may be *C. defoliarti*), *C. grandensis* (as "n. sp."), and *C. jamesi*. I was able to rear *C. crepuscularis* along with *C. sonorensis*, *C. occidentalis*, and *C. mortivallis* from mud collected on 10 September 2020 from nonvegetated sunlit alkaline pools in a stream bed in Grand County at 38.96339°N 109.33585°W and 1315 m elevation in the same wash as Jones's Cisco pupae collection site.

Culicoides crepuscularis immatures have been collected or reared from alkaline dung-polluted direct sunlit soil (Hair et al. 1966), drainage ditches, freshwater seepage ponds (Rowley 1967), mud flats (Rowley 1967; Childers and Wingo 1968), high-organic fresh- to salt-marsh (Blanton and Wirth 1979), muddy areas in pastures, mud contaminated by effluent from a milking parlor (Kline and Greiner 1985), and in greatest abundance at the water's edge of pond marshes, slow streams in meadows, and forest and grassland bogs with pH 6.2–9.5 and low to high salinity (McMullen 1978).

Culicoides crepuscularis immatures often share habitats with other species. In particular, Jones (1967) collected pupae of *C. crepuscularis*, along with *C. sonorensis* (as *C. variipennis*) and a species close to *Culicoides wisconsinensis* Jones, from 20 April into May, which had overwintered as larvae in mud in Weld County, Colorado; and Pfannenstiel and Ruder (2015) found *C. crepuscularis* along with *C. sonorensis* and *C. haematopotus* in mud in relict (long unused) and active bison (*Bison bison* [Linnaeus], Bovidae) wallows in Kansas about two weeks after they were flooded by rain.

Adult behavior. *Culicoides crepuscularis* is an opportunistic feeder on birds and mammals. Reported hosts are crow (*Corvus brachyrhynchos* Brehm, Corvidae), white-throated sparrow (*Zonotrichia albicollis* [Gmelin], Passerellidae), ruffed grouse (*Bonasa umbellus* [Linnaeus], Phasianidae), saw-whet owl (*Aegolius acadicus* [Gmelin], Strigidae) (Bennett 1961; Fallis and Bennett 1961a), domestic duck (*Anas boschas* Linnaeus), American robin (*Turdus migratorius* Linnaeus, Turdidae), purple finch (*Haemorhous purpureus* [Gmelin], Fringillidae), blue jay (*Cyanocitta cristata* [Linnaeus], Corvidae), Canada jay (*Perisoreus canadensis* [Linnaeus], Corvidae) (Bennett 1961), flicker (Fallis and Bennett 1961a), starling (Robinson 1961), magpie (*Pica pica hudsonia* [Sabine], Corvidae) (Hibler 1963), grackle (*Quiscalus quiscula versicolor* [Vieillot], Icteridae) (Robinson 1971), mourning dove (*Zenaida macroura* [Linnaeus]) (Greiner 1975), turkey (*Meleagris gallopavo* Linnaeus) (Atkinson 1988), house finch (*Haemorhous mexicanus* [Müller], Fringillidae) (Hopken et al. 2017), chicken (*Gallus gallus* [Linnaeus]) (Sloyer et al. 2019a), human (Edmunds and Keener 1954; Snow 1955; Hair 1966; Hair and Turner 1968), cow (Roberts 1965; Zimmerman and Turner 1983), raccoon, domestic rabbit (Wright and DeFoliart 1970), sheep (Zimmerman and Turner 1983), and eastern gray squirrel (*Sciurus carolinensis* Gmelin, Sciuridae) (McGregor et al. 2018). Furthermore, Hair (1966) collected blood-engorged *C. crepuscularis* from drop traps baited with domestic rabbit (*Oryctolagus cuniculus*), guinea pig (*Cavia porcellus* [Linnaeus]), rat (*Rattus*), chicken, turkey, mallard duck (*Anas boschas*), bobwhite quail (*Colinus virginianus* [Linnaeus]), and mourning dove; and Hood and Welch (1980) collected *C. crepuscularis* from red-winged blackbird (*Agelaius phoeniceus* [Linnaeus], Icteridae) nests.

Edmunds and Keener (1954) reported crepuscular-biting with a peak 15–45 minutes after sunset, and Nelson and Bellamy (1971) reported flight activity in Kern County, California, July–September, peaked near dusk and gradually diminished through the night without a peak near dawn. However, in Weld County, Colorado, *C. crepuscularis* activity was similar but showed a secondary peak either just before dawn in the hotter months of June and July or after dawn in the cooler months of May and August–October (Barnard and Jones 1980b).

Snow (1955) reported crepuscular-biting on humans in the forest canopy (rather than in the understory), which is behavior consistent with ornithophilic or arboreal mammalophilic preferences. However, Murray (1957) reported *C. crepuscularis* adults were most active in lowland fields and pastures rather than forested areas; but this habitat distinction may be biased by his use of light traps, which are more effective in open areas.

Clarifying this, McGregor et al. (2018) found *C. crepuscularis* more abundant (40 of 40 specimens with UVLT) 6–9 m up in the forest canopy rather than at ground-level within the forest—a distinction Murray did not make.

Vector potential. *Culicoides crepuscularis* has been found naturally infected with: an unidentified filarial nematode of starlings (Robinson 1961); *Chandlerella quiscali* Linstow (Nematoda: Filarioidea), a parasite of grackles (*Quiscalus quiscula*) (Robinson 1971; Huizinga and Granath 1984); *Splendidofilaria picacardina* Hibler (Nematoda: Filarioidea) and *Eufilaria longicaudata* Hibler (Nematoda: Filarioidea), parasites of magpies (Wirth and Hubert 1989); bluetongue virus (BTV) in Colorado (White et al. 2005) and Louisiana (Becker et al. 2010; Becker et al. 2020); and epizootic hemorrhagic disease virus (EHDV) in Texas (Schoenthal 2015). Texas specimens have also been found infected with DNA identical to that of *Chandlerella quiscali* from an Illinois grackle and with DNA identical to that of the avian malarial parasite *Haemoproteus sacharovi* Novy and MacNeal (Aconoidasida: Haemoproteidae) from an Arizona mourning dove (Martin et al. 2019). They noted *H. sacharovi* is also vectored by the pigeon louse fly, *Pseudolynchia canariensis* (Macquart) (Diptera: Hippoboscidae)—unusual in that the two vectors are in different Diptera suborders.

Bennett and Fallis (1960) found *C. crepuscularis* in Canada to be a natural vector of *Haemoproteus* Kruse (reported as *Haemoproteus danilewskii* Kruse by Santiago-Alarcon et al. 2012b) and experimentally found sporozoites in *C. crepuscularis* salivary glands 8 d after feeding on infected crows and white-throated sparrows (Fallis and Bennett 1961a). In addition, they demonstrated experimental vectorial competence of *C. crepuscularis* for transmission of *Haemoproteus fringillae* Labbé (Fallis and Bennett 1961b); and Greiner (1975) collected *C. crepuscularis* feeding on mourning doves when *Haemoproteus* was being transmitted among doves in Nebraska.

Experiments also support *C. crepuscularis* being a competent vector of filarial nematodes. Hibler (1963) demonstrated complete development of *Eufilaria longicaudata* and *Splendidofilaria picacardina* in *C. crepuscularis* after feeding on an infected magpie, and Robinson (1971) found active *Chandlerella quiscali* microfilaria in the head and mouthparts of 11 of 23 *C. crepuscularis* 10 d after feeding on an infected grackle.

Symbionts. *Culicoides crepuscularis* is sometimes heavily parasitized by mermithid nematodes, which often produce intersexes in surviving adult. Smith and Perry (1967) found eight of eight males collected with NJLTs in Florida were mermithid-induced intersexes; Jorgensen (1969) collected 44 mermithid-induced intersexes (23% of males) in Washington, with intersex rates up to 74%; Wieser-Schimpf et al. (1991) collected 110 intersexes (50% of males) in Louisiana, but did not check for parasitism; and, Atchley (1967) collected two intersex specimens in New Mexico, however, he did not say if they were parasitized.

Eight of eleven male *C. crepuscularis* collected in Grand County 16 May 2002 were parasitized by larval mites (Table 10). Three other mites were loose and may have come off any of the males or four females in that collection.

Erram (2016) studied the bacterial flora on adult female *C. crepuscularis* and found that Proteobacteria were predominant. In addition, *Wolbachia* infections, which can alter dipteran reproduction by killing male embryos, inducing gamete incompatibility, or feminizing genetic males (Stouthamer 1999), have been found in a *C. crepuscularis* population in Florida (Covey 2020), suggesting the possibility of using *Wolbachia* to control *C. crepuscularis* populations or reduce pathogen transmission.

Atypical biology. A specimen with diminished distal pale wing spots (Fig. 172) and having one normally large and two small ovoid spermathecae, 0.28 and 0.33 as long as the large spermatheca, was collected with UVLT on 16 July 2019 at 43.73340°N 114.27168°W and 1974 m elevation in Blaine County, Idaho.

Remarks. Across its extremely wide geographic range, considerable *C. crepuscularis* wing pattern variation has been documented by Atchley (1967) and figured in Wirth et al. (1985). Several specimens collected in the present study have reduced or lack distal pale spots in r_3, m_1, or m_2: two Blaine County, Idaho, females have greatly diminished wing spots (Fig. 172); the Bonneville County, Idaho, female in Figure 171 lacks the medial pale spot in m_2; and the Grand County male in Figure 143 lacks the medial pale spot in m_1. Also, the ventral apodeme of the gonocoxite illustrated from Florida specimens in Figure 55h of Blanton and Wirth (1979) is somewhat different from those illustrated from New Mexico specimens in Figure 33 of Atchley (1967) and collected in the present study (Fig. 89). *Culicoides crepuscularis* may be a species complex, but further study would be needed.

Subgenus *Diphaomyia* Vargas

***Culicoides* (*Diphaomyia*) *bergi* Cochrane**

(Fig. 194)

Culicoides bergi Cochrane, 1973: 311 (female, male; fig. female head, antenna, palpus, wing, spermathecae, male genitalia, parameres; New York).

Culicoides (*Diphaomyia*) *bergi*: Wirth et al. 1985: 16 (numerical characters; fig. female wing).

Culicoides baueri Hoffman, misidentified: James 1943: 149 (seasonal distribution; Colorado). Wirth 1952a: 183 (key; female; male genitalia; fig. dorsal thoracic pattern, female palpus, wing, male genitalia). Rees and Bullock 1954 (Utah: Salt Lake County). Foote and Pratt 1954: 16 (in part; key; female; male genitalia; fig. male genitalia). Fox 1955: 229 (in part; key and diagnoses of subgenera; species key; taxonomy).

Culicoides (*Diphaomyia*) *baueri*, misidentified: Vargas 1960: 40 (subgenus *Diphaomyia* Vargas; designated *C. baueri* as type species). Jones 1961a: 741 (key; pupa; fig. respiratory trumpet, operculum, chaetotaxy; Texas). Jamnback 1965: 42 (key; female; male genitalia; pupa; distribution; fig. female wing, antenna, palpus, eye separation, pupa). Atchley 1967: 985 (key; numerical characters; female; male genitalia; variation; fig. female wing, palpus, spermathecae, male genitalia, parameres). Battle and Turner 1971: 24 (in part; female, male; biology; fig. female eye separation, palpus, wing, spermathecae, male genitalia).

Diagnosis. (Tables 14, 15) Wing pattern distinct; r_2 dark; distal pale spot in r_3 bilobed and 8-shaped; pale spots at ~0.3 on M_1 and ~0.5 on M_2; CuA fork and CuA_1 and CuA_2 entirely within pale stripes; ventral apodeme of gonocoxite with two widely divergent processes, footlike, the posterior one small and sometimes unapparent (as in Fig. 78 *C. salihi*); basal arms of aedeagus each with spurlike process on posterior margin (as in Fig. 73 *C. defoliarti-haematopotus*), median process of aedeagus with a median pair of lateral hyaline posterior-projecting points, aedeagal ratio ~0.55; parameres separate, without submedian lobe, with subapical fringe of spines (as in Fig. 77 *C. salihi*).

Distribution. California, Utah (Box Elder, Cache, Garfield, Grand, Salt Lake, Uintah counties), Wyoming, Colorado, South Dakota, Nebraska, Missouri, Arizona, New Mexico, Texas, Wisconsin, New York, West Virginia, Virginia. Records for *C. baueri* from the northern and western United States before 1973 were for *C. bergi* (Cochrane 1973).

Larval ecology. Immatures have been collected from a grassy puddle and from fresh-water spring, creek, and pond margins (Jones 1961b as *C. baueri*; Cochrane 1973), usually from feces-enriched mud (Knausenberger 1986).

Adult behavior. Cochrane (1973) reports *C. bergi* collections from quail-baited traps; and Weinmann et al. (1979) collected blood-engorged *C. bergi* (as *C. baueri*) from California quail (*Callipepla californica*)-baited traps; however, they found no *C. bergi* infected with quail heartworm (*Splendidofilaria californiensis*) or other evidence it can transmit the parasite.

***Culicoides* (*Diphaomyia*) *defoliarti* Atchley and Wirth**

(Fig. 73, 74, 126, 127, 204)

Culicoides (*Diphaomyia*) *defoliarti* Atchley and Wirth, 1979: 527 (key; numerical characters; female; male genitalia; pupa; fig. female antenna, palpus, wing, mesonotum, eye separation, spermathecae, male genitalia, parameres; Arizona). Wirth et al. 1985: 18 (numerical characters; fig. female wing).

Culicoides haematopotus Malloch, misidentified: Wirth 1952a: 182 (in part; key; female; male genitalia; distribution; fig. dorsal thoracic pattern, female palpus, wing). Jones 1961a: 739 (in part from Utah specimens; key; pupa; fig. respiratory trumpet, operculum, chaetotaxy, anal segment). Atchley 1967: 987 (in part; key; numerical characters; female; male genitalia; variation; fig. female wing, palpus, tibial comb, spermathecae, male genitalia, parameres).

Diagnosis. (Tables 14, 15) Wing pattern distinct; r_2 dark; isolated pale spots straddling at ~0.3 on M_1 and ~0.5 on M_2; r_3 mostly dark with distal pale spot small and entirely within distal 0.2 of cell and often not reaching wing margin; pale areas anterior along CuA broken by dark areas at base and after midpoint; spermathecae unequal by ~1.2, sclerotized necks >2× longer than wide; ventral apodeme of gonocoxite with two widely divergent processes, footlike; basal arms of aedeagus each with spurlike process on posterior margin, median process of aedeagus narrow parallel-sided, aedeagal ratio ~0.5; parameres separate, each with bulbous submedian lobe and subapical fringe of spines.

Distribution. Oregon, Utah (Garfield, Grand, San Juan, Uintah counties), Wyoming, Colorado (Montrose County, **new state record**), California, Arizona, New Mexico. McMullen (1978) reports "*Culicoides* near *haematopotus*" from British Columbia, which may be for *C. defoliarti*. The Colorado record is of one female collected with UVLT on 30 July 2020 at 38.32234°W and 108.18359°W and 2934 m elevation on the Uncompahgre Plateau.

Larval ecology. Wirth reared immatures collected from a seepage area below a dam in Arizona (Atchley and Wirth 1979). Jones (1961b) collected pupae (as *C. haematopotus*; may be *C. defoliarti*) from two Utah sites: the nonvegetated sunlit margin of an alkaline stream near Cisco (47 km north-northeast of Moab), Grand County, along with immatures of a Stonei group species (as *C. stonei*), *C. occidentalis* or *C. sonorensis* (as *C. variipennis australis*), *C. jamesi*, *C. grandensis* (as "n. sp."), and *C. crepuscularis*; and a freshwater seep in Garfield County, along with *C. sonorensis* (as *C. variipennis*) and *C. jamesi*.

Adult behavior. The mandibular and lacinial teeth on the female and collection in CO_2-baited traps indicate it feeds on vertebrate blood; however, its hosts are unknown.

Symbionts. Female *C. defoliarti* and indeterminate male *C. defoliarti-haematopotus* were parasitized by larval mites (Table 10). Ten indeterminate *C. defoliarti-haematopotus* intersex specimens were also collected: one apparently unparasitized, eight parasitized by mermithid nematodes, and one parasitized by a mermithid nematode and a mite (Table 11). Atchley (1967) collected a possible *C. defoliarti* (as *C. haematopotus*) intersex in New Mexico; however, he did not say if it was parasitized.

Remarks. The SCo patterns on the feminized antennae of the nine parasitized intersex *C. defoliarti-haematopotus* specimens fell into two distinct groups: 1, 8–13 (n = 5) and 1, 11–13 (n = 4). These patterns are the same as for normal *C. defoliarti* females and normal indeterminate *C. defoliarti-haematopotus* males, respectively; however, mandibular teeth were absent from four of the 8–13 set and present on three of the 11–13 set, which were opposite of expectation based on sex.

Only a portion of the ~5580 *C. defoliarti* and *C. haematopotus* collected was closely examined. Of 1188 specimens tentatively identified by wing pattern in alcohol, 22% seemed to be *C. defoliarti*. However, when 38 females were slide-mounted and identified by antennal ratio and SCo pattern, 11 (29%) had been misidentified, indicating that distinguishing these species in alcohol was not reliable. Thus, these species are combined as "*defoliarti-haematopotus*" in the trap comparison and seasonal distribution Tables 4 and 5. These species are differentiated in the other tables only if the females were slide-mounted and positively identified and the males were associated with these positively identified females.

Culicoides (*Diphaomyia*) *erikae* Atchley and Wirth

(Fig. 76, 129, 240, 271)

> *Culicoides* (*Diphaomyia*) *erikae* Atchley and Wirth, 1979: 532 (key; numerical characters; female; male genitalia; pupa; fig. female antenna, palpus, wing, eye separation, spermathecae, male antenna, parameres, genitalia; New Mexico). Wirth et al. 1985: 18 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing pattern reduced; r_2 dark; distal pale spots absent from r_3, m_1, m_2, often cua_1; spermathecae with sclerotized necks ~2× longer than wide; sclerotized ring on spermathecal duct; ventral apodeme of gonocoxite with two widely divergent processes, footlike; basal arms of aedeagus each with spurlike process on posterior margin, median process of aedeagus narrow parallel-sided, aedeagal ratio ~0.4; parameres separate, each with bulbous submedian lobe and subapical fringe of spines.

Distribution. Utah (Box Elder, Grand, Uintah counties), Arizona, New Mexico. Nine of the 14 *C. erikae* collected were from 2436 m elevation in Uintah County (Table 7), suggesting it is more common at higher elevations than were routinely sampled.

Larval ecology. Atchley collected or reared pupae from Silver Creek Canyon, Otero County, New Mexico, in May of 1973 and from Cedar Creek Canyon, Lincoln County, New Mexico, in June of 1973 but did not report details of the habitats (Atchley and Wirth 1979).

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; however, its hosts are unknown.

Culicoides (*Diphaomyia*) *haematopotus* Malloch

(Fig. 73, 74, 127, 205, 268)

Culicoides haematopotus Malloch, 1915: 302 (key; male, female; fig. male genitalia, antenna, female wing; Illinois). Hoffman 1925: 299 (key; female; fig. wing, mesonotum). Root and Hoffman 1937: 161 (key; female; male genitalia; fig. male genitalia). Thomsen 1937: 69 (key; larva, pupa; fig. respiratory trumpet). James 1943: 149 (seasonal distribution; Colorado). Knowlton and Fronk 1950: 114 (Utah: Grand County). Wirth 1952a: 182 (in part; key; female; male genitalia; distribution; fig. dorsal thoracic pattern, female palpus, wing). Bullock 1952: 21 (key; female; Utah: Salt Lake County). Rees and Bullock 1954 (Utah: Salt Lake County). Foote and Pratt 1954: 23 (key; diagnoses of female, male, pupa; fig. female wing, mesonotum, palpus, male genitalia).

Culicoides (*Oecacta*) *haematopotus*: Khalaf 1954: 37 (assignment to subgenus *Oecacta*). Fox 1955: 240 (in part; key and diagnoses of subgenera; species key; taxonomy). Wirth and Bottimer 1956: 263 (Texas ecology).

Culicoides (*Diphaomyia*) *haematopotus*: Vargas 1960: 40 (assignment to subgenus *Diphaomyia*). Jones 1961a: 739 (in part; key; pupa; fig. respiratory trumpet, operculum, chaetotaxy, anal segment). Jamnback 1965: 70 (key; female; male genitalia; pupa, larva; biology; fig. male genitalia, female wing, antenna, palpus, eye separation, pupa, larva). Atchley 1967: 987 (in part; key; numerical characters; female; male genitalia; variation; fig. female wing, palpus, tibial comb, spermathecae, male genitalia, parameres). Childers and Wingo 1968: 14 (key; biology; fig. female wing, spermathecae). Jorgensen 1969: 17 (quantitative characters; key; female, male; seasonal distribution; fig. female wing, spermathecae, palpus, antenna, male genitalia, parameres). Battle and Turner 1971: 47 (female; male genitalia; larval habitats; feeding habits; seasonal distribution; fig. female eye separation, palpus, wing, spermathecae, male genitalia, parameres). Blanton and Wirth 1979: 95 (key; numerical characters; female; male genitalia; pupa, larva; fig. female antenna, palpus, wing, eye separation, spermatheca, leg, male genitalia, parameres; larval habitat; feeding habits; seasonal distribution). Atchley and Wirth 1979: 537 (key; numerical characters; female; male genitalia; pupa, larva; fig. female antenna, palpus, wing, eye separation, spermathecae, leg, male genitalia, parameres). Downes and Wirth 1981: 415 (fig. male genitalia). Wirth et al. 1985: 18 (numerical characters; fig. female wing). Wirth et al. 1988: 32 (numerical characters; fig. female wing). Murphree and Mullen 1991: 324 (key; larva; numerical characters; fig. head, epipharynx, hypostoma, caudal segment, mandible). Borkent and Spinelli 2000: 30 (in Neotropical catalog). Borkent 2012: 73 (fig. pupal abdominal segment 4). Borkent 2014: 24 (key to genera of pupae of Ceratopogonidae; fig. pupal abdominal segment 4, thorax, abdominal segment 9).

Diagnosis. (Tables 14, 15) Wing pattern distinct; r_2 dark; isolated pale spots straddling at ~0.3 on M_1 and at ~0.5 on M_2; r_3 mostly dark with distal pale spot small and entirely within distal 0.2 of cell and reaching wing margin; pale areas anterior along CuA broken by dark areas at base and after midpoint; spermathecae unequal by ~1.2, sclerotized necks >2× longer than wide; ventral apodeme of gonocoxite with two widely divergent processes, footlike; basal arms of aedeagus each with spurlike process on posterior margin, median process of aedeagus narrow parallel-sided, aedeagal ratio ~0.5; parameres separate, each with bulbous submedian lobe and subapical fringe of spines.

Distribution. Southern Canada (British Columbia to Nova Scotia), through the United States and Mexico, to Honduras. Utah: Grand, Salt Lake counties.

Biology. In 1979, *C. defoliarti* was described from specimens of *C. haematopotus* collected in the western United States where their distributions are now recognized to overlap; thus, earlier western bionomic records for these species are conflated. For this reason, unless indicated as possibly for *C. defoliarti*, the following information is from outside the known range of *C. defoliarti* and, hence, likely specific for *C. haematopotus*.

Larval ecology. Jones (1961b) collected pupae he identified as *C. haematopotus*, which may be *C. defoliarti*, from two Utah sites (see *C. defoliarti* biology). Others have collected or reared *C. haematopotus* immatures from heavily vegetated and bare moist mud with rotting leaves at pond margins, a shaded stream margin with decaying leaves (Williams 1955), stream edges with damp sand and leaf mold (Murray 1957), moist alkaline dung-polluted direct sunlit soil, leaves in stream and pond margins, low-organic freshwater pond margins (Hair et al. 1966), mud flats, freshwater seepage ponds (Rowley 1967), low-organic pond and stream margins (Blanton and Wirth 1979), pond margins, and muddy areas in pastures (Kline and Greiner 1985). Pfannenstiel and Ruder (2015) found *C. haematopotus* along with *C. sonorensis* and *C. crepuscularis* in mud in relict (long unused) and active bison (*Bison bison*) wallows in Kansas about two weeks after they were flooded by rain.

Erram et al. (2019) reared *C. haematopotus* from mud substrate samples collected over three months in Florida from the edges of various stream, puddle, and seepage habitats, which produced 280, 69, and 2 adults, respectively. They also characterized the habitat samples for P, K, Mg, Ca, Cu, Mn, Zn, organic matter, pH, moisture, electrical conductivity, and microbes and found that adult production in the stream samples was positively correlated with Zn and P concentrations, pH, moisture, and microbe levels, but was negatively correlated with Mn concentration and electrical conductivity.

Adult behavior. Snow (1955) reported *C. haematopotus* blood-feeds at different levels in a forest ecosystem, starting in low shady areas late in the afternoon, moving into the shrub and tree canopy as light intensity and temperatures drop, feeding in the canopy through warm nights with an early crepuscular activity peak, and returning to the understory at dawn. However, Murray (1957) reported *C. haematopotus* adults were most active in lowland fields and pastures rather than wooded areas; but this habitat distinction may be biased by his use of light traps, which are more effective in open areas. Clarifying this, McGregor et al. (2018) found *C. haematopotus* significantly more abundant in UVLTs 6–9 m up in the forest canopy rather than at ground-level within the forest—a distinction Murray did not make.

Using only ground-level NJLTs, Hair (1966) found flight activity in Virginia greatest during 2100–0300 hours, with half as much activity during 0300–0600 hours. However, his use of light traps misses diurnal and underreports crepuscular activity. More thoroughly, Nelson and Bellamy (1971) used truck traps at 2 h intervals in Kern County, California, and found *C. haematopotus* (may be *C. defoliarti*) flight activity through the night with activity peaks near dusk and dawn.

Culicoides haematopotus is an opportunistic feeder with a preference for birds. Known hosts are human (Edmunds and Keener 1954; Snow 1955; Hair 1966; Hair and Turner 1968; Sloyer et al. 2019a), crow (*Corvus brachyrhynchos*) (Fallis and Bennett 1961a), mourning dove (Greiner 1975), cow (*Bos taurus*) (Hayes et al. 1984; Sloyer et al. 2019a), turkey (*Meleagris gallopavo*) (Atkinson 1988; Sloyer et al. 2019a), northern cardinal (*Cardinalis cardinalis* [Linnaeus] Cardinalidae), red-eyed vireo (*Vireo olivaceus* [Linnaeus], Vireonidae) (McGregor et al. 2018), white-throated sparrow (*Zonotrichia albicollis*) (Swanson and Turnbull 2014), chicken (*Gallus gallus*), and white-tailed deer (*Odocoileus virginianus* [Zimmermann], Cervidae) (Sloyer et al. 2019a). Also, Sloyer et al. (2019a) found no statistically significant seasonal host preference variation in Florida.

Hair (1966) collected blood-engorged *C. haematopotus* from drop traps baited with domestic rabbit (*Oryctolagus cuniculus*), eastern cotton-tail rabbit (*Sylvilagus*), guinea pig (*Cavia porcellus*), opossum (*Didelphis*), rat (*Rattus*), chicken, turkey, mallard duck (*Anas boschas*), bobwhite quail (*Colinus virginianus*), and mourning dove.

Vector potential. *Culicoides haematopotus* has been found naturally infected with the magpie filarial worms *Eufilaria longicaudata* (Wirth and Hubert 1989) and *Chandlerella striatospicula* Hibler (Nematoda: Filarioidea), which Hibler (1963) showed are transmitted by *C. haematopotus*. Robinson (1971) found active *Chandlerella quiscali* microfilaria in the head and mouthparts of *C. haematopotus* 10 d after feeding on an infected grackle. Greiner (1975) collected *C. haematopotus* feeding on mourning doves during a period when avian malarial *Haemoproteus* Kruse (Aconoidasida: Haemoproteidae) was being transmitted among doves in Nebraska, though the midges were not tested for the avian malarial parasite; however, Atkinson (1988) found *Haemoproteus mansoni* Castellani and Chalmers sporozoites (as *Haemoproteus meleagridis* Levine) in *C. haematopotus* salivary glands in Florida. Though not previously considered a virus vector, one *C. haematopotus* was found infected with bluetongue virus (BTV) in Louisiana (Becker et al. 2010).

Symbionts. *Culicoides haematopotus* is sometimes heavily parasitized by mermithid nematodes, which produce intersexes in surviving adult midges. Smith and Perry (1967) collected 123 mermithid-induced intersexes (42% of males) in Florida, with intersex rates up to 51%; Atchley (1967) collected an intersex specimen (possibly *C. defoliarti*) in New Mexico, however, he did not say if it was parasitized; and, Erram et al. (2019) found 4% of the adults reared from streambank and puddle samples collected over three months in Florida were mermithid-parasitized intersexes. Ten indeterminate *C. defoliarti-haematopotus* intersex specimens were collected in the present study: one apparently unparasitized, eight parasitized by mermithid nematodes, and one parasitized by a mermithid nematode and a larval mite (Table 10). In addition, several normal indeterminate male *C. defoliarti-haematopotus* and a female *C. haematopotus* were parasitized by larval mites (Table 10).

Erram (2016) studied the bacterial flora on adult female *C. haematopotus* and found that Proteobacteria were predominant, likely because of its relatively unpolluted larval habitat. In addition, *Wolbachia* infections, which can alter dipteran reproduction by killing male embryos, inducing gamete incompatibility, or feminizing genetic males (Stouthamer 1999), have been found in a *C. haematopotus* population in Florida (Covey 2020), suggesting the possibility of using *Wolbachia* to control *C. haematopotus* populations or reduce pathogen transmission.

Remarks. *Culicoides haematopotus* conflates with *C. defoliarti* in records from the southwestern United States before 1979. See *C. defoliarti* remarks.

Culicoides (*Diphaomyia*) *inyoensis* Wirth and Blanton

(Fig. 75, 128, 211, 212)

Culicoides (*Diphaomyia*) *inyoensis* Wirth and Blanton, 1969a: 565 (female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, leg, male genitalia, parameres; California). Atchley and Wirth 1979: 541 (key; numerical characters; female; male genitalia; fig. female antenna, palpus, wing, eye separation, spermathecae, leg, male genitalia, parameres). Wirth et al. 1985: 18 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing pattern extensive; r_2 dark; large distal pale spots in r_3, m_1, m_2, cua_1, but may be diffuse and indistinct; distal pale spot in r_3 centered at ~0.7 the distance from apex of costa to apex of M_1, extending into distal 0.1 of cell; M_1 dark; pale spot barely on M_2 at ~0.4, spreading anterior into m_1; spermathecae subequal, with sclerotized necks; ventral apodeme of gonocoxite with two widely divergent processes, footlike; basal arms of aedeagus each with spurlike process on posterior margin, median process of aedeagus slightly tapering to blunt tip, aedeagal ratio ~0.5; parameres separate, each with bulbous submedian lobe and subapical fringe of spines.

Distribution. California, Utah (Garfield, Grand counties).

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; and though its hosts are unknown, the SCo presence on only the proximal flagellomeres suggests it is mammalophilic.

Symbionts. Male and female *C. inyoensis* were parasitized by larval mites (Table 10), which species may indicate its pupal habitat or oviposition site.

Remarks. Wirth and Blanton (1969a) discuss *C. inyoensis*' similarity to *Culicoides mohave* Wirth, which have similar wing and SCo patterns. In the present study, I identified a female *C. inyoensis* collected by J. N. Belkin from Saratoga Spring, Death Valley, San Bernardino County, California, 30 May 1953, that had been misidentified as *C. mohave*. It seems likely other specimens identified as *C. mohave* before *C. inyoensis*' 1969 description are also misidentified.

The *C. inyoensis* type series was collected from Resting Springs, Inyo County, California, 29–30 May 1955, along with several *C. mohave*. Saratoga Spring is only 32 km away from and ~465 m lower than Resting Springs; thus, their habitats overlap in the Mojave Desert environment, with *C. inyoensis* ranging more northern into the Canyonlands of Utah and *C. mohave* more southern into the Sonoran Desert of Baja California.

Culicoides (*Diphaomyia*) *salihi* Khalaf (new status)

(Fig. 77, 78, 130, 213, 252, 269)

Culicoides salihi Khalaf, 1952a: 351 (female; male genitalia; fig. male genitalia, parameres, female antenna, palpus, seasonal incidence; Oklahoma).

Culicoides (*Oecacta*) *salihi*: Khalaf 1954: 43 (male genitalia; assignment to Haematopotus group of subgenus *Oecacta*). Fox 1955: 254 (key and diagnoses of subgenera; species key; taxonomy). Wirth and Bottimer 1956: 263 (Texas ecology). Khalaf 1957: 201, 206 (diagnosis; Oklahoma distribution; June, July; fig. Oklahoma distribution). Wirth et al. 1985: 38 (numerical characters; Oklahoma, Texas, Arizona, California; fig. female wing).

Diagnosis. (Tables 14, 15) Light yellowish brown; small, wing length <1 mm; wing pattern of faint pale plots, but reduced; r_2 dark; pale spots not straddling M_1, absent distally from r_3, m_1, m_2; mandible with nine tiny teeth, half normal size; palpal sensory pit enlarged internally; two subequal sclerotized ovoid spermathecae, with slender sclerotized necks ~0.3 as long as the spermathecae, and heavily sclerotized ring on the spermathecal duct; male tergite 9 apicolateral processes projecting, pointed; ventral apodeme of gonocoxite with two widely divergent processes, footlike, posterior process appearing appressed against gonocoxite, difficult to see; basal arms of aedeagus each with spurlike process on posterior margin, median process of aedeagus with a median pair of lateral hyaline posterior-projecting points, aedeagal ratio ~0.45; parameres separate, moderately slender and tapering, without submedian lobe, with subapical fringe of spines and slender pointed tip.

Distribution. California, Utah (Garfield County, **new state record**), Arizona, New Mexico, Oklahoma, Texas.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; and though its hosts are unknown, the SCo presence on only the proximal flagellomeres suggests it is mammalophilic.

Its week 17 and week 43 data in Table 5 represent the earliest and latest collection dates (27 April and 23 October) in south-central Texas (Wirth and Bottimer 1956), a warmer climate. Hence, this range probably represents a much wider season of activity than would be likely in Utah.

Remarks. Khalaf (1954) placed this species in the Haematopotus group (now part of subgenus *Diphaomyia*). The combination of narrowly separated eyes, long-necked spermathecae, sclerotized ring, paired submedian posterior processes on the basal aedeagal arms, and paramere with a fringe of spines suggest assignment to the subgenus *Diphaomyia*. However, *C. salihi* lacks the distinct hooklike posterior process of the ventral apodeme of the gonocoxite and the submedian lobe on the paramere characteristic of the Haematopotus group; thus, its placement in that group is incorrect.

However, the posterior process of the ventral apodeme of the gonocoxite is relatively reduced in the Baueri group of subgenus *Diphaomyia*. Cochrane (1973: 314), in his description of *C. bergi*, states the posterior "heel" of the ventral apodeme on the gonocoxite is "abbreviated, in some specimens not apparent". Similarly, on *C. salihi*, this heel process is ventro-posteriorly aimed, overlapping the medial side of the gonocoxite and difficult to see, often appearing as only a dark sclerotization on the gonocoxite (Fig. 78). In addition, both *C. bergi* and *C. salihi* have a pair of pointed hyaline processes on the median process of the aedeagus and lack submedian lobes on the parameres. Hence, because Cochrane described *C. bergi* from a subset of *C. baueri*, which is the type species for the subgenus *Diphaomyia*, I propose inclusion of *C. salihi* in subgenus *Diphaomyia* (**new status**).

Subgenus *Drymodesmyia* Vargas

The species of the subgenus *Drymodesmyia* are some of the more difficult to identify. The only key to the Nearctic species was Wirth and Hubert (1960), which relied heavily on somewhat variable wing patterns and occasionally on spermathecal or ambiguous male genitalia characteristics. I have attempted to clarify some of the ambiguity; however, for several species, a best-fit determination using several characters must be used; and then, sometimes only a tentative identification can be made. Current research using molecular methods at the University of California at Riverside (Xinmi Zhang, personal communication) may solve this problem.

So far as is known, the Nearctic *Drymodesmyia* use either treeholes (*C. byersi* and *C. hinmani*) or cactus rot holes (the other species) for their larval habitats. *Culicoides byersi* replaces the common eastern North American treehole species, *C. hinmani*, in similar treehole habitats in the southwestern United States. However, treeholes wet enough for larval development are lacking in the arid areas of the southwest except in relatively uncommon and isolated riparian, spring-fed, and other areas with sufficient water for trees to maintain moist treeholes. It seems likely that occupation of cactus rot holes is a relatively recent adaptation to the increasingly dry climate. This and the frequent occupation of rot holes of the same cactus species by different *Drymodesmyia* species (Wirth and Hubert 1960; Ryckman 1960) suggests that their morphological similarity may be due to interbreeding and incomplete speciation. A good summary of the biology of the cactiphilic species is provided by Ryckman (1960).

Culicoides (*Drymodesmyia*) *arizonensis* Wirth and Hubert

(Fig. 111, 164, 215)

Culicoides (*Oecacta*) *arizonensis* Wirth and Hubert, 1960: 655 (key; numerical characters; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres; Arizona).

Culicoides (*Drymodesmyia*) *arizonensis*: Wirth 1965: 130 (placement in subgenus *Drymodesmyia*). Wirth et al. 1985: 14 (numerical characters; fig. female wing). Wirth et al. 1988: 24 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 30 (in Neotropical catalog).

Diagnosis. (Tables 14, 15) Dark brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 nearly filling distal 0.3–0.4 of cell, cut into on proximal side by dark spot; pale spots at ~0.3 on M_1 and ~0.5 on M_2; one pale spot in distal half of anal cell; tips of M_1, M_2 dark; CuA_1 and CuA_2 within dark areas; pore of sensory pit on palpal segment 3 ~0.3 the diameter of segment, widening internally (as in Fig. 248 *C. sitiens*); femora and tibiae without subapical pale band; spermathecae unequal by ~1.5×, pyriform; ventro-posterior membrane of male sternite 9 densely spiculate; ventral apodeme of gonocoxite simple, ~0.5 as long as dorsal apodeme; aedeagus V-shaped, truncate tip ~0.25 width of arm spread, aedeagal ratio ~0.6; parameres separate, apices simple pointed bent.

Distribution. California, Arizona, Baja California.

Larval ecology and adult behavior. *Culicoides arizonensis* has been reared from rot holes in *Carnegiea gigantea* (Ryckman 1960) and in *Pachycereus schottii* (Engelmann) D. R. Hunt (Cactaceae) (Wirth and Hubert 1960). However, its adult hosts are unknown, though the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Culicoides (*Drymodesmyia*) *bakeri* Vargas

(Fig. 197, 259)

Culicoides bakeri Vargas, 1954: 27 (female; male genitalia; fig. female wing, palpus, antenna, male genitalia; Federal District, Mexico). Wirth and Hubert 1960: 652 (key; numerical characters; female; male genitalia; fig. female palpus, spermathecae).

Culicoides (*Glaphiromyia*) *bakeri*: Vargas 1960: 41 (assignment to subgenus *Glaphiromyia* Vargas).

Culicoides (*Drymodesmyia*) *bakeri*: Wirth et al. 1988: 24 (numerical characters). Borkent and Spinelli 2000: 30 (in Neotropical catalog). Huerta 2007: 24 (female; male; fig. female antenna, head, spermathecae, thorax, wing, male genitalia, aedeagus, parameres; Federal District, Mexico).

Diagnosis. (Tables 14, 15) (Measurement and ratio data in Table 14 are averages of Mexico data (Huerta 2007) and the data from the specimen collected in California.) Dark brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 bilobed and 8-shaped into two separated spots; pale spots at ~0.3 on M_1 and ~0.5 on M_2; two pale spots in distal half of anal cell; tips of M_1, M_2, CuA_1 pale, pale apices of M_1 and M_2 connected thinly along wing margin, with thin pale margin extending partway up along margin of r_3; most of CuA_1 and CuA_2 within dark areas; pore of sensory pit on palpal segment 3 <0.3 the diameter of segment, widening internally (as in Fig. 248 *C. sitiens*); combined distal five flagellomeres (including intersegmental spaces) on female equal to or slightly longer than combined proximal eight; pale bands basal on all femora, subapical on fore and mid femora, basal on all tibiae; spermathecae slightly pyriform, unequal by 1.2×, with necks longer than wide tapering to 0.15 diameter of spermatheca; ventro-posterior membrane of male sternite 9 not spiculate; ventral apodeme of gonocoxite simple; aedeagus V-shaped, nearly straight-sided tapering to blunt tip 0.19 width of arm spread, aedeagal ratio 0.50; parameres separate, apices with 4–6 spines.

Distribution. California (Riverside County, **new United States record**), Mexico City. Xinmi Zhang collected one female with UVLT on 28 June 2019 at the Boyd Deep Canyon Desert Research Center, Riverside County, California, 33.64239°N 116.38414°W at 318 m elevation.

Larval ecology and adult behavior. *Culicoides bakeri*'s larval habitat is unknown; however, like other *Drymodesmyia*, its larval habitat is likely the abundant cacti at the collection site. Also, its adult hosts are unknown, though the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Remarks. Though far from its Mexico type locality and only other known collection site, the female collected readily keys to *C. bakeri* in Wirth and Hubert (1960) and agrees with Huerta's 2007 redescription (except for having 18 mandibular teeth), notably in having a double distal pale spot in r_3, two distinct distal pale spots in the anal cell (Fig. 197), and unequal spermathecae with distinct narrow necks (Fig. 259).

Culicoides (*Drymodesmyia*) *butleri* Wirth and Hubert

(Fig. 104, 105, 158, 159, 198, 257)

Culicoides (*Oecacta*) *butleri* Wirth and Hubert, 1960: 650 (key; numerical characters; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres; Arizona).

Culicoides (*Drymodesmyia*) *butleri*: Wirth 1965: 130 (placement in subgenus *Drymodesmyia*). Wirth et al. 1985: 14 (numerical characters; fig. female wing). Wirth et al. 1988: 24 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 30 (in Neotropical catalog).

Diagnosis. (Tables 14, 15) Dark brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 bilobed and 8-shaped; pale spots at ~0.3 on M_1 and ~0.5 on M_2; two pale spots in distal half of anal cell; tips of M_1, M_2, CuA_1 pale; most of CuA_1 and CuA_2 within dark areas; pore of sensory pit on palpal segment 3 <0.3 the diameter of segment, widening internally (as in Fig. 248 *C. sitiens*); combined distal five flagellomeres (including intersegmental spaces) on female distinctly shorter than combined proximal eight; pale band subapical on fore femora, basal on all tibiae; spermathecae unequal by ~1.2×, >2× longer than wide, opening ~0.3 as wide as spermatheca, without necks; ventro-posterior membrane of male sternite 9 not spiculate; ventral apodeme of gonocoxite simple; aedeagus somewhat Y-shaped, constricting at base of median process, tapering to truncated tip 0.17 (0.14–0.22) width of arm spread, aedeagal ratio 0.38–0.45 (n = 2); parameres separate, narrowest diameter of paramere before first ~90° bend in apical half 0.0031–0.0034 mm (n = 2), apices simple pointed bent.

Distribution. Arizona, Texas (Vigil et al. 2014), Nuevo León, Trinidad (Wirth and Hubert 1960).

Larval ecology and adult behavior. *Culicoides butleri*'s larval habitat is unknown; however, like other *Drymodesmyia*, its larval habitat is likely the abundant cholla (*Cylindropuntia* [Engelmann] F. M. Knuth, Cactaceae) and barrel cactus (*Ferocactus* Britton and Rose, Cactaceae) at the Greenlee County, Arizona, collection site. Also, its adult hosts are unknown, though the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Atypical biology. One female, collected with UVLT in Greenlee County, Arizona, had three fully developed spermathecae with a vestigial fourth, instead of two with a vestigial third (Table 12).

Remarks. The height of the aedeagal arch of the male collected in Greenlee County, Arizona, (Fig. 104) more closely matches the description of Wirth and Hubert (1960) but is somewhat different from the specimen identified by W. W. Wirth from Gila County, Arizona (Fig. 105); so, genitalia and wing images (Fig. 158, 159) are included for both specimens.

Culicoides (*Drymodesmyia*) *byersi* Atchley

(Fig. 114, 168, 214, 250)

Culicoides (*Drymodesmyia*) *byersi* Atchley, 1967: 983 (key; numerical characters; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres; New Mexico). Wirth et al. 1985: 14 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Brown; wing pattern moderately faint; r_2 dark; pale spot at end of costa oval and not extending back beneath r_2; distal pale spots present in r_3, m_1, m_2, cua_1 and anal cell; in r_3 and m_1, not close to wing margin; in r_3, elongate and aimed diagonally toward costa, but often faint; mandible with 9–11 minute teeth; pore of sensory pit on palpal segment 3 <0.3 the diameter of segment, widening internally (as in Fig. 249 *C. hinmani*); pale banding absent subapically from mid femora, basally and subapically from hind femora, subapically from hind tibiae; ventro-posterior membrane of male sternite 9 not spiculate; ventral apodeme of gonocoxite simple, up to 2× longer and only a little more slender than dorsal apodeme; aedeagus simple, nearly V-shaped, median process evenly tapering to broad truncate tip, aedeagal ratio ~0.3; parameres separate, apices simple contorted pointed.

Distribution. California, Utah (Grand County), Colorado, Arizona, New Mexico. *Culicoides byersi* is the southwestern treehole-inhabiting counterpart to the morphologically similar and more northern and eastern *C.* (*Drymodesmyia*) *hinmani*, which known ranges overlap in only Utah and Colorado.

Larval ecology and adult behavior. *Culicoides byersi* has been reared from a cottonwood treehole in Colorado (Pappas et al. 1991), and the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood. Furthermore, the combination of its unusually minute teeth and treehole larval habitat with its frequent collection in low-level CO_2-baited traps (Table 4) suggests a small mammal, ground-dwelling bird, or generalist small-animal feeding preference.

Culicoides (*Drymodesmyia*) *cacticola* Wirth and Hubert

(Fig. 106, 160, 199, 258)

Culicoides (*Oecacta*) *cacticola* Wirth and Hubert, 1960: 653 (as *C. cacticolus*; key; numerical characters; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres; California).

Culicoides (*Drymodesmyia*) *cacticola*: Wirth 1965: 131 (placement in subgenus *Drymodesmyia*). Wirth et al. 1985: 14 (numerical characters; fig. female wing). Wirth et al. 1988: 24 (numerical characters; fig. female wing). Murphree and Mullen 1991: 319 (key; larva; numerical characters; fig. epipharynx, hypostoma, mandible). Breidenbaugh and Mullens 1999a: 855 (egg, larva, pupa; fig. egg, larval head, mouthparts, caudal segment, pupal respiratory trumpet, operculum, caudal segment, chaetotaxy). Borkent and Spinelli 2000: 30 (in Neotropical catalog).

Diagnosis. (Tables 14, 15) Dark brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 bilobed and 8-shaped; pale spots at ~0.3 on M_1 and ~0.5 on M_2; one pale spot in distal half of anal cell; tips of M_1, M_2, usually CuA_1, pale; otherwise CuA_1 and CuA_2 within dark areas; pore of sensory pit on palpal segment 3 <0.3 the diameter of segment, widening internally (as in Fig. 248 *C. sitiens*); tibiae with faint subapical pale band; spermathecae unequal by ~1.2×, ~1.2× longer than wide; ventro-posterior membrane of male sternite 9 not spiculate; ventral apodeme of gonocoxite simple; aedeagus somewhat Y-shaped, constricting at base of median process, tapering to rounded ventrally bent tip ~0.17 width of arm spread, aedeagal ratio 0.46 (0.44–0.50, n = 10); parameres separate, narrowest diameter before first ~90° bend in apical half 0.0024 mm (0.0022–0.0031, n = 10), apices simple pointed bent.

Distribution. California, Nevada (Clark County, **new state record**), Utah (Washington County, **new state record**), Arizona, Texas, Baja California Sur, Sonora (Monarch 2021). A male was collected with UVLT on 2 April 2019 at 36.14032°N 114.72704°W and 384 m elevation in Nevada.

Larval ecology. *Culicoides cacticola* has been reared from rot holes in *Opuntia* Miller, *Carnegiea gigantea* (Ryckman 1960), and *Ferocactus cylindraceus* (Engelmann) Orcutt (Cactaceae) (Breidenbaugh and Mullens 1999a). Apparently, *C. cacticola* uses a wide variety of cacti as larval habitats: the Utah specimens were collected from an area where only one species of cactus (*Cylindropuntia acanthocarpa* [Engelmann and Bigelow] F. M. Knuth, Cactaceae) was present.

Adult behavior. Blood-engorged females have been collected from Japanese quail (*Coturnix japonica*) and bighorn sheep (*Ovis canadensis nelsoni*) (Mullens and Dada 1992a). Mullens and Dada (1992b) collected *C. cacticola* with CO_2-baited traps and, more abundantly, at window lights.

Life cycle. Laboratory studies by Breidenbaugh and Mullens (1999a) found that wild-caught females laid an average of 103 eggs, of which 93% hatched in ~3 d at 21–25 °C. The larvae fed on the bacterial-feeding nematodes *Panagrellus redivivus* (Linnaeus) (Rhabditidae) and *Pelodera*, pupated ~19 d after hatch, and eclosed ~3 d later with a male to female ratio of 31:7.

Symbionts. Mullens et al. (1997b) experimented with the potential biocontrol parasitic nematode, *Heleidomermis magnapapula* in the laboratory and found it readily entered, infected, developed, and emerged from and killed *C. cacticola* larvae.

Atypical biology. A female collected in Riverside County, California, by Xinmi Zhang had three fully developed spermathecae instead of two with a vestigial third (Table 12).

Remarks. The differentiation of *C. cacticola* and *C. torridus* in the Wirth and Hubert (1960) key, where the double distal pale spot in r_3 is conjoined in *C. cacticola* but separated in *C. torridus*, fails to reliably differentiate males and some females. No other characteristic was indicated to distinguish female *C. cacticola* from *C. torridus*. And though some male specimens of *C. cacticola* and *C. torridus* can be distinguished by comparing the relatively small differences of the height of the basal arch of their aedeagi and the narrowest paramere diameter before the 90° bend of the apical portion (indicated in Wirth and Hubert [1960] for *C. torridus* as only "relatively stout"), preliminary data from Xinmi Zhang (personal communication) show that they cannot be differentiated using either the Cytochrome c oxidase I (CO1) or 28S rDNA genes, which readily separate the other *Drymodesmyia* species studied. This suggests that the wing spot and genitalia distinctions are intraspecific variations and that *C. torridus* should be demoted to a synonym of *C. cacticola*.

A male identified by genitalia as intermediate between *C. cacticola* and *C. torridus* (and confirmed by CO1 and 28S rDNA genetics [Xinmi Zhang, personal communication]), collected by Xinmi Zhang with a CO_2-baited trap on 28 June 2019 at the Boyd Deep Canyon Desert Research Center, Riverside County, California, 33.67653°N 116.36969°W at 190 m elevation, had a subapical spine on each paramere (similar to those circled in Fig. 90 *C. calexicanus*). Within the *Drymodesmyia* of North America this characteristic is described for only *C. bakeri* (but with 4–6 spines). However, the specimen's distinct single distal pale spot that does not reach the wing margin in the anal cell excludes that identification.

Culicoides (*Drymodesmyia*) *copiosus* Root and Hoffman

(Fig. 112, 165, 217, 218, 260, 261)

Culicoides copiosus Root and Hoffman, 1937: 171 (female, male; fig. male genitalia, parameres; Federal District, Mexico). Wirth 1952a: 191 (in part; key; female; male genitalia; fig. female wing, palpus, male genitalia).

Culicoides (*Oecacta*) *copiosus*: Khalaf 1954: 37 (assignment to subgenus *Oecacta*). Fox 1955: 232 (in part; key and diagnoses of subgenera; species key; taxonomy). Wirth and Hubert 1960: 657 (key; numerical characters; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres).

Culicoides (*Drymodesmyia*) *copiosus*: Vargas 1960: 40 (subgenus *Drymodesmyia* Vargas; designated *C. copiosus* as type species). Downes and Wirth 1981: 402, 407 (fig. female wing, palpus). Wirth et al. 1985: 14 (numerical characters; fig. female wing). Wirth et al. 1988: 26 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 30 (in Neotropical catalog).

Culicoides (*Drymodesmyia*) *pilosus* Wirth and Blanton, 1959: Vargas 1960: 40 (synonym).

Diagnosis. (Tables 14, 15) Dark brown; wing pattern usually distinct, but may be diffuse; r_2 dark; distal pale spot in r_3 simple, often nearly circular on female; pale spots at ~0.3 on M_1 and ~0.5 on M_2; one or two pale spots in distal half of anal cell, the second one faint if present; tips of M_1, M_2 dark; CuA_1 and CuA_2 within dark areas; pore of sensory pit on palpal segment 3 ~0.3 the diameter of segment, widening internally (as in Fig. 248 *C. sitiens*); tibiae without subapical pale band; spermathecae unequal by ~1.2×, pyriform, largest is larger than flagellomere 1; ventro-posterior membrane of male sternite 9 sparsely to densely spiculate; ventral apodeme of gonocoxite simple, longer than dorsal apodeme; aedeagus V-shaped, rounded tip ~0.15 width of arm spread, aedeagal ratio ~0.4; parameres separate, apices simple pointed bent.

Distribution. California, Utah (Washington County, **new state record**), Arizona, Texas, northern Mexico.

Larval ecology. *Culicoides copiosus* has been reared from rot holes in *Opuntia* and *Pachycereus schottii* (Ryckman 1960). The Utah specimens were collected from an area where only one species of cactus (*Cylindropuntia acanthocarpa*) was present. Wirth's (1952a) description and records (at least in part) of *C. copiosus*, and Ryckman's (1953) report of rearing *C. copiosus* from *Carnegiea gigantea* were misidentifications of *C. ryckmani* (Wirth and Hubert 1960).

Adult behavior. Wirth and Hubert (1960) describe the mandibular teeth on the female as "very fine, almost vestigial", which suggested the possibility *C. copiosus* does not blood-feed. However, *C. ryckmani*, which has been collected blood-engorged (Ryckman 1960), was also described as having "very fine, practically vestigial teeth", much like those of *C. hinmani*, a species known to be ornithophilic.

Culicoides (*Drymodesmyia*) *hinmani* Khalaf

(Fig. 115, 169, 216, 249, 250)

Culicoides hinmani Khalaf, 1952a: 353 (female; male genitalia; fig. male genitalia, parameres, female antenna, palpus; seasonal incidence; Oklahoma).

Culicoides (*Oecacta*) *hinmani*: Khalaf 1954: 37 (assignment to subgenus *Oecacta*). Fox 1955: 241 (key and diagnoses of subgenera; species key; taxonomy). Khalaf 1957: 207 (diagnosis; seasonal incidence). Jones and Wirth 1958: 87 (redescription; *C. hinmani* misidentified by some authors as *C. borinqueni* Fox and Hoffman, which is not Nearctic). Wirth and Hubert 1960: 658 (key; fig. female wing, palpus, spermathecae, male genitalia, parameres).

Culicoides (*Drymodesmyia*) *hinmani*: Wirth 1965: 131 (placement in subgenus *Drymodesmyia*). Childers and Wingo 1968: 15 (key; fig. female wing, spermathecae). Battle and Turner 1971: 49 (female; male genitalia; larval habitats; feeding habits; seasonal distribution; fig. female eye separation, palpus, wing, spermathecae, male genitalia, parameres). Blanton and Wirth 1979: 99 (key; numerical characters; female; male genitalia; fig. female antenna, palpus, wing, eye separation, spermathecae, leg, male genitalia, parameres; larval habitat, feeding habits, seasonal distribution). Guirgis 1984: 402 (female diagnosis). Wirth et al. 1985: 16 (numerical characters; fig. female wing). Murphree and Mullen 1991: 321 (key; larva; numerical characters; fig. head, hypostoma, epipharynx, caudal segment, mandible). Lamberson et al. 1992: 111 (key; pupa; fig. respiratory trumpet, operculum, abdominal segment 9, dorsal tubercles, abdominal chaetotaxy).

Culicoides borinqueni Fox and Hoffman, misidentified: Wirth 1952b: 238 (larval habitat). Snow 1955: 517 (feeding behavior). Wirth and Bottimer 1956: 261 (Texas ecology). Wirth and Jones 1956: 161 (Nearctic).

Diagnosis. (Tables 14, 15) Yellow; wing pattern distinct; r_2 dark; pale spot at end of costa bilobed and wrapping back and beneath r_2; distal pale spots present in r_3, m_1, m_2, cua_1 and anal cell; in r_3 and m_1, not close to wing margin; in r_3, almost round; mandible with 13–15 minute teeth, half normal size; pore of sensory pit on palpal segment 3 <0.3 the diameter of segment, about as deep as wide, slightly widening internally; pale banding subapical on mid femora, basal and subapical on hind femora, subapical on hind tibiae; ventro-posterior membrane of male sternite 9 not spiculate; ventral apodeme of gonocoxite simple, about as long as and only a little more slender than dorsal apodeme; aedeagus simple, nearly V-shaped, median process evenly tapering to broad rounded tip, aedeagal ratio ~0.4; parameres separate, apices simple pointed.

Distribution. Wyoming, North Dakota (Anderson and Holloway 1993) to New York (Guirgis 1984), south to Utah (Grand County), Colorado, Texas to Florida. *Culicoides hinmani* is the northern and eastern treehole-inhabiting counterpart to the morphologically similar and southwestern *C.* (*Drymodesmyia*) *byersi*, which known ranges overlap in only Utah and Colorado.

Larval ecology. *Culicoides hinmani*'s larval habitat is moist treeholes without standing water (Kruger et al. 1990) of pH 8.7–9.3 (Smith and Varnell 1967; Pappas and Pappas 1990). It has been reared from treeholes in tulip tree (*Liriodendron tulipifera* Linnaeus, Magnoliaceae) (Wirth 1952b, as *C. borinqueni*), oak (Wirth and Bottimer 1956, as *C. borinqueni*), magnolia (*Magnolia grandiflora* Linnaeus, Magnoliaceae) (Smith 1965), buckeye (*Aesculus octandra* March, Sapindaceae) (Hair et al. 1966), boxelder, linden, persimmon, post oak, and elm (Pappas et al. 1991).

Adult behavior. Known hosts are unspecified birds (Smith and Varnell 1967; Blanton and Wirth 1979), humans (Snow 1955 as *C. borinqueni*; Smith and Varnell 1967; Hair 1966; Hair and Turner 1968), and turkeys (*Meleagris gallopavo*) (Tanner and Turner 1974; Atkinson 1988); and Hair (1966) collected blood-engorged *C. hinmani* from drop traps baited with domestic rabbit (*Oryctolagus cuniculus*), guinea pig (*Cavia porcellus*), and rat (*Rattus*). Furthermore, consistent with bird-feeding behavior, Atkinson et al. (1983) found *C. hinmani* naturally infected with *Haemoproteus mansoni* (as *H. meleagridis*), a parasite of turkeys.

Snow (1955, as *C. borinqueni*) reported *C. hinmani* to be a diurnal biter with an afternoon activity peak from ground-level into the canopy of a Tennessee forest. This diurnal feeding behavior may explain why *C. hinmani* was poorly represented in light traps, but readily collected in CO_2-baited traps, in the present study (Table 4).

Culicoides (*Drymodesmyia*) *insolatus* Wirth and Hubert

(Fig. 110, 166, 200)

Culicoides (*Oecacta*) *insolatus* Wirth and Hubert, 1960: 654 (key; numerical characters; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres; Baja California).

Culicoides (*Drymodesmyia*) *insolatus*: Wirth et al. 1985: 16 (numerical characters; fig. female wing). Wirth et al. 1988: 26 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 30 (in Neotropical catalog).

Diagnosis. (Tables 14, 15) Dark brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 roundly squarish to slightly bilobed with small anterior cap, oriented perpendicular to M_1; pale spots at ~0.3 on M_1 and ~0.5 on M_2, sometimes the spot at ~0.3 only touching anterior of, not straddling, vein; one distinct pale spot in distal half of anal cell; tips of M_1, M_2, CuA_1 dark; most of CuA_1, all of CuA_2 within dark areas; pore of sensory pit on palpal segment 3 <0.3 the diameter of segment, widening internally (as in Fig. 248 *C. sitiens*); tibiae without subapical pale band; spermathecae unequal by ~1.2×, ~1.1× longer than wide; ventro-posterior membrane of male sternite 9 spiculate; ventral apodeme of gonocoxite simple; aedeagus V-shaped, papilliform tip <0.1 width of arm spread, aedeagal ratio ~0.4; parameres separate, apices simple pointed bent hooklike.

Distribution. California, Baja California, Sonora. The single female I collected with UVLT on 4 April 2019 at 34.81440°N 115.61413°W and 1219 m elevation in the Granite Mountains of San Bernardino County, California, may be near the northern limit for this hot-desert species.

Larval ecology and adult behavior. *Culicoides insolatus* has been reared from rot holes in *Pachycereus schottii* (Ryckman 1960). The specimen I collected was from an area where the cacti flora was predominately several *Opuntia* species, with a few *Ferocactus*, *Echinocereus* Engelmann, and *Mammillaria* Haworth (Cactaceae). However, its adult hosts are unknown, though the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Culicoides (*Drymodesmyia*) *jonesi* Wirth and Hubert

(Fig. 107, 161, 201, 256)

Culicoides (*Oecacta*) *jonesi* Wirth and Hubert, 1960: 650 (key; numerical characters; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres; Texas).

Culicoides (*Drymodesmyia*) *jonesi*: Wirth 1965: 131 (placement in subgenus *Drymodesmyia*). Wirth et al. 1985: 16 (numerical characters; fig. female wing). Murphree and Mullen 1991: 323 (key; larva; numerical characters; fig. epipharynx, hypostoma, mandible).

Culicoides jamaicensis Edwards, misidentified: Wirth and Bottimer 1956: 263 (biology; Texas).

Diagnosis. (Tables 14, 15) Dark brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 bilobed and 8-shaped; pale spots at ~0.3 on M_1 and ~0.5 on M_2; two pale spots in distal half of anal cell; tips of M_1, M_2, CuA_1 pale; most of CuA_1 and CuA_2 within dark areas; pore of sensory pit on palpal segment 3 <0.3 the diameter of segment, widening internally (as in Fig. 248 *C. sitiens*); combined distal five flagellomeres (including intersegmental spaces) on female distinctly shorter than combined proximal eight; pale band subapical on fore femora, basal on all tibiae; spermathecae unequal by ~1.2×, ~1.7× longer than wide, opening ~0.3 as wide as spermatheca, without necks; mean male wing length 0.86 mm (n = 7); ventro-posterior membrane of male sternite 9 not spiculate; ventral apodeme of gonocoxite simple; aedeagus V-shaped, straight-sided until flaring truncate tip ~0.25 width of arm spread, aedeagal ratio ~0.3; parameres separate, apices simple pointed bent.

Distribution. Arizona (Greenlee County, **new state record**), New Mexico (USNM), Texas. Ten males and ten females were collected with UVLT on 10 October 2019 at 32.96215°N 109.30566°W and 1056 m elevation in Arizona. This collection site was in the northwest portion of the Chihuahuan Desert (Brown 1982), as was R. H. Jones's *C. jonesi* collection site in Big Bend National Park, Texas (Wirth and Hubert 1960), suggesting *C. jonesi* may be the Chihuahuan Desert counterpart to the closely related Sonoran Desert inhabiting *C. sitiens*.

Larval ecology and adult behavior. *Culicoides jonesi* has been reared from *Opuntia lindheimeri* Engelmann (Cactaceae) (Wirth and Hubert 1960). My Arizona collection was from an area with abundant cholla (*Cylindropuntia*) and barrel cactus (*Ferocactus*) and included five other cactiphilic *Culicoides* species (Table 9). However, its adult hosts are unknown though the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Wirth and Bottimer (1956) reported their earliest Texas collection of *C. jonesi* adults was 18 February, and their latest was 20 October.

Culicoides (*Drymodesmyia*) *ryckmani* Wirth and Hubert

(Fig. 113, 167, 219, 220, 262)

Culicoides (*Oecacta*) *ryckmani* Wirth and Hubert, 1960: 656 (key; numerical characters; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres; Arizona).

Culicoides (*Drymodesmyia*) *ryckmani*: Wirth 1965: 131 (placement in subgenus *Drymodesmyia*). Wirth et al. 1985: 16 (numerical characters; fig. female wing). Wirth et al. 1988: 28 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 31 (in Neotropical catalog).

Culicoides copiosus, misidentified: Wirth 1952a: 191 (female; male genitalia; fig. female wing, palpus, male genitalia). Ryckman 1953: 164 (biology). Fox 1955: 232 (in part; key and diagnoses of subgenera; species key; taxonomy).

Diagnosis. (Tables 14, 15) Dark brown; wing pattern diffuse, relatively faint; r_2 dark; distal pale spot in r_3 simple, elongate parallel with M_1, ~2× longer than wide; isolated pale spot at ~0.5 on M_2, faint at ~0.3 on or touching anterior to M_1 or absent; one pale spot in distal half of anal cell; tips of M_1, M_2 dark; CuA_1 and CuA_2 within dark areas; pore of sensory pit on palpal segment 3 ~0.3 the diameter of segment, widening internally (as in Fig. 248 *C. sitiens*); tibiae without subapical pale band; spermathecae subequal, subspherical, tiny, smaller than flagellomere 1; ventro-posterior membrane of male sternite 9 not spiculate; ventral apodeme of gonocoxite simple, much more slender and often shorter than the broad, pointed dorsal apodeme; aedeagus V-shaped, truncate tip ~0.2 width of arm spread, aedeagal ratio ~0.36; parameres separate, apices simple pointed bent.

Distribution. California, Utah (Washington County, **new state record**), Arizona, Texas, Baja California, Baja California Sur.

Larval ecology. *Culicoides ryckmani* has been reared from rot holes in *Opuntia*, *Carnegiea gigantea*, *Pachycereus pringlei*, and *Pachycereus schottii* (Ryckman 1960). Apparently, *C. ryckmani* uses a wide variety of cacti as larval habitats: the California specimens I collected were from an area where the cacti flora was predominately several *Cylindropuntia* and *Opuntia* species, with a few *Ferocactus*, *Echinocereus*, and *Mammillaria*; and the Utah specimens were collected from an area where only *Cylindropuntia acanthocarpa* was present.

Adult behavior. Blood-engorged females have been collected from the occupied nest of a house finch (*Haemorhous mexicanus*) (Ryckman 1960). Mullens and Dada (1992b) collected *C. ryckmani* with CO_2-baited traps and, more abundantly, at window lights.

Symbionts and atypical biology. A male I collected in Mohave County, Arizona, was parasitized by a larval mite (Table 10); and a female collected in San Diego County, California, by S. Anthony had three fully developed spermathecae instead of two with a vestigial third (Table 12).

Culicoides (*Drymodesmyia*) *sitiens* Wirth and Hubert

(Fig. 108, 162, 202, 248, 255)

Culicoides (*Oecacta*) *sitiens* Wirth and Hubert, 1960: 652 (key; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres; California).

Culicoides (*Drymodesmyia*) *sitiens*: Wirth 1965: 131 (placement in subgenus *Drymodesmyia*). Atchley 1967: 981 (key; numerical characters; female; male genitalia; fig. female wing, palpus, tibial comb, male genitalia, parameres). Wirth et al. 1985: 16 (numerical characters; fig. female wing). Wirth et al. 1988: 28 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 31 (in Neotropical catalog).

Diagnosis. (Tables 14, 15) Dark brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 bilobed and 8-shaped; pale spots at ~0.3 on M_1 and ~0.5 on M_2; tips of M_1, M_2 pale; CuA_1 and CuA_2 within dark areas except at tip of CuA_1; pore of sensory pit on palpal segment 3 <0.3 the diameter of segment, widening internally; combined distal five flagellomeres (including intersegmental spaces) on female distinctly longer than combined proximal eight; tibiae without subapical pale band; spermathecae unequal by ~1.1×, ~1.3× longer than wide, opening ~0.3 as wide as spermatheca, without necks; mean male wing length 0.98 mm (n = 5); ventro-posterior membrane of male sternite 9 not spiculate; ventral apodeme of gonocoxite simple; aedeagus V-shaped, straight-sided until flaring truncate tip ~0.25 width of arm spread, aedeagal ratio ~0.3; parameres separate, apices simple pointed bent back hooklike.

Distribution. California, Utah (Grand County), Arizona, New Mexico, Baja California. *Culicoides sitiens* seems to be the Sonoran Desert counterpart to the closely related Chihuahuan Desert inhabiting *C. jonesi*.

Larval ecology. *Culicoides sitiens* has been reared from *Opuntia* and *Pachycereus schottii* rot holes (Ryckman 1960; Wirth and Hubert 1960).

Adult behavior. Known hosts are Japanese quail (*Coturnix japonica*) and domestic rabbit (*Oryctolagus cuniculus*) (Mullens and Dada 1992a).

Culicoides (*Drymodesmyia*) *torridus* Wirth and Hubert

(Fig. 109, 163, 203)

Culicoides (*Oecacta*) *torridus* Wirth and Hubert, 1960: 654 (key; numerical characters; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres; Arizona).

Culicoides (*Drymodesmyia*) *torridus*: Wirth et al. 1985: 16 (numerical characters; fig. female wing). Wirth et al. 1988: 28 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 31 (in Neotropical catalog).

Diagnosis. (Tables 14, 15) Dark brown; wing pattern distinct; r_2 dark; distal pale spot in r_3 bilobed, divided into two distinct spots; pale spots at ~0.3 on M_1 and at ~0.5 on M_2; one pale bilobed spot in distal half of anal cell; tips of M_1, M_2, sometimes CuA_1 pale; most of CuA_1 and CuA_2 within dark areas; pore of sensory pit on palpal segment 3 <0.3 the diameter of segment, widening internally (as in Fig. 248 *C. sitiens*); tibiae without subapical pale band; spermathecae unequal by ~1.2×, ~1.1× longer than wide; ventro-posterior membrane of male sternite 9 not spiculate; ventral apodeme of gonocoxite simple; aedeagus somewhat Y-shaped, constricting at base of median process, tapering to truncate tip ~0.17 width of arm spread, aedeagal ratio 0.38 (0.33–0.41, n = 15); parameres separate, narrowest diameter of paramere before first ~90° bend in apical half 0.0032 mm (0.0025–0.0037, n = 15), apices simple pointed bent.

Distribution. California, Nevada (Clark County, **new state record**), Arizona (Greenlee County, **new state record**), Baja California, Baja California Sur, San Luis Potosi (**new state record** [Monarch 2021]), Puebla (**new state record** [Monarch 2021]), Oaxaca (**new state record** [Monarch 2021]). A male was collected with UVLT on 2 April 2019 at 36.14032°N 114.72704°W and 384 m elevation in Nevada; and a female and three males were collected with UVLT on 10 October 2019 at 32.96215°N 109.30566°W and 1056 m elevation in Arizona.

Larval ecology and adult behavior. *Culicoides torridus* has been reared from rot holes in *Pachycereus schottii* (Ryckman 1960) and *Ferocactus cylindraceus* (data from slide labeled Riverside County, California, 9 April 1996, collector M. Breidenbaugh). However, its adult hosts are unknown though the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Remarks. Males of *C. torridus* and *C. cacticola* can be difficult to distinguish, and there is genetic evidence that they are conspecific (Xinmi Zhang, personal communication). The *C. torridus* males were collected in the same traps in Clark County, Nevada, and Greenlee County, Arizona, as the *C. cacticola* males (Table 9), lending circumstantial evidence to this. See *C. cacticola* remarks.

Subgenus *Haematomyidium* Goeldi

Culicoides (*Haematomyidium*) *kettlei* Breidenbaugh and Mullens

(Fig. 80, 133, 187, 188)

Culicoides (*Haematomyidium*) *kettlei* Breidenbaugh and Mullens, 1999b: 150 (egg, larva, pupa, adult female; male genitalia; fig. egg, larval head, caudal segment, mouthparts, pupal respiratory trumpet, operculum, caudal segment, chaetotaxy, female eyes, antenna, palpus, legs, wing, spermathecae, male genitalia; California).

Diagnosis. (Tables 14, 15) Brown; r_2 dark; distal pale spot in r_3 irregular, crude C- or mushroom-shaped, sometimes extending faintly along anterior wing margin into apex of cell to form an arch; two irregular pale spots in m_1; distal pale spots in m_2, cua_1, anal cell; M_1 and M_2 without pale spots; one pale spot in distal half of anal cell, not reaching wing margin; male tergite 9 apicolateral processes as long as ~0.4 the distance between them; ventral apodeme of gonocoxite with two well-developed widely divergent processes, footlike; aedeagus simple, median process tapering to blunt minutely serrate tip, aedeagal ratio ~0.6; parameres separate, with distinct bulbous submedian lobe smaller than width of paramere, and with subapical fringe of spines. (Male genitalia indistinguishable from that of *C. stellifer.*)

Distribution. California, Baja California.

Larval ecology and adult behavior. Breidenbaugh and Mullens (1999a) collected adults with emergence traps from soil margins of an ephemeral creek at 300–350 m elevation in San Bernardino County, California. They (1999b) also report collections of *C. kettlei* females with CO_2-baited traps, and Mullens and Dada (1992a, as "*Culicoides* n. sp. near *lahillei*") collected an unfed female from a bighorn sheep, which, along with its SCo pattern reduced to only the proximal flagellomeres, strongly suggests it is mammalophilic.

Life cycle. Laboratory studies by Breidenbaugh and Mullens (1999b) found that wild-caught *C. kettlei* laid an average of 74 eggs and the larvae fed on bacterial-feeding *Pelodera* nematodes and started pupating 26 d after egg hatch at 21 °C.

Symbionts. Mullens et al. (1997b) experimented with the potential biocontrol parasitic nematode, *Heleidomermis magnapapula* in the laboratory and found it readily penetrated but did not develop or emerge from *C. kettlei* (as "*C.* n. sp. near *lahillei* [Iches]") larvae, which continued to develop to adults with no sign of the nematode.

Remarks. Willis Wirth referred to this species as new species number 120 (Breidenbaugh and Mullens 1999b).

Culicoides kettlei has considerable wing pattern variation (Fig. 133, 187, 188) and is often similar to *C. stellifer* (Fig. 134, 135, 189); and their quantitative characters (Table 14), leg-banding (Table 15), and genitalia are nearly identical. Other than for the number of distal pale spots in m_1 and the anal cell, I could find no consistent ways to distinguish adult *C. kettlei* from *C. stellifer.* In addition, other than the lack of hypostomal teeth on *C. kettlei*, I could find no distinct differences between the larval and pupal descriptions of *C. kettlei* in Breidenbaugh and Mullens (1999b) and those of *C. stellifer* in Blanton and Wirth (1979) and Murphree and Mullen (1991). See *C. stellifer* remarks.

Culicoides (*Haematomyidium*) *stellifer* (Coquillett) (new status)

(Fig. 134, 135, 189)

Ceratopogon stellifer Coquillett, 1901: 603 (key; female; District of Columbia).

Culicoides stellifer (Coquillett): Kieffer 1906: 55 (combination). Malloch 1915: 300 (key; male, female; distribution; fig. male wing). Hoffman 1925: 295 (key; female; fig. wing, mesonotum). Root and Hoffman 1937: 162 (key; female; male genitalia; fig. male genitalia). Fox 1942: 419 (pupa; fig. respiratory trumpet, female anal segment). James 1943: 148 (seasonal distribution; Colorado). Knowlton and Fronk 1950: 114 (Utah: Cache County). Knowlton and Kardos 1951: 163 (Utah: Kane County). Wirth 1952a: 184 (key; male genitalia; fig. dorsal thoracic pattern, aedeagus). Bullock 1952: 20 (key; female; male genitalia; biology; seasonal distribution; Utah: Salt Lake County). Rees and Bullock 1954 (Utah: Salt Lake County). Foote and Pratt 1954: 32 (key; diagnoses of female, male, pupa; fig. female wing, mesonotum, palpus, male genitalia).

Culicoides (*Oecacta*) *stellifer*: Khalaf 1954: 37 (assignment to subgenus *Oecacta*). Fox 1955: 255 (key and diagnoses of subgenera; species key; taxonomy). Wirth and Bottimer 1956: 263 (Texas ecology). Forattini 1957: 421 (key; female; male genitalia; fig. female eyes, flagellomeres 8–9, palpus, mesonotum, wing and wing variation, male genitalia, aedeagus, parameres, pupal anal segment, respiratory trumpet; distribution map). Jamnback 1965: 99 (key; female; male genitalia; pupa, larva; biology; fig. male genitalia, female wing, antenna, palpus, eye separation, pupa, larva). Atchley 1967: 992 (key; numerical characters; female; male genitalia; fig. female wing, palpus, tibial comb, spermathecae, male genitalia, parameres). Childers and Wingo 1968: 18 (key; biology; fig. female wing, spermathecae). Battle and Turner 1971: 81 (female; male genitalia; larval habitats; feeding habits; seasonal distribution; fig. female eye separation, palpus, wing, spermathecae, male genitalia, parameres). Blanton and Wirth 1979: 149 (key; numerical characters; female; male genitalia; pupa, larva; fig. female antenna, palpus, wing, eye separation, spermathecae, leg, male genitalia, parameres; larval habitat; feeding habits; seasonal distribution). Wirth et al. 1985: 28 (numerical characters; fig. female wing). Murphree and Mullen 1991: 352 (key; larva; numerical characters; fig. thorax, epipharynx, mandible, hypostoma, caudal segment).

Culicoides (*Haematomyidium*) *stellifer*: Vargas 1960: 42 (assignment to subgenus *Haematomyidium*).

Diagnosis. (Tables 14, 15) Brown; wing pattern distinct; r_2 dark; three pale spots past end of costa in r_3, the first at tip of costa bilobed 8-shaped and not extending to M_1 or r-m crossvein, the second a crude C-shape almost always connected along anterior wing margin to a small third spot at apex of cell to form an arch; three irregular pale spots in m_1, sometimes conjoined narrowly along posterior margin of cell; m_2, cua_1 with pale spots; M_1 and M_2 without pale spots; two pale spots in distal half of anal cell, the second reaching wing margin, on male the spots merged forming a lobed spot reaching wing margin; male tergite 9 apicolateral processes as long as ~0.4 the distance between them; ventral apodeme of gonocoxite with two well-developed widely divergent processes, footlike; aedeagus simple, median process tapering to blunt minutely serrate tip, aedeagal ratio ~0.6; parameres separate, with blunt submedian lobe smaller than width of paramere, and with subapical fringe of spines. (Male genitalia indistinguishable from that of *C. kettlei* Fig. 80.)

Distribution. North America from Idaho, Montana to Nova Scotia, south to California, Florida, Mexico, Trinidad, Venezuela. Utah: Box Elder, Cache, Garfield, Grand, Kane, Salt Lake, Summit counties.

Larval ecology. Immatures have been collected or reared from ooze from tree wounds (Wirth 1952a), heavily vegetated and bare moist mud with rotting leaves at pond margins, a shaded stream margin with decaying leaves (Williams 1955), mud at pond margins (Wirth and Bottimer 1956), shallow stream-edge depressions with decaying leaves (Murray 1957), freshwater soil (Jones 1961b), moist alkaline dung-polluted sunlit soil, leaves in stream and pond margins, buckeye (*Aesculus octandra*) treeholes (Hair et al. 1966), sand bank of pool adjacent to creek (Childers and Wingo 1968), and muddy lake, pond, marsh, and stream margins often with wet leaves and grass (Blanton and Wirth 1979). In laboratory studies, Erram and Burkett-Cadena (2018) determined *C. stellifer* prefers to oviposit on low-organic mud and *Sphagnum* moss rather than field water- or manure-polluted mud.

Erram et al. (2019) reared *C. stellifer* from mud substrate samples collected over three months in Florida from the edges of puddle, seepage, and stream habitats, which produced 94, 12, and 10 adults, respectively. They also characterized the samples for P, K, Mg, Ca, Cu, Mn, Zn, organic matter, pH, moisture, electrical conductivity, and microbes and found that adult production in the puddle samples was correlated (in descending order of importance) positively with K and Zn concentrations and negatively with pH, P concentration, electrical conductivity, Mg concentration, and organic matter.

Life cycle. When experimenting with rearing *C. stellifer* in the laboratory at 26 °C, Erram and Burkett-Cadena (2020) found development took an average of 28 d from oviposition to adult emergence when reared on agar with nematodes as the food source; and survivorship was 38%. The egg stage lasted 3–4 d with a 56% hatch rate. The larval stage lasted an average of 21 d with 71% survival to pupation, which lasted an average of 3.5 d with 95% survival to adult emergence.

Adult behavior. Murray (1957) reported *C. stellifer* to be day-biters and most active in lowland fields and pastures in Virginia. However, Blanton and Wirth (1979) said this record likely refers to *Culicoides paraensis* (Goeldi); and Hair (1966) found flight activity in Virginia was through the night, greatest during 2100–2400 hours, then tapering off to 0600 hours. Furthermore, Murray's habitat distinctions may be biased by his use of light traps, which are more effective in open areas. Possibly clarifying this, Swanson and Adler (2010), using CO_2-baited unlit traps, collected 10% of their *C. stellifer* at 1.5 m, 77% at 5 m, and 12% at 10 m up in the forest canopy; and McGregor et al. (2018) found *C. stellifer* significantly more abundant in UVLTs 6–9 m up rather than at ground-level within the forest—a distinction Murray did not make. In addition, Sloyer (2018), using light traps with and without CO_2, characterized 23 Florida habitat variables for temperature, precipitation, and vegetation for predicting *C. stellifer* host-seeking activity; however, the results are of limited usefulness in the generally more arid and higher altitude southwestern United States.

Culicoides stellifer is mostly mammalophilic. Known hosts are human (Bullock 1952; Hair 1966; Reeves et al. 2004; Sloyer et al. 2019a), goat, turkey (Humphreys and Turner 1973), cow (Schmidtmann et al. 1981; Zimmerman and Turner 1983; Mullen et al. 1985a), sheep (Zimmerman and Turner 1983), blue jay (*Cyanocitta cristata*) (Garvin and Greiner 2003), white-tailed deer (*Odocoileus virginianus*) (Mullen et al. 1985a; Smith and Stallknecht 1996; Hopken et al. 2017; McGregor et al. 2018; Sloyer et al. 2019a), raccoon (*Procyon lotor* [Linnaeus], Procyonidae), eastern gray squirrel (*Sciurus carolinensis*) (McGregor et al. 2018), and chicken (*Gallus gallus*) (Sloyer et al. 2019a). In Florida, McGregor et al. (2019c) found *C. stellifer* prefers to feed on red deer (*Cervus* sp.) and fallow deer (*Dama dama* [Linnaeus], Cervidae) rather than Bovidae and white-tailed deer.

Hair (1966) collected blood-engorged *C. stellifer* from drop traps baited with domestic rabbit, eastern cottontail rabbit (*Sylvilagus*), guinea pig (*Cavia porcellus*), opossum (*Didelphis*), and turkey (*Meleagris gallopavo*). Gerhardt (1986) collected *C. stellifer* from white-tailed deer and cow-baited drop traps. Schmidtmann et al. (1981) reported *C. stellifer* strongly preferred biting calves on the belly instead of on the head, back, or legs. Wieser-Schimpf et al. (1991) compared collections from New Jersey UVLTs with and without CO_2 in Louisiana and found those with CO_2 collected a greater but statistically insignificant number of nulliparous, parous empty, engorged, and gravid females.

Vector potential. *Culicoides stellifer* has been found naturally infected with vesicular stomatitis New Jersey virus (VSV) (*Vesiculovirus*, Rhabdoviridae) (Walton et al. 1987, Kramer et al. 1990), bluetongue virus (BTV) (Mellor et al. 2000; McGregor et al. 2019b; Becker et al. 2020), West Nile virus (WNV) (Sabio 2005; Sabio et al. 2006), and epizootic hemorrhagic disease virus (EHDV) (McGregor et al. 2019b). The infection rates and estimated concentrations of WNV were similar to those known for mosquito vectors of WNV. Mullen et al. (1985b) demonstrated female *C. stellifer* could be infected by intrathoracic inoculation and harbor BTV, though the experiment did not prove *C. stellifer*'s ability to be naturally infected with BTV. More recently, McGregor et al. (2019b) collected *C. stellifer*, with no visible blood in the gut, infected with EHDV and BTV retained from feeding on white-tailed deer, fallow deer, and elk (*Cervus* spp.) during EHDV and BTV episodes in Florida.

Furthermore, if *C. stellifer* is found to be a competent vector, its May to September seasonal distribution in both Grand County (Table 5) and Salt Lake County (Bullock 1952) would likely give it an important role in transmitting EHDV and BTV in the western United States.

Symbionts. *Culicoides stellifer* is sometimes heavily parasitized by mermithid nematodes, which produce intersexes in surviving adult midges. Smith and Perry (1967) collected 44 mermithid-induced intersexes (27% of males) in Florida, with intersex rates up to 62%; Wieser-Schimpf et al. (1991) collected 31 intersexes (2% of total males and females) in Louisiana, but did not check for parasitism; and, Erram et al. (2019) found 5% of the adults reared from puddle samples collected over three months in Florida were mermithid-parasitized intersexes. Another symbiont study (Erram 2016) found that the bacterial flora on adult female *C. stellifer* consisted predominately of Proteobacteria—likely because of its relatively unpolluted larval habitat.

Remarks. North American authors (Blanton and Wirth 1979; Wirth et al. 1985; et al.) and the most recent catalog (Borkent and Dominiak 2020) list *C. stellifer* in subgenus *Oecacta* Poey, whereas European authors (Meiswinkel et al. 2004; EFSA 2009) follow Vargas's (1960) placement of *C. stellifer* in subgenus *Haematomyidium*. Because of the close similarity of *C. stellifer* to *C.* (*Haematomyidium*) *kettlei* (see *C. kettlei* remarks), because of the closer similarity of the male genitalia of *C. stellifer* to that of *C. paraensis* (the subgenus *Haematomyidium* type species) than to that of *Culicoides furens* (Poey) (the subgenus *Oecacta* type species), and because Forattini (1957) keys *C. stellifer* and *C. paraensis* to the same terminal couplet in his subgenus *Oecacta* key, I am following Vargas's (1960) assignment of *C. stellifer* to subgenus *Haematomyidium* (**new status**) Furthermore, of the 152 species of subgenus *Oecacta* listed in Borkent and Dominiak (2020), only *C. stellifer* has a Nearctic type and only six (*Culicoides alahialinus* Barbosa, *Culicoides barbosai* Wirth and Blanton, *Culicoides cancer* Hogue and Wirth, *C. furens*, *Culicoides furensoides* Williams, and *Culicoides gorgasi* Wirth and Blanton) have Neotropical types, indicating subgenus *Oecacta* is presently a predominantly Afro-Eurasian assemblage.

Mitochondrial DNA CO1 gene sequences suggest *C. stellifer* is a species complex (Shults et al. 2020). Specimens from Texas, South Carolina, and Florida showed relatively little genetic divergence between populations, whereas specimens from Ontario clustered in a divergent genetic group more in accordance with that of a different species.

Subgenus *Monoculicoides* Khalaf

***Culicoides* (*Monoculicoides*) *grandensis* Grogan and Phillips**

(Fig. 53, 173)

> *Culicoides* (*Monoculicoides*) *grandensis* Grogan and Phillips, 2008: 196 (diagnosis, male, female; fig. female antenna, palpus, spermatheca, wing; male genitalia; Utah: Grand County). Grogan and Lysyk 2015: 9 (key; diagnosis; bionomics; assignment to "*C. nubeculosus-stigma* complex"; not "n. sp. 113"). Shults and Borkent 2018: 458 (key; numerical characters; female pupa; fig. dorsal apotome).

Diagnosis. (Tables 14, 15) Pale brown; wing with faint pattern; in r_3, m_1, m_2, cua_1 extensive and more of dark irregular curves and pale streaks than ovoid spots; scutum without dark spots at seta bases; legs without apparent banding; mandibular and lacinial teeth vestigial; one sclerotized spermatheca, ovoid, with opening >0.5 the diameter of the spermatheca, without neck; aedeagus bare, entire; parameres fused basally.

Distribution. Utah (Grand County).

Larval ecology. Jones (1961b) collected *C. grandensis* (as "n. sp.") pupae from the nonvegetated sunlit margin of an alkaline stream near Cisco (47 km north-northeast of Moab), Grand County, along with immatures of a Stonei group species (as *C. stonei*), *C. occidentalis* or *C. sonorensis* (as *C. variipennis australis*), *C. haematopotus* (may be *C. defoliarti*), *C. jamesi*, and *C. crepuscularis*.

Adult behavior. The absence of mandibular and lacinial teeth on the female indicates *C. grandensis* does not blood-feed.

One female was incandescent light-trapped 18 September 2001 at 38.54606°N 109.59159°W in Grand County. Additional data from Jones's 30 May 1958 collection of two pupae reared with a probable emergence date of 20 June 1958 (Grogan and Phillips 2008) are also included in the seasonal distribution (Table 5).

Remarks. *Culicoides grandensis* was originally thought to be Willis Wirth's and Antony Downes's "n. sp. 113" (Grogan and Phillips 2008). It is now thought that "n. sp. 113" is likely *Culicoides stigma* (Meigen) (Grogan and Lysyk 2015).

Culicoides (*Monoculicoides*) *occidentalis* Wirth and Jones

(Fig. 48, 49, 51)

Culicoides (*Monoculicoides*) *variipennis occidentalis* Wirth and Jones, 1957: 21 (diagnosis; fig. female palpus, mesonotum, wing; California). Jorgensen 1969: 27 (in part; key; quantitative characters; female; male genitalia; seasonal distribution; fig. male genitalia, parameres, female wing, spermatheca, palpus, antenna; Washington). Wirth et al. 1985: 30 (numerical characters). Wirth et al. 1988: 56 (numerical characters; fig. female wing). Tabachnick 1992 (genetic comparison of *C. v. sonorensis*, *C. v. occidentalis*, and *C. v. variipennis*). Velten and Mullens 1997 (comparison of *C. v. sonorensis* and *C. v. occidentalis*; fig. pupal terminalia, male aedeagi; biology).

Culicoides (*Monoculicoides*) *occidentalis*: Jorgensen 1969: 32 (status change). Downes 1978: 63 (status change as *C. o. occidentalis*; fig. female palpus). Holbrook et al. 2000: 70 (key; diagnosis; fig. female palpus, aedeagus). Borkent and Spinelli 2000: 36 (in Neotropical catalog). Shults and Borkent 2018: 459 (key; numerical characters; male pupa, female pupa; fig. habitus, respiratory organ, female dorsal apotome, mouthparts, thoracic setae, abdominal segments 8–9, male abdominal segment 4).

Culicoides variipennis (Coquillett), misidentified in part: Wirth 1952a: 180, 252 (key; female; male genitalia; pupa, larva; distribution; fig. female wing, dorsal thoracic patterns, palpus, pupa, larva). Bullock 1952: 18 (key; female; male genitalia; biology; habitat and biotic associations; fig. larvae, pupae; seasonal distribution; Utah: Salt Lake County). Rees and Bullock 1954 (Utah: Salt Lake County). Foote and Pratt 1954: 34 (key; diagnoses of female, male, pupa; biology; fig. female wing, mesonotum, palpus, male genitalia). Fox 1955: 258 (key and diagnoses of subgenera; species key; taxonomy). Hensleigh and Atchley 1977: 379 (morphometric analysis). Blanton and Wirth 1979: 161 (key; numerical characters; female; male genitalia; pupa, larva; fig. female antenna, palpus, wing, eye separation, spermatheca, leg, male genitalia, parameres; larval habitat; feeding habits; seasonal distribution). Wirth and Morris 1985: 165 (reevaluation of *C. variipennis* complex). Murphree and Mullen 1991: 354 (Borax Lake, California; key; larva; numerical characters; fig. head, thorax, epipharynx, hypostoma, mandible, caudal segment).

Culicoides variipennis australis Wirth and Jones, misidentified: Jones 1961b: 703 (in part; pupal habitats; Utah). Atchley 1967: 975 (synonym subordinate to *C. v. sonorensis*, in part; New Mexico).

Culicoides variipennis sonorensis Wirth and Jones, misidentified: Atchley 1967: 974 (in part; key; numerical characters; female; male genitalia; variation; feeding habits; fig. female wing, palpus, tibial comb, spermatheca, male genitalia, parameres; New Mexico).

Diagnosis. (Tables 14, 15). (Females morphologically indistinguishable from *C. sonorensis*.) Dark brown; wing with prominent pattern; in r_3, m_1, m_2, cua_1 extensive and more of dark irregular curves, pale streaks, and zigzags than ovoid spots; scutum with dark spots at seta bases (as in Fig. 55 *C. sonorensis*); legs with distinct pale banding; female palpal segment 3 swollen 1.8–3.0× longer than wide, with medium to large rounded or irregularly shaped and often partly divided sensory pit; one sclerotized spermatheca, U-shaped, with opening >0.5 the diameter of the spermatheca, without neck (as in Fig. 54 *C. sonorensis*); parameres fused basally; ventral surface of aedeagus bare, apex deeply bifurcated into bladelike tips.

Distribution. British Columbia, Alberta, south through Washington, Oregon, California, Nevada, Utah (Grand, Salt Lake counties, **new state record**), Arizona (**new state record** [Monarch 2021]), to Baja California, Baja California Sur, with disjunct populations in New Mexico, Texas, Puebla (Huerta et al. 2012).

Biology. Because of the complex synonymy of the Variipennis group, *C. occidentalis*, *C. sonorensis*, and *C. variipennis* conflate in many records before 2000. Though I have tried to present only data associated with *C. occidentalis*, it is possible some of it refers to *C. sonorensis*, *C. variipennis*, or a combination.

Larval ecology. *Culicoides occidentalis* is likely to be widespread in highly alkaline or saline sites in Utah. Bullock (1952) collected and reared immatures likely to be *C. occidentalis* (as *C. variipennis*) from a brine (21% salts) borrow pit in Salt Lake County. Jones (1961b) also collected pupae likely to be *C. occidentalis* (as *C. variipennis*) from a sunlit sandy seep area along the margin of a highly saline-water pool near the Great Salt Lake in Salt Lake County; and pupae likely to be both *C. occidentalis* and *C. sonorensis* (as *C. variipennis australis*) from the nonvegetated sunlit margin of an alkaline stream near Cisco (47 km north-northeast of Moab), Grand County, along with immatures of a Stonei group species (as *C. stonei*), *C. jamesi*, *C. haematopotus* (may be *C. defoliarti*), *C. grandensis* (as "n. sp."), and *C. crepuscularis*. I was able to rear *C. occidentalis* along with *C. sonorensis*, *C. crepuscularis*, and *C. mortivallis* from mud collected on 10 September 2020 from nonvegetated sunlit alkaline pools in a stream bed in Grand County at 38.96339°N 109.33585°W and 1315 m elevation in the same wash as Jones's Cisco pupae collection site. Further confirmation of the presence of *C. occidentalis* and *C. sonorensis* at that site and *C. occidentalis* in Salt Lake County was from CO1 gene analysis of specimens collected and tested by Phillip Shults (personal communication).

Rowley (1967) collected or reared immatures from highly alkaline potholes of pH 9.9 in Washington. Colwell (1981) collected larvae in Northern California from near the shoreline of Borax Lake (38.985°N 122.673°W), a highly alkaline pond with conductivity of 3–130 mS/cm, pH 9.2–10, 1000–5000 ppm alkalinity, and 200–900 ppm boron. He found eggs laid in the eulittoral zone or on floating algae and collected adults near the site February to November. Schmidtmann et al. (2000) reported aquatic habitats of *C. occidentalis* immatures had significantly higher conductivity, boron, potassium, and chloride, but lower organic matter and significantly lower phosphate, than *C. sonorensis* habitats. Among these variables, the most significant discriminator was electrical conductivity, which averaged ~9× higher in the *C. occidentalis* habitats, which included desert lake margins, sloughs at a dry lake edge, a shallow desert pond, a salt marsh, a saline creek, and a saline hot spring (Schmidtmann 2006).

Adult behavior. Tempelis and Nelson (1971) identified 325 blood meals from mixed *C. sonorensis* and *C. occidentalis* in Kern County, California, as: 51% Bovidae (cattle and sheep), 46% Leporidae (rabbits and hares), 1% Canidae (dogs), 1% Equidae (horses), and 1% unidentified mammals. *Culicoides occidentalis* collected in Northern California had blood meals from black-tailed deer (*Odocoileus hemionus* Rafinesque, Cervidae), black-tailed jackrabbit (*Lepus californicus*), cow (*Bos taurus*), dog (*Canis lupus* Linnaeus, Canidae), goat (*Capra aegagrus*), sheep (*Ovis aries*), donkey (*Equus africanus* Linnaeus, Equidae), horse (*Equus ferus*), pig (*Sus scrofa* Linnaeus, Suidae), and emu (*Dromaius novaehollandiae* [Latham], Casuariidae) (Hopken et al. 2017). They proposed the aberrant bird (emu) record may be due to the similarity of the emu's size and CO_2 output to *C. occidentalis*'s normal mammalian hosts; and, Koch and Axtell's (1979) study of *Culicoides* host attraction support this possibility. It can also be a severe biting pest of humans (Colwell 1981).

Nelson (1965) and Nelson and Bellamy (1971) collected many males (as *C. v. occidentalis*) with CO_2-baited traps, suggesting the males seek hosts to find females for mating. In addition, *C. occidentalis* male swarms have been observed at ~2 m above the ground, above and downwind of bushes (Holbrook et al. 2000).

Vector potential. *Culicoides occidentalis* has not been implicated in bluetongue virus (BTV) or other arbovirus epizootics, and its saline larval habitats tend to be separate from the normal habitats of bovid hosts. In addition, laboratory studies have shown it to have a significantly lower susceptibility to oral infection by BTV than *C. sonorensis* (Holbrook and Tabachnick 1995). However, Hopken et al. (2017) found *C. occidentalis* more abundant and *C. sonorensis* less abundant than previously thought in Lake County, California, which has had BTV and epizootic hemorrhagic disease virus (EHDV) activity (Roug et al. 2012), suggesting *C. occidentalis* should be studied further as a potential vector.

Symbionts. Mullens et al. (1997b) experimented with the potential biocontrol parasitic nematode, *Heleidomermis magnapapula* in the laboratory and found it readily entered, infected, developed, emerged from, and killed *C. occidentalis* larvae. Also, Mullens et al. (2008) reported that others have found *C. occidentalis* larvae naturally parasitized by nematodes (likely *H. magnapapula*) in mud having 6–20 g/L salt content in Virginia.

Remarks. Tabachnick (1992) provided genetic evidence that *C. v. variipennis*, *C. v. sonorensis*, and *C. v. occidentalis* are distinct over their wide geographic ranges and are likely different species. In addition, Velten and Mullens (1997) were able to hybridize *C. v. occidentalis* and *C. v. sonorensis* in the laboratory and produce fertile hybrids, but summarized information showing no gene flow between the species in nature, concluding the subspecies are distinct but closely related. Based on this and more genetic evidence, Holbrook et al. (2000) elevated *C. variipennis*, *C. sonorensis*, and *C. occidentalis* to species status; and Hopken (2016) and Hopken et al. (2017) reported CO1 gene evidence confirming *C. occidentalis* to be distinct from both *C. sonorensis* and *C. variipennis*. See *C. sonorensis* remarks.

Culicoides (*Monoculicoides*) *sonorensis* Wirth and Jones

(Fig. 2, 46, 47, 50, 54, 55, 174)

Culicoides (*Monoculicoides*) *variipennis sonorensis* Wirth and Jones, 1957: 18 (diagnosis; fig. aedeagus, female palpus, mesonotum, wing; Arizona). Atchley 1967: 974 (in part; key; numerical characters; female; male genitalia; variation; feeding habits; fig. female wing, palpus, tibial comb, spermatheca, male genitalia, parameres; New Mexico). Childers and Wingo 1968: 20 (key; numerical characters; biology; fig. female wing, spermathecae). Wirth et al. 1985: 30 (numerical characters; fig. female wing). Wirth et al. 1988: 56 (numerical characters; fig. female wing). Tabachnick 1992 (genetic comparison of *C. v. sonorensis*, *C. v. occidentalis*, and *C. v. variipennis*). Velten and Mullens 1997 (comparison of *C. v. sonorensis* and *C. v. occidentalis*; fig. pupal terminalia, male aedeagi; biology).

Culicoides (*Monoculicoides*) *sonorensis*: Holbrook et al. 2000: 70 (status change; key; diagnosis; fig. female palpus, aedeagus; Arizona). Borkent and Spinelli 2000: 36 (in Neotropical catalog). Reeves 2008: 372 (osmoregulatory anal papillae and cutaneous chloride cells stained and identified; fig. larva, pupa). Borkent 2012: 70 (fig. pupal habitus, cephalothorax, head). Borkent 2014: 24 (key to genera of pupae of Ceratopogonidae; fig. pupal habitus, cephalothorax). Abubekerov 2014: 66 (egg, larva, pupal respiratory trumpet; biology; fig.). Nayduch et al. 2014: 1 (transcriptome). Shults et al. 2016: 280 (pupa; fig.). Abubekerov and Mullens 2018: 554 (egg, larval instars; fig. egg, head, mandibles, antenna, proleg, epipharynx, hypopharynx; comparison of colony-reared with wild-collected fourth instar larvae). Shults and Borkent 2018: 453 (key; numerical characters; fig. female dorsal apotome, male abdominal segment 4). Morales-Hojas et al. 2018 (full genome sequence). Rozo-Lopez et al. 2020: 8 (male and female reproductive tracts; fig.).

Culicoides variipennis (Coquillett), misidentified: Root and Hoffman 1937: 158 (in part; key; female; male genitalia; fig. spermatheca, male genitalia). James 1943: 148 (seasonal distribution; Colorado). Knowlton and Fronk 1950: 113 (Utah: Grand, Juab, Millard counties). Knowlton and Kardos 1951 (Utah: Kane, Davis, Washington counties). Wirth 1952a: 180, 252 (in part; key; female; male genitalia; pupa, larva; distribution; fig. female wing, dorsal thoracic patterns, palpus, pupa, larva). Bullock 1952: 18 (in part; key; female; male genitalia; biology; habitat and biotic associations; fig. larvae, pupae; seasonal distribution; Utah: Salt Lake County). Rees and Bullock 1954 (in part; Utah: Salt Lake County). Foote and Pratt 1954: 34 (in part; key; diagnoses of female, male, pupa; biology; fig. female wing, mesonotum, palpus, male genitalia).

Culicoides (*Monoculicoides*) *variipennis*: Khalaf 1954: 40 (assignment to subgenus *Monoculicoides*). Fox 1955: 258 (in part; key and diagnoses of subgenera; species diagnosis; taxonomy). Hensleigh and Atchley 1977: 379 (morphometric analysis). Wirth and Morris 1985: 165 (reevaluation of *C. variipennis* complex).

Culicoides variipennis albertensis Wirth and Jones, 1957: 17 (diagnosis; Alberta). Wirth et al. 1985: 8 (numerical characters).

Culicoides variipennis australis Wirth and Jones, 1957: 15 (diagnosis; fig. female palpus, antenna, mesonotum, wing; Louisiana). Atchley 1967: 975 (synonym subordinate to *C. v. sonorensis*, in part; New Mexico). Childers and Wingo 1968: 20 (key; numerical characters; biology; fig. female wing, spermathecae). Wirth et al. 1985: 30 (numerical characters; fig. female wing).

Culicoides variipennis occidentalis Wirth and Jones, misidentified: Rowley 1967: 501 (in part; larval habitats).

Culicoides occidentalis, misidentified: Jorgensen 1969: 27 (in part; proposed status change; key; quantitative characters; female; male genitalia; seasonal distribution; fig. male genitalia, parameres, female wing, palpus, spermatheca, antenna; Washington).

Culicoides occidentalis albertensis, misidentified: Downes 1978: 63 (combination).

Culicoides occidentalis australis, misidentified: Downes 1978: 63 (combination).

Culicoides occidentalis sonorensis, misidentified in part: Downes 1978: 63 (combination; fig. female palpus).

Diagnosis. (Tables 14, 15) (Females morphologically indistinguishable from *C. occidentalis*.) Dark brown; wing with prominent pattern; in r_3, m_1, m_2, cua_1 extensive and more of dark irregular curves, pale streaks, and zigzags than ovoid spots; scutum with dark spots at seta bases; legs with distinct pale banding; female palpal segment 3 swollen 1.8–3.0× longer than wide, with medium to large rounded or irregularly shaped and often partly divided sensory pit; one sclerotized spermatheca, U-shaped, with opening >0.5 the diameter of the spermatheca, without neck; parameres fused basally; ventral surface of aedeagus spiculate, apex deeply bifurcated into bladelike tips.

Distribution. British Columbia, Alberta, Montana, North Dakota, Ontario, south through the western half of the United States to California, Utah (Davis, Garfield, Grand, Juab, Kane, Morgan, Salt Lake, Sevier, Uintah, Washington counties), Colorado, Arizona, New Mexico, Texas, Louisiana; into Mexico to Guerrero and Puebla; generally scattered populations east of the Mississippi River to Vermont, Maryland, Virginia, Kentucky, Tennessee, North Carolina, Georgia, Florida (Holbrook et al. 2000; Borkent and Spinelli 2000; Schmidtmann et al. 2011; Huerta et al. 2012; Vigil et al. 2014; Jewiss-Gaines et al. 2017).

Biology. *Culicoides sonorensis* is recognized as a significant animal virus vector and is arguably the most economically important *Culicoides* species in North America. This has resulted in a relatively large body of scientific literature, which I attempt to briefly summarize below. Because of the complex synonymy of the Variipennis group, *C. occidentalis*, *C. sonorensis*, and *C. variipennis* conflate in many records before 2000. Though I have tried to present only data associated with *C. sonorensis*, it is possible some of it refers to *C. occidentalis*, *C. variipennis*, or a combination, and larval habitats cited with especially high (~20%) dissolved salts and relatively low organic matter may be *C. occidentalis* sites. Unless otherwise indicated, *C. sonorensis* records from before 2000 were originally reported for *C. variipennis*. Detailed procedures for the large-scale rearing and colonization of *C. sonorensis* and associated summaries of longevity, larval and adult habitats and feeding behavior, and reproduction are described by Hunt (1994).

Larval ecology. *Culicoides sonorensis* habits are widespread in Utah. Bullock (1952) collected and reared immatures from bulrush (*Schoenoplectus americanus* [Persoon] Volkart ex Schinz and Keller, Cyperaceae) swamps, spikerush (*Eleocharis acicularis* and *E. macrostachya* Britton, Cyperaceae) mats, and saltgrass (*Distichlis stricta*) pastures and ditch banks in Salt Lake County. Jones (1961b) collected pupae from a freshwater seep in Garfield County, along with *C. jamesi*, *C. haematopotus* (may be *C. defoliarti*); from freshwater at the margin of a manure-polluted slough in Morgan County; and from the nonvegetated sunlit margin of an alkaline stream near Cisco (47 km north-northeast of Moab), Grand County, along with immatures of a Stonei group species (as *C. stonei*), *C. jamesi*, *C. haematopotus* (may be *C. defoliarti*), *C. grandensis* (as "n. sp."), and *C. crepuscularis*. I was able to rear *C. sonorensis* along with *C. occidentalis*, *C. crepuscularis*, and *C. mortivallis* from mud collected on 10 September 2020 from nonvegetated sunlit alkaline pools in a stream bed in Grand County at 38.96339°N 109.33585°W and 1315 m elevation in the same wash as Jones's Cisco pupae collection site.

Others have collected or reared immatures from 12 kinds of organic-polluted or saline agricultural, urban, industrial, and natural habitats (O'Rourke et al. 1983). *Culicoides sonorensis* larvae have been found in soils heavily polluted with human fecal effluent (Jones 1959; Childers and Wingo 1968), swine-polluted puddles, a salt spring (having clay, algae, slime, and 2% dissolved salts [Shepard 1907]; Childers and Wingo 1968), and dairy wastewater (Mullens 1989). Pfannenstiel and Ruder (2015) found *C. sonorensis* along with *C. crepuscularis* and *C. haematopotus* in mud in active bison (*Bison bison*) wallows in Kansas a week after they were flooded by rain; however, *C. sonorensis* did not colonize relict (long unused) wallows—presumably because these relict wallows had much less animal waste. Erram and Zurek (2018) found mud mixed with feces from cattle, goats, pigs, horses, and white-tailed deer supported *C. sonorensis* larval development, whereas mud mixed with chicken feces did not. Wong et al. (2018) found the greatest density of viable eggs were laid ~5 cm above the waterline in a dairy wastewater pond with ~5° slope, and these eggs had greater survivorship than eggs laid either closer or farther from the waterline.

Culicoides sonorensis prefers highly fecal-polluted sites and can tolerate high concentrations of some salts when high levels of organic matter are also present. Schmidtmann et al. (2000) found immatures in soils with high levels of organic material, phosphate, nitrate, and boron; however, these *C. sonorensis* habitats had significantly lower conductivity, boron, potassium, and chloride, and higher organic matter and significantly higher phosphate than *C. occidentalis* habitats. Cole and Whiteside (1965) collected larvae in Apache County, Arizona, 34.800°N 109.407°W, from saline ponds having 6% to 26% total dissolved solids, pH 9–10, "remarkably high" phosphate, the green alga *Ctenocladus circinnatus* Borzi (Ctenocladaceae), a *Mastogloia* Thwaites ex W. Smith (Mastogloiaceae) diatom, an *Oscillatoria* Vaucher ex Gomont (Oscillatoriaceae) cyanobacterium, and a green bacterium. Though they did not mention fecal contamination, the high levels of phosphorus and microorganisms, along with the brown coloration of the water evident in Google Earth imagery of 5 November 2015, suggest high organic matter content. In addition, from experiments with manure-loading in test ponds, Mullens and Rodriguez (1988) found the most highly polluted mud produced the highest larval densities (up to 11,300 in 30 ml) and the largest adults.

Bullock (1952) observed colonized *C. sonorensis* larvae to feed on living and dead ephydrid pupae and collected second instar larvae with their gut full of *Chlamydomonas vorhiesi* Jones (Chlamydomonadaceae) algae. Campbell et al. (2004) identified 14 genera of bacteria of the divisions Proteobacteria, Fibrobacteres/Acidobacteria, Actinobacteria, and Firmicutes in the midgut of adult female *C. sonorensis* and found the species composition differed from that of *C. variipennis* and altered after a blood meal. Erram (2016) compared the bacteria on field-collected adult female *C. sonorensis* with three other species of *Culicoides*. Proteobacteria were predominant on *C. crepuscularis*, *C. haematopotus*, and *C. stellifer*, whereas Proteobacteria and Firmicutes shared predominance on *C. sonorensis*, likely because of its manure-infused larval habitat. Furthermore, Neupane et al. (2020) isolated from the gut of *C. sonorensis* larvae a new species of bacteria, *Culicoidibacter larvae* Neupane et al., representing a novel family, order, and class in the phylum Firmicutes.

Adult behavior. *Culicoides sonorensis* is mammalophilic. Field hosts include cow (Gerry et al. 2001), horse (Foulk 1966; Jones et al. 1977; Crane et al. 1983; Gerry et al. 2001), burro (Jones et al. 1977), human (Stanford 1931; Knowlton and Fronk 1950; Foulk 1966; Foulk 1969), rabbit (Crane et al. 1983), domestic sheep (Jones 1961c), and bighorn sheep (*Ovis canadensis nelsoni*) (Mullens and Dada 1992a). Laboratory studies found *C. sonorensis* would readily feed on cattle, sheep, rabbits, mice, humans, chickens (Jones 1959), jirds (*Meriones unguiculatus* Milne-Edwards, Muridae) (Collins and Jones 1978), patas monkeys (*Erythrocebus patas* [Schreber], Cercopithecidae) (Lowrie et al. 1982), and guinea pigs (*Cavia porcellus*) (Pérez de León et al. 2006; Seblova et al. 2015).

Tempelis and Nelson (1971) identified 325 blood meals from mixed *C. sonorensis* and *C. occidentalis* in Kern County, California, as: 51% Bovidae (cattle and sheep), 46% Leporidae (rabbits and hares), 1% Canidae (dogs), 1% Equidae (horses), and 1% unidentified mammals. *Culicoides sonorensis* (as "*C. variipennis* complex", distinct from *C. occidentalis*; see remarks) collected in Northern California had blood meals from black-tailed deer (*Odocoileus hemionus*), black-tailed jackrabbit (*Lepus californicus*), cow (*Bos taurus*), dog (*Canis lupus*), sheep (*Ovis aries*), donkey (*Equus africanus*), horse (*Equus ferus*), pig (*Sus scrofa*), and emu (*Dromaius novaehollandiae*) (Hopken et al. 2017). They proposed the aberrant bird (emu) record may be due to the similarity of the emu's size and CO_2 output to *C. sonorensis*' normal mammalian hosts; and, Koch and Axtell's (1979) study of *Culicoides* host attraction support this possibility.

Jones et al. (1977) collected *C. sonorensis* males along with females from horses and burros, and Gerry and Mullens (1998) observed males coupled with blood-feeding females on the venter of a tethered calf. This unusual behavior suggests males seek hosts to find females for mating and correlates with Nelson's (1965) and Nelson and Bellamy's (1971) collections of males with CO_2-baited traps and my relatively high proportion of males collected with CO_2-baited traps (Table 4).

Foulk (1969) reported a crepuscular feeding pattern with peaks just after dawn and at sunset with <1% of the activity during the period from ~2 h after sunrise to ~3 h before sunset. Jones (1961c) collected *C. sonorensis* feeding on sheep during the evening crepuscular period in Colorado, and Jones et al. (1977) observed primarily morning-crepuscular feeding on horses and burros when both crepuscular periods were sampled. At three locations in Southern California, Gerry et al. (2008) collected *C. sonorensis* with a CO_2-baited trap and from a horse at various times to obtain 24 hour samplings July through September and found host-seeking was from ~1900 to ~0800 hours, with a peak at ~2000 and a larger one at ~0600.

In Weld County, Colorado, Akey and Barnard (1983) used a vehicle-mounted trap and found that diel flight patterns of nulliparous, parous, and gravid females differed significantly. They also found that nullipars decreased from 100% in April to 0% by November, averaging 25% for the season. This latter discovery compared favorably with Nelson and Scrivani (1972), who were able to collect only nullipars during early emergence in February in Kern County, California, suggesting that adult midges are unlikely to provide a major way for arboviruses to overwinter in that environment.

Linhares and Anderson (1990) found that female *C. sonorensis* flight activity in Northern California occurred only at 7–29 °C. Activity peaked highest at about sunset, continued on moonlit nights, and rose to a lower peak about dawn. When temperatures were >12 °C, activity continued through the night on moon-lit nights but diminished ~2 h after sunset on dark nights; and, when temperatures were <12 °C, both night and dawn activity were greatly reduced. Similarly, Barnard and Jones (1980b) observed flight activity only when temperatures were 7–37 °C in Weld County, Colorado. Summer activity was highest from about sunset until midnight, diminished through the night, and peaked again about sunrise; however, during the cooler months, activity started earlier, decreased more at night, and increased later after dawn. In the same study, Barnard (1980) found that female *C. sonorensis* collections using NJLTs were inversely correlated with truck trap collections during summer full moons—likely because moonlight diminishes the contrast of a trap's white light.

McDermott et al. (2015) have shown *C. sonorensis* are more averse to light when infected by bluetongue virus (BTV)—presumably because of high virus loads in the eyes. In addition, Mills et al. (2017) found epizootic hemorrhagic disease virus (EHDV) infection in *C. sonorensis* was associated with damaged ommatidia. This condition may reduce night activity and light-trap collection rates as BTV or EHDV infection rates increase through the season. Nayduch et al. (2019) went further and studied gene expression in EHDV-infected *C. sonorensis*, finding that the virus altered the expression of genes associated with tissue and cellular integrity, immune response, nervous system function, olfaction, and vision within 36 h after ingestion and likely produced important changes in phenotypic expressions involving host-seeking and other behaviors.

Wieser-Schimpf et al. (1991) compared *C. sonorensis* collections from New Jersey UVLTs with and without CO_2 and found that traps with CO_2 collected significantly more nulliparous (5.4×) and parous empty (3.9×) females, fewer engorged (0.3×) females, and about the same number of gravid females. Furthermore, McDermott et al. (2016) compared traps with CO_2 or UV alone or in combination, along with placement near or away from livestock or dairy wastewater ponds, and found: parous female collections did not consistently correlate with trap type; traps with UV light collected a higher proportion of males than did traps with CO_2 alone; CO_2-baited traps collected significantly more nulliparous females than males or parous females at all locations; and CO_2-baited traps collected more males and females in open fields than near livestock or ponds. These results make sense because ~7× more *C. sonorensis* males and females are attracted to cattle than to traps baited with CO_2 alone (Mullens and Gerry 1998) and because mate-seeking males and host-seeking females are more likely to be foraging in open fields or near livestock, which outcompete CO_2-baited traps, than near ponds.

Vector potential. *Culicoides sonorensis* has been found naturally infected with Main Drain virus (MDV) (Bunyaviridae) (Nelson and Scrivani 1972; Elbel et al. 1977; Crane et al. 1983), Lokern virus (LOKV) (Bunyaviridae) (Nelson and Scrivani 1972; Crane et al. 1983; Kramer et al. 1990), Buttonwillow virus (BUTV) (*Orthobunyavirus*, Bunyaviridae) (Reeves et al. 1970; Nelson and Scrivani 1972; Hayes et al. 1976; Kramer et al. 1990), EHDV (Foster et al. 1980), BTV (Price and Hardy 1954; Foster et al. 1980; Kramer et al. 1990; White et al. 2005), vesicular stomatitis New Jersey virus (VSV) (Walton et al. 1987; Kramer et al. 1990), West Nile virus (WNV) (Naugle et al. 2004), and *Onchocerca cervicalis* Railliet and Henry (Nematoda: Filarioidea) (Foil et al. 1984; Higgins et al. 1988), a parasite of horses.

Collins and Jones (1978) demonstrated *C. sonorensis* readily became infected with *O. cervicalis* after membrane-feeding on infected blood and was able to transmit the parasite to jirds; and Foil et al. (1984) found wild-caught *C. sonorensis* had an infection rate of 7% after feeding on infected horses. *Culicoides sonorensis* has also been shown to be a competent laboratory vector of human serous cavity filariasis, *Mansonella ozzardi* (Manson) (Nematoda: Filarioidea), after feeding on infected patas monkeys (Lowrie et al. 1982).

Culicoides sonorensis can also transmit some medically important trypanosomes. It has been shown to develop late stage infections (thoracic midgut and stomodeal valve colonization) of two species of *Leishmania* Borovsky (Kinetoplastida: Trypanosomatidae) at rates up to 80% after feeding on guinea pigs; however, three species of human *Leishmania* failed to produce similar infections (Seblova et al. 2015). Chanmol et al. (2019) showed that *C. sonorensis* acquired disseminated *Leishmania orientalis* Jariyapan et al. infections after feeding on infected blood. Further studies by Becvar et al. (2021) were able to show that *C. sonorensis* was able to efficiently acquire four strains of *Leishmania* subgenus *Mundinia* Espinosa et al. and infect naïve mice after feeding on infected blood or after probing infected mice without taking a blood meal.

Culicoides sonorensis has been infected by VSV after feeding on infected bovine blood or serum (Nunamaker et al. 2000); and other experiments showed *C. sonorensis* can orally transmit the virus to cattle (Pérez de León and Tabachnick 2006) and guinea pigs (Pérez de León et al. 2006). In a comparison of potential dipteran vectors, Drolet et al. (2005) stated *C. sonorensis* is likely a highly competent vector of VSV, and Rozo-Lopez et al. (2018) review the evidence for *C. sonorensis* being an important vector of this virus. Furthermore, Rozo-Lopez et al. (2020) found that females orally-infected with VSV were able to venereally infect 20–32% of males with infectious virus; intrathoracically injected males were able to venereally infect 49% of females with infectious virus; and venereally-infected males were able to venereally-infect 10% of females with infectious virus.

Culicoides sonorensis is the primary western North American vector of EHDV of deer, elk, pronghorn antelope, cattle, bighorn and domestic sheep, goats, and bison and of BTV of cattle, sheep, goats, and bison (Holbrook 1988; Sohn and Yuill 1991; Mellor et al. 2000; Tessaro and Clavijo 2001; Ruder et al. 2012; Stevens et al. 2015). Experiments conducted by McGregor et al. (2019a) showed *C. sonorensis* to be a highly competent vector for Florida and Canada strains of EHDV, with 100% infection, >76% dissemination, and >55% transmission rates by day 7 after feeding on infected blood.

The potential for *C. sonorensis* to transmit more obscure viruses and important exotic diseases is significant. It has been shown experimentally to be able to transmit Buttonwillow virus (BUTV) of leporids (Hardy et al. 1972). Experiments have shown it able to transmit some strains of African horse sickness virus (AHSV) (*Orbivirus*, Reoviridae) (Wittmann et al. 2002) and to have a 19% probability of developing a transmissible infection of Schmallenberg virus (SBV) (*Orthobunyavirus*, Bunyaviridae)—which causes premature birth, stillbirth, or fetal malformation in ruminants—after feeding on infected blood (Veronesi et al. 2013). Other experiments (Möhlmann et al. 2018) found Shuni virus (SHUV) (*Orthobunyavirus*, Bunyaviridae)—which produces encephalitis, abortions, and fetal malformations in horses, ruminants, and other animals, and can infect humans—produced a 60% infection rate and disseminated to the salivary glands of 10% of *C. sonorensis* that had fed on SHUV-infected blood, suggesting high vector competency for this African virus. Experiments by Stokes et al. (2020) found that colonized *C. sonorensis* developed a disseminated infection for bovine ephemeral fever virus (BEFV) (*Ephemerovirus*, Rhabdoviridae) after feeding on infected blood (1–2%) and by intrathoracic injection (100%); however, they were unable to show that the infected midges were able to transmit the virus to naïve cattle. Furthermore, *C. sonorensis* produced a significant disseminated and salivary infection of Oropouche virus (OROV) (*Orthobunyavirus*, Bunyaviridae) after feeding on infected blood (McGregor et al. 2021), suggesting a high vector potential for this Neotropical zoonosis that causes considerable incidence of febrile illness in humans.

Lehiy et al. (2018) characterized the physiological responses of mice fed upon by uninfected *C. sonorensis* and determined that the immune responses and recruitment of cells susceptible to *Orbivirus* (Reoviridae) infection likely enabled the high rates of BTV transmission found by Baylis et al. (2008), who had demonstrated that a single infected *C. sonorensis* has a >80% chance of transmitting BTV to a naive sheep. However, Baylis et al. (2008) had also found that <4% of naive *C. sonorensis* acquired a disseminated infection after feeding on infected sheep, with the highest rates of transmission occurring early during the sheep's infection when viremia was highest, suggesting the midges have significant barriers to BTV infection. In contrast, Mills et al. (2017) found *C. sonorensis* that fed on EHDV-infected blood in the laboratory at 25 °C acquired a disseminated and replicating infection by day five with a 50% infection rate by day ten, suggesting a high potential for virus transmission 5 d post infection. These results compared favorably with Carpenter et al. (2011) who estimated average *C. sonorensis* infection and virus replication rates of 0.14 and 0.018 for BTV, 0.92 and 0.084 for EHDV, and 0.52 and 0.017 for AHSV; suggesting especially high vector competency for EHDV transmission. Of note, there are many variables in these studies that likely affected infection rates. Sources of variation include environmental (e.g., incubation temperature and time, or larval nutrition), genetic (e.g., insect population differences over space or time), and experimental (e.g., virus strain, lab maintenance history and titer) factors, so direct comparisons among experiments are often difficult. However, as a group, the studies provide strong evidence for *C. sonorensis* serving as a natural vector particularly of BTV and EHDV in the western USA.

Life cycle. Jones (1957, 1960) colonized *C. sonorensis* and found the laboratory life cycle to average 30 d: 2 d egg, 21 d larva, 3 d pupa, 1 d pre-blood-meal adult, and 3 d gonotrophic cycle. Barnard and Jones (1980a) reported *C. sonorensis* in Weld County, Colorado, overwintered as fourth (last) instar larvae, started emerging as adults in March, had generations as short as two weeks at the peak of summer, and produced seven generations a year by October. However, in the subtropical Chino Basin of Southern California, *C. sonorensis* has 9–11 generations and larvae present late January to December, with an average generation period of 4.8–6.5 weeks, shortening to 3–4.5 weeks in the hotter months (Mullens and Lii 1987).

It is not known how much of a role autogeny plays in the number of *C. sonorensis* generations per year. The only report of autogeny in *C. sonorensis* is from Downes in 1958 (reported by Linley 1983) for *C. variipennis albertensis*, now considered a subordinate synonym of *C. sonorensis*.

Work et al. (1991) estimated a 3 d gonotrophic cycle, a 0.242 life-stage-specific survivorship, and a 0.623 daily adult survivorship for wild *C. sonorensis* in Yolo County, Northern California. In addition, Mullens and Holbrook (1991) determined that temperature greatly influence the gonotrophic cycle from blood meal to oviposition, which varied from 14 d at 13 °C to <3 d at 34 °C. They also found midges held at 13 °C laid an average of only ~4 eggs per female, whereas midges held at temperatures of 17–34 °C laid averages of 62–69 eggs per female.

In Southern California, Gerry and Mullens (2000) found *C. sonorensis* to have a gonotrophic cycle varying from 3–4 d in hot months to 14 d in cool months, a daily survivorship varying from <60% during hot months to >95% during cool months, and an extrinsic incubation period for BTV as short as 9–10 d in late summer, but suggested the low survivorship during that time reduced virus transmission potential. However, Wittmann et al. (2002) concluded EHDV, BTV, and AHSV transmission potential was higher in warmer weather because the reduced midge survivorship was more than offset by the shorter viral extrinsic incubation period.

Lysyk (2007) studied the population dynamics of *C. sonorensis* in southern Alberta, Canada; and Lysyk and Danyk (2007) compared Alberta and Colorado populations with regard to the effect of temperature on survivorship, gonadotrophic cycle, and life history and determined populations in the warmer southern United States would have a temperature-dependent 1.8–2.6 times greater vectorial capacity for BTV transmission. Furthermore, Lysyk and Dergousoff (2014) evaluated the effects of climate, weather, and geography on current abundance and distribution of *C. sonorensis* to establish a baseline for future evaluation of the effect of climate change.

Adult vector life span is causally related to its ability to transmit disease. Reeves and Jones (2010) found that colony *C. sonorensis* that were fed on melezitose, a sugar in homopteran honeydew secretions, lived significantly longer than those fed on either sucrose or stachyose and concluded that the availability of honeydew could play a role in BTV and EHDV transmission. However, they found no significant difference in viral persistence between the groups after feeding on BTV- or EHDV-infected blood, though a larger number of melezitose-fed infected midges survived.

Phenology. *Culicoides sonorensis* immatures exhibit behavioral and physiological adaptations for surviving drought and extreme cold. Though their larvae cannot survive desiccation (Mullens and Rodriguez 1992), they can migrate horizontally with a slowly receding waterline (Mullens and Rodriguez 1989) or vertically 7–10 cm into sandy-loam soil (Mullens and Rodriguez 1992) to avoid it. McDermott and Mullens (2014) reported some (>1%) older (>28 h) *C. sonorensis* embryos can survive severe desiccation with up to 60% water loss, suggesting *C. sonorensis* eggs are able to survive the dry periods of some ephemeral habitats. Laboratory studies (McDermott et al. 2017) of *C. sonorensis* immatures from both subtropical Southern California and temperate Weld County, Colorado, found their eggs can tolerate temperatures to –20 °C, larvae to −4 °C, and pupae to −9 °C without complete mortality, but with reduced survivorship. Lower temperatures caused complete mortality for larvae and pupae. These mortality threshold temperatures are higher than their freeze temperatures, suggesting larvae and pupae are able to move to tolerable microhabitats until death.

From 29 March to 20 May in Weld County, Colorado, Jones (1967) collected pupae of *C. sonorensis* that had overwintered as larvae in unfrozen mud along with *C. crepuscularis* and a species close to *Culicoides wisconsinensis* Jones. Furthermore, Mayo et al. (2014a, 2014b) found late-winter collections of diapausing parous *C. sonorensis* female adults in Northern California positive for BTV, indicating the virus can overwinter in *C. sonorensis* in temperate regions. However, studies by Jones and Foster (1969) and Osborne et al. (2015) found no evidence for vertical (transovarial) transmission.

In Grand County, Utah, *C. sonorensis* was the earliest midge to be collected, with four females between two CO_2-baited traps on 9 March 2005 in week 10. Whether adults collected in early March in the present study are from a cohort that overwintered as larvae or as adults has implications for local BTV and EHDV transmission.

Symbionts. Mermithid nematodes have been studied as possible biocontrol agents against *C. sonorensis*. In Southern California dairy wastewater ponds, larvae are parasitized by *Heleidomermis magnapapula* (Poinar and Mullens 1987), which tolerates the moderate salinity and organic pollution levels common to *C. sonorensis* habitats (Mullens and Luhring 1996). Parasitism rates ranged from 0% to 69% in immatures but were <0.06% in adults sampled with emergence traps, CO_2-baited traps, and light traps—indicating a high mortality rate for the parasitized immatures (Paine and Mullens 1994).

Bacterial endosymbionts such as *Wolbachia* and "*Candidatus* Cardinium" are being studied as potential biocontrol agents. *Wolbachia* can alter dipteran reproduction by killing male embryos, inducing gamete incompatibility, or feminizing genetic males (Stouthamer 1999) and can make vectors incompatible with some pathogens (Pagès et al. 2017). "*Candidatus* Cardinium" has been found to alter reproduction in parasitoid wasps by various means, including by inducing parthenogenesis, and is being investigated for its effect on *Culicoides* (Pagès et al. 2017; Möhlmann 2019; Pilgrim et al. 2020). Möhlmann (2019) found *C. sonorensis* colonies in Europe infected with *Wolbachia* and "*Candidatus* Cardinium"; and *Wolbachia* infections in *C. sonorensis* have been found in several laboratory colonies and in wild populations in Colorado and South Carolina (Covey 2020). Furthermore, Ghosh et al. (2019) were able to infect *C. sonorensis* cell cultures with *Wolbachia*, suggesting the possibility of introducing it to control *C. sonorensis* populations or reduce pathogen transmission.

One female collected in Grand County was parasitized by a larval mite (Table 10); a female (likely *C. sonorensis*, but possibly *C. occidentalis*) reared from mud collected from a pool in an alkaline wash in Grand County had androgenized antennae but otherwise appeared normal and not parasitized; 4 of 19 males reared from the same site contained remnants of dead nematodes (Table 11); and a male and a female collected near the Gila River in Greenlee County, Arizona, were parasitized by apparently live mermithid nematodes (Table 11). Wieser-Schimpf et al. (1991) collected an intersex (0.5% of males) in Louisiana but did not check for parasitism.

Predators. Potential predators have also been studied. Reeves (2010) investigated the avoidance behavior of colonized *C. sonorensis* larvae as they were fed on by *Hydra littoralis* (Anthomedusae: Hydridae), a common aquatic invertebrate that can kill and consume 2–7 *C. sonorensis* larvae per day.

Remarks. Using CO1 gene analysis, Hopken (2016) concluded *C. occidentalis* and *C. sonorensis* are distinct species, and Hopken et al. (2017) provided evidence to suggest *C. sonorensis* and *C. variipennis* are conspecific. This correlates with Tabachnick (1992) finding *C. v. sonorensis* and *C. v. variipennis* more genetically similar to each other than to *C. v. occidentalis*. See *C. occidentalis* remarks.

Subgenus *Selfia* Khalaf

Slide-mounted specimens of brown female *Culicoides* (*Selfia*) *brookmani* Wirth, *C.* (*Selfia*) *denningi*, and *Culicoides* (*Selfia*) *multipunctatus* Malloch can be reliably distinguished from the other brown subgenus *Selfia* females: *C. hieroglyphicus*, *C. jamesi*, *Culicoides jacksoni* Atchley, and *Culicoides tenuistylus* Wirth (Atchley 1970). However, the thousands of specimens collected made slide-mounting and identification impractical; hence, nearly all the brown females of the subgenus *Selfia* were not identified to species and are listed as "unidentified" in the data tables. Both sexes of *C. moabensis* (which are distinctively yellow) and the males of other subgenus *Selfia* species were readily identified without slide-mounting.

Larval ecology. Approximately 66,500 brown subgenus *Selfia* females were collected in Grand County and 761 in Garfield County. Species of this subgenus were only 14% of the species diversity but were 58% of specimens collected in Grand County, likely because of the local abundance of stream-bank larval habitats.

Vector potential. Subgenus *Selfia* females that were not identified to species have been found infected with Main Drain virus (MDV), Lokern virus (LOKV), Buttonwillow virus (BUTV) (Kramer et al. 1990), and vesicular stomatitis New Jersey virus (VSV) (Walton et al. 1987; Kramer et al. 1990). The females positive for VSV were collected with subgenus *Selfia* males identified to be 56% *C. jamesi*, 23% *C. denningi*, and 21% *C. hieroglyphicus* (Walton et al. 1987). Furthermore, subgenus *Selfia* distribution in the southwestern United States and Great Plains correlates with VSV outbreaks (Rozo-Lopez et al. 2018).

Symbionts. Three intersex specimens, collected and identified as either *C. hieroglyphicus*, *C. jamesi*, or *C. jacksoni*, and one intersex specimen, identified as either *C. denningi*, *C. hieroglyphicus*, *C. jamesi*, or *C. jacksoni*, with female wings and genitalia and male heads (one with male and female palpi and two shriveled and melanized worms) were parasitized by mermithid nematodes (Table 11).

Culicoides (*Selfia*) *brookmani* Wirth

(Fig. 34)

Culicoides brookmani Wirth, 1952a: 179 (key; female; male genitalia; fig. male genitalia, female wing, palpus; California).

Culicoides (*Selfia*) *brookmani*: Khalaf 1954: 38 (assignment to subgenus *Selfia*). Fox 1955: 230 (key and diagnoses of subgenera; species key; taxonomy). Jones and Wirth 1958: 86 (corrections to keys and original description). Atchley 1967: 960 (key; numerical characters; female; male genitalia; fig. female wing, palpus, tibial comb, male genitalia). Atchley 1970: 223 (key; female, male, pupa; 29 fig.). Wirth et al. 1985: 32 (numerical characters; fig. female wing). Breidenbaugh and Mullens 1999a: 859 (egg, larva; fig. egg, larval head, mouthparts, thorax, caudal segment). Phillips 2015: 847 (key).

Diagnosis. (Tables 14, 15) Brown; wing without pattern of pale spots; three unsclerotized or faintly sclerotized long fingerlike spermathecae; female and male scutella with four setae; hind tarsomeres without apical spines; posterior margin of sternite 9 convex over base of aedeagus, without paired median lobes; basal third of gonocoxite abruptly expanded and bent mesally; gonocoxal apodeme simple, without hooklike process; aedeagus about as long as wide, lateral arms in the form of boomerang-shaped sclerites, apical portion trifurcate with lateral processes shorter than wide; parameres fused, 2–3× wider than long, median process short hemispherical.

Distribution. California, Utah (Grand, Washington counties), Kansas (Swanson et al. 2018), Arizona, New Mexico, Texas.

Larval ecology. *Culicoides brookmani* is a primarily warm- to hot-desert-inhabiting species. Atchley (1970) collected pupae from the muddy margins of a small, slow, algae-choked stream at ~1320 m elevation in Coconino County in north central Arizona and from an intermittent Sonoran Desert stream in Sycamore Canyon in Santa Cruz County in southern Arizona; and Breidenbaugh and Mullens (1999a) collected immatures from sandy and silty soil margins of a desert creek having filamentous algae at 300–350 m elevation in Riverside County, California.

Adult behavior. Known hosts are deer, jackrabbit (Atchley 1970), bighorn sheep (*Ovis canadensis nelsoni*), and domestic rabbit (*Oryctolagus cuniculus*) (Mullens and Dada 1992a). Mullens and Dada (1992b) reported high parity rates (averaging ~40%) for CO_2-with-light-trapped females, suggesting a high vector potential. They also reported double activity peaks of March–June and September–October in the Santa Rosa Mountains of Southern California, which, because of the shorter season of the Utah Canyonlands, compares favorably with the double peaks of late May (week 21) and late August (week 34) in the present study.

Life cycle. Laboratory studies by Breidenbaugh and Mullens (1999a) found that a wild-caught *C. brookmani* female laid 94 eggs that hatched 5 d later, and the larvae fed on bacterial-feeding *Pelodera* and *Panagrellus redivivus* nematodes and started pupating 13 d later at 27 °C.

Symbionts. Mullens et al. (1997b) experimented with the potential biocontrol parasitic nematode, *Heleidomermis magnapapula* in the laboratory and found it readily penetrated but did not develop or emerge from *C. brookmani* larvae, which continued to develop to adults with no sign of the nematodes.

Remarks. *Culicoides brookmani* is more closely related to *C. moabensis* and *C. multipunctatus* of the Multipunctatus group than to other *Selfia* species (Phillips 2015).

Culicoides (*Selfia*) *denningi* Foote and Pratt

(Fig. 36, 281)

Culicoides denningi Foote and Pratt, 1954: 20 (key; female, male; fig. female wing, mesonotum, palpus, male genitalia; Saskatchewan).

Culicoides (*Selfia*) *denningi*: Fox 1955: 235 (assignment to subgenus *Selfia*; key and diagnoses of subgenera; species key; taxonomy). Atchley 1970: 229 (key; female, male, pupa, larva; 24 fig.). Atchley 1971b: 55 (pupa; geographic variation; comparison with *C. jamesi* and *C. hieroglyphicus*). Atchley 1973: 630 (female, pupa; comparison with *C. jamesi* and *C. hieroglyphicus*). Wirth et al. 1985: 32 (numerical characters; fig. female wing). Murphree and Mullen 1991: 362 (key; larva; numerical characters; fig. head, mandible, hypostoma, epipharynx).

Culicoides hieroglyphicus Malloch, misidentified: James 1943: 148 (in part; male genitalia variant; seasonal distribution, Colorado).

Diagnosis. (Tables 14, 15) Brown; wing without pattern of pale spots; three unsclerotized or faintly sclerotized long fingerlike spermathecae; male scutellum with six setae; hind tarsomeres with apical spines; posterior margin of male sternite 9 with pair of prominent caudomedial lobes slightly longer than wide; gonocoxal apodeme simple, expanded apically, without hooklike process; gonocoxite not abruptly expanded basally; apex of gonostylus rounded clublike, without tooth; aedeagus Y-shaped; parameres fused, about as long as wide, median process slightly longer than wide, rounded.

Distribution. Washington, Saskatchewan, Alberta, south through Idaho (Custer County, **new state record**), Montana, Wyoming, South Dakota, to Oregon, Nevada, Utah (Cache, Duchesne, Garfield, Grand, Juab, Millard, Uintah counties), Colorado, Kansas (Swanson et al. 2018), Nebraska.

Larval ecology. Atchley (1970) collected pupae from a clear 25 °C stream at 1590 m in Elko County, Nevada, from small to large and fresh to polluted 17–33 °C stream and river margins at 1370–2160 m elevation in Garfield, Juab, Millard, and Uintah counties, Utah, and, along with larger numbers of immature *C. jamesi*, from a small highly polluted creek at 730 m elevation in Montana. During a multi-year study, Fredeen (1969) found that *C. denningi* larvae migrate from the margin to the mid-channel of the South Saskatchewan River (Canada) before it freezes, overwinter in the vegetation-free riverbed sand, and swim to shore to pupate in the spring.

Adult behavior. *Culicoides denningi* can be a severe crepuscular pest of horses and humans to at least 1.2 km from its larval habitat but would also bite throughout calm cloudy days (Fredeen 1969). Jones (1965) reported sheep as a host for *C. hieroglyphicus*; however, Atchley (1970) states that the report may be mistaken and instead be for *C. denningi*. Two female *C. denningi* were collected in Grand County while biting humans: one 11 August 1999 in Castle Valley (38.64°N 109.41°W) and one on my ear midday 3 May 2000 in east Moab. Two females were collected by T. Graham while biting a human 12 November 2017 in Canyonlands National Park, San Juan County (38.15339°N 109.82893°W).

Symbionts. Female and male *C. denningi* were parasitized by larval mites (Table 10).

Remarks. James's (1943) description of a *C. hieroglyphicus* male genitalia variant collected in Larimer County, Colorado, is that of *C. denningi*. The distributions of *C. denningi* and *C. hieroglyphicus* overlap in northern Colorado, Utah, and Wyoming; and they are more closely related to each other than to other *Selfia* species (Atchley 1970).

***Culicoides* (*Selfia*) *hieroglyphicus* Malloch**

(Fig. 37)

Culicoides hieroglyphicus Malloch, 1915: 297 (key; female; fig. mesonotum; Arizona). Hoffman 1925: 280 (key; female; fig. wing, mesonotum). Root and Hoffman 1937: 158 (key; female; male genitalia; fig. male genitalia). James 1943: 148 (in part; seasonal distribution; Colorado). Wirth 1952a: 176 (key; female; male genitalia; distribution; fig. dorsal thoracic pattern, female palpus, male genitalia). Knowlton and Kardos 1951: 163 (Utah: Kane, Washington counties). Bullock 1952 (key).

Culicoides (*Selfia*) *hieroglyphicus*: Khalaf 1954: 38 (subgenus *Selfia* Khalaf; designated *C. hieroglyphicus* as type species). Foote and Pratt 1954: 24 (key; diagnosis; fig. female wing, mesonotum, palpus, male genitalia). Fox 1955: 241 (key and diagnoses of subgenera; species key; taxonomy). Wirth and Bottimer 1956: 263 (Texas ecology). Jones 1961a: 737 (key; pupa; fig. respiratory trumpet, operculum, cephalothoracic chaetotaxy). Atchley 1967: 962 (key; numerical characters; female; male genitalia; variation; feeding habits; fig. female wing, palpus, male genitalia, parameres). Atchley 1970: 242 (key; female, male, pupa, larva; 33 fig.). Atchley 1971b: 60 (pupa; geographic variation; comparison with *C. denningi* and *C. jamesi*). Atchley 1973: 630 (female, pupa; comparison with *C. denningi* and *C. jamesi*). Downes and Wirth 1981: 415, 418 (fig. male genitalia, spermathecae). Wirth et al. 1985: 32 (numerical characters; fig. female wing). Wirth et al. 1988: 56 (numerical characters; fig. female wing). Murphree and Mullen 1991: 363 (key; larva; numerical characters; fig. mandible, epipharynx). Borkent and Spinelli 2000: 37 (in Neotropical catalog).

Diagnosis. (Tables 14, 15) Brown; wing without pattern of pale spots; three unsclerotized or faintly sclerotized long fingerlike spermathecae; male scutellum with six setae; hind tarsomeres with apical spines; posterior margin of male sternite 9 with pair of prominent caudomedial lobes ~4× longer than wide; gonocoxal apodeme simple, expanded distally, without hooklike process; gonocoxite not abruptly expanded basally; apex of gonostylus expanded foot-shaped, without tooth; aedeagus Y-shaped; parameres fused, longer than wide, median process 3–4× longer than wide, tonguelike.

Distribution. California, Nevada, Idaho (Bonneville County, **new state record**), Wyoming, South Dakota, south through Utah (Carbon, Garfield, Grand, Kane, San Juan, Uintah, Washington, Wayne counties), Colorado, Nebraska, Kansas, Oklahoma, Arizona, New Mexico, Texas, Sonora, to Baja California, Durango, Aguascalientes. Reports for Montana in Root and Hoffman (1937), Foote and Pratt (1954), and Fox (1955) were erroneous (Atchley 1970).

Larval ecology. Atchley (1970) collected pupae from small to medium and fresh to alkaline warm stream and river margins at 1280–1650 m elevation in Carbon, Garfield, Grand, Kane, San Juan, and Wayne counties, Utah. The most productive habitat was in a small alkaline wash southwest of Cisco (47 km north-northeast of Moab) in Grand County with density of several hundred immatures per dm^2, along with some *C. occidentalis* or *C. sonorensis* (as *C. variipennis*). The coldest collection site was in Wayne County, which had a water temperature of 22 °C and also had small numbers of *C. jamesi*. The other Utah sites had water temperatures >27 °C and no other *Selfia* species. Jones (1961b) reared many immatures from mudflats from a hot spring in Texas and few from lake margins in Oklahoma—exceptional habitats for this species.

Adult behavior. Known hosts are sheep (Jones 1965; however, Atchley [1970] questions this may be for *C. denningi*), jackrabbit (Atchley 1970), burro (Jones et al. 1977), and horse (Elbel et al. 1977; Jones et al. 1977). In Weld County, Colorado, *C. hieroglyphicus* was most active during daylight hours April–October (Barnard and Jones 1980b).

Symbionts. A female—likely *C. hieroglyphicus*—collected in Grand County was parasitized by a shriveled, and melanized mermithid nematode. Three females and an intersex male collected in Greenlee County, Arizona, were also parasitized by mermithids (Table 11). In addition, Atchley (1967, 1970) reports a high incidence of intersex males parasitized by mermithid nematodes near Glenwood, Catron County, New Mexico; and my collections near the Gila River in Greenlee County, Arizona, and Grant County, New Mexico, included many *C. hieroglyphicus* parasitized by larval mites (Table 10).

Culicoides (*Selfia*) *jacksoni* Atchley

(Fig. 39)

Culicoides (*Selfia*) *jacksoni* Atchley, 1970: 258 (key; female, male, pupa, larva; 30 fig.; New Mexico). Wirth et al. 1985: 32 (numerical characters; fig. female wing). Murphree and Mullen 1991: 364 (key; larva; numerical characters; fig. mandible, epipharynx).

Diagnosis. (Tables 14, 15) Brown; wing without pattern of pale spots; three unsclerotized or faintly sclerotized long fingerlike spermathecae; male scutellum with six setae; hind tarsomeres with apical spines; posterior margin of male sternite 9 concave or cleft, without caudomedial lobes; gonocoxite slightly tapering, not basally expanded or bent; gonocoxal apodeme with a small posterior mesally directed hooklike process; apex of gonostylus rounded blunt clublike, without tooth; aedeagus Y-shaped, with moderately sclerotized median cross-bar connecting the heavily sclerotized basal arms; parameres fused, longer than wide, with heavily sclerotized abrupt knoblike shoulders at ~0.5, median process 4–5× longer than wide, narrow, parallel-sided fingerlike.

Distribution. California, Utah (Duchesne, Grand counties), Arizona, New Mexico.

Larval ecology. Atchley (1970) collected pupae 12 July 1968 from mud margins of small cold (19–21 °C) shallow pools in a freshwater stream with weedy vegetation at 2300 m elevation in a spruce-Douglas fir forest in Duchesne County, Utah. His New Mexico collection of larvae and pupae were from a similar habitat having 17 °C water at 2200 m elevation in a pine-Douglas fir forest. And, Breidenbaugh and Mullens (1999a) collected an adult female above 823 m elevation in Riverside County, California, that laid 85 eggs, which hatched 5 d later at 21–25°C, and which larvae fed on bacterial-feeding *Pelodera* nematodes in the laboratory.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; and though its hosts are unknown, the SCo presence on only the proximal flagellomeres suggests it is mammalophilic.

Culicoides (*Selfia*) *jamesi* Fox

(Fig. 38)

Culicoides jamesi Fox, 1946: 244 (female; male genitalia; fig. female mesonotum, wing, palpus, male genitalia, parameres; Montana). Wirth 1952a: 178 (key; female; male genitalia; fig. dorsal thoracic pattern, female palpus, male genitalia).

Culicoides (*Selfia*) *jamesi*: Khalaf 1954: 38 (assignment to subgenus *Selfia*). Foote and Pratt 1954: 26 (key; diagnosis; fig. male genitalia). Fox 1955: 243 (key and diagnoses of subgenera; species key; taxonomy). Jones 1961a: 737 (key; pupa; fig. respiratory trumpet, operculum, anal segment). Atchley 1967: 965 (key; numerical characters; female; male genitalia; fig. female wing, palpus, tibial comb, male genitalia). Jorgensen 1969: 19 (key; quantitative characters; female; male genitalia; seasonal distribution; fig. female wing, palpus, antenna, male genitalia, parameres). Atchley 1970: 269 (key; female, male, pupa, larva; 24 fig.). Atchley 1971b: 65 (pupa; geographic variation; comparison with *C. denningi* and *C. hieroglyphicus*). Atchley 1973: 630 (female, pupa; comparison with *C. denningi* and *C. hieroglyphicus*). Wirth et al. 1985: 32 (numerical characters; fig. female wing). Murphree and Mullen 1991: 364 (key; larva; numerical characters; fig. epipharynx).

Diagnosis. (Tables 14, 15) Brown; wing without pattern of pale spots; three unsclerotized or faintly sclerotized long fingerlike spermathecae; male scutellum with six setae; hind tarsomeres with apical spines; posterior margin of male sternite 9 cleft, without caudomedial lobes; gonocoxite slightly tapering, not basally expanded or bent; gonocoxal apodeme with a small posterior mesally directed hooklike process; apex of gonostylus markedly expanded and foot-shaped, without tooth; aedeagus elongate, almost parallel-sided, without median cross-bar; parameres fused, longer than wide, median process ~3× longer than wide, tapering tonguelike.

Distribution. British Columbia, Alberta (Lysyk 2006), Montana, South Dakota, south through Washington, Idaho (Blaine County, **new state record**), Wyoming, Oregon, Nevada, Utah (Box Elder, Duchesne, Garfield, Grand, Kane, Morgan, Summit, Uintah, Washington, Wayne counties), and Colorado, to California, Arizona, New Mexico. Khalaf's (1957) record of *C. jamesi* from Oklahoma is dubious (Atchley 1970).

Larval ecology. *Culicoides jamesi* seems to have wider ecological tolerance than other *Selfia* species, being distributed over the entire western United States except for the extreme Desert Southwest. Jones (1961b) collected immatures from the nonvegetated sunlit margin of an alkaline stream near Cisco (47 km north-northeast of Moab), Grand County, along with immatures of a Stonei group species (as *C. stonei*), *C. occidentalis* or *C. sonorensis* (as *C. variipennis australis*), *C. haematopotus* (may be *C. defoliarti*), *C. grandensis* (as "n. sp."), and *C. crepuscularis*; and from a freshwater seep in Garfield County, along with *C. sonorensis* (as *C. variipennis*) and *C. haematopotus* (may be *C. defoliarti*). Atchley (1970) collected pupae from mud margins of small cold (19–21 °C) shallow pools in a freshwater stream with weedy vegetation at 2320 m elevation in a spruce-Douglas fir forest in Duchesne County; from the margin of a warm (27–30 °C) freshwater stream at 1600 m elevation in a pinyon-juniper woodland in Kane County; and from cold stream mudflats at 1800 m elevation in Garfield County. He also reared immatures from New Mexico and Wyoming, and from a small shallow highly polluted creek at 730 m elevation in Montana, which also had lesser numbers of *C. denningi*. In addition, McMullen (1978) reared *C. jamesi* from mud from a stream in a heavily manured pasture in British Columbia.

Adult behavior. Known hosts are cow (Jorgensen 1969) and horse (Atchley 1970).

Culicoides (*Selfia*) *moabensis* Phillips

(Fig. 33, 35)

Culicoides (*Selfia*) *moabensis* Phillips, 2015: 842 (key; diagnosis, male, female; fig. male head, thorax, wing, genitalia; female head, thorax, color, wing, genitalia; seasonal activity; Utah: Grand County).

Diagnosis. (Tables 14, 15) Yellowish to reddish yellow; wing without pattern of pale spots; three unsclerotized or faintly sclerotized long fingerlike spermathecae; male scutellum with four setae; hind tarsomeres without apical spines; posterior margin of sternite 9 convex over base of aedeagus, without paired median lobes; basal third of gonocoxite abruptly expanded and bent mesally; gonocoxal apodeme simple, without hooklike process; aedeagus ~2× longer than wide, lateral arms not boomerang-shaped sclerites, apical third trifurcate into subparallel lobes >2× longer than wide; parameres fused, as long as wide, median process elongate triangular tonguelike.

Distribution. Grand County, Utah.

Adult behavior. The mandibular and lacinial teeth on the female and collection in CO_2-baited traps indicate it feeds on vertebrate blood; and though its hosts are unknown, the SCo presence on only the proximal flagellomeres suggests it is mammalophilic.

Culicoides moabensis was collected from mid-April through October, with strong peaks in late May (week 21) and early October (week 41), suggesting it is bivoltine in Grand County, which may not be the case in other areas (see *C. brookmani* biology).

Remarks. *Culicoides moabensis* is more closely related to *C. brookmani* and *C. multipunctatus* of the Multipunctatus group than to other *Selfia* species (Phillips 2015).

Culicoides (*Selfia*) *tenuistylus* Wirth

(Fig. 40)

Culicoides tenuistylus Wirth, 1952a: 178 (female; male genitalia; fig. female palpus, male genitalia; California).

Culicoides (*Selfia*) *tenuistylus*: Khalaf 1954: 38 (assignment to subgenus *Selfia*). Atchley 1970: 263 (key; female, male, pupa, larva; 19 fig.). Wirth et al. 1985: 34 (numerical characters; fig. female wing). Murphree and Mullen 1991: 365 (key; larva; numerical characters; fig. epipharynx).

Diagnosis. (Tables 14, 15) Brown; wing without pattern of pale spots; three unsclerotized or faintly sclerotized long fingerlike spermathecae; male scutellum with six setae; hind tarsomeres with apical spines; posterior margin of male sternite 9 nearly straight, without caudomedial lobes; gonocoxite slightly tapering, not basally expanded or bent; posterior portion of gonocoxal apodeme with tiny coarse fingerlike processes on mesal surface and a spinelike process at base; apex of gonostylus rounded blunt clublike, without tooth; aedeagus Y-shaped, with moderately sclerotized median cross-bar connecting the heavily sclerotized basal arms; parameres fused, little longer than wide, with broad tapering blunt triangular median process.

Distribution. California. Cole and Schlinger (1969) report *C. tenuistylus* from Arizona and New Mexico; however, because the closely similar *C. jacksoni*—which has an Arizona and New Mexico distribution—was described later by Atchley (1970), these may be misidentifications.

Larval ecology and adult behavior. Immatures have been reared from a sandy stream margin in Mendocino County, California; and females have been collected from the ears of deer and from jackrabbits (Atchley 1970). Furthermore, Weinmann et al. (1979) collected blood-engorged *C. tenuistylus* from California quail (*Callipepla californica*)-baited traps; however, they found no *C. tenuistylus* infected with quail heartworm (*Splendidofilaria californiensis*) or other evidence it can transmit the parasite.

Subgenus *Sensiculicoides* Shevchenko

Culicoides (*Sensiculicoides*) *kibunensis* Tokunaga

(Fig. 98, 152, 231, 273)

Culicoides kibunensis Tokunaga, 1937: 298 (male, female; fig. female wing, antenna, male genitalia; Japan).

Culicoides (*Oecacta*) *kibunensis*: Khalaf 1954: 36 (assignment to subgenus *Oecacta*). Arnaud 1956: 107 (female, male; fig. female head, antenna, palpus, mouthparts, mesonotum, wing, legs, tibial spines, spermathecae, genitalia, male antenna, palpus, mesonotum, wing, ventral genitalia, dorsal genitalia, parameres and aedeagus; synonyms: *Culicoides ponkikiri* Kono and Takahasi, *Culicoides sitinohensis* Okada). Jorgensen 1969 (as species 75): 36 (key; quantitative characters; female; male genitalia; fig. female antenna, spermathecae, palpus, wing, male genitalia, parameres; seasonal distribution; Washington). Wirth and Blanton 1969a: 560 (female, male; fig. antenna, palpus, wing, eye separation, spermathecae, male genitalia, parameres; synonym: *Culicoides cubitalis* Edwards). Wirth et al. 1985: 38 (numerical characters; fig. female wing).

Culicoides (*Sensiculicoides*) *kibunensis*: Szadziewski et al. 2016: 420 (resurrection and diagnosis of subgenus *Sensiculicoides* Shevchenko, 1977; placement of *C. kibunensis* in *Sensiculicoides*).

Culicoides cubitalis Edwards, 1939: Edwards et al. 1939: 40, 139 (male; fig. genitalia; Britain). Kettle and Lawson 1952: 438, 460 (larva, pupa; fig.). Campbell and Pelham-Clinton 1960: 244 (male, female). Callot and Kremer 1963: 113 (male, female, intersexes; numerical characters; fig. palpi, wings).

Culicoides ponkikiri Kono and Takahasi, 1940: 74 (key; female; fig. wing, antenna, palpus; Japan).

Culicoides sitinohensis Okada, 1941: 18 (female).

Culicoides albicans (Winnertz), misidentified: Callot 1959: 439 (intersex; fig. female, head, male head; France).

Diagnosis. (Tables 14, 15) Wing pattern reduced; r_2 dark; pale spots at tip of costa, on r-m crossvein, absent or faint in apices of r_3, m_1, m_2, cua_1; antennal ratio 1.13–1.65; proboscis ratio 0.74–0.90; palpal ratio 1.57–2.78;

spermathecae usually slightly unequal by 1.05× but up to 1.26× in some specimens, sclerotized necks shorter than wide or absent; sclerotized ring on spermathecal duct; ventral apodeme of gonocoxite simple; gonostylus almost straight, midportion of lateral contour concave; aedeagus Y-shaped, median process stout at base, tapering to blunt tip, sometimes with a pair of lateral finlike distally pointed processes at ~0.7 (these difficult to see), aedeagal ratio ~0.5; parameres separate, apices simple, pointed, curved ventrally.

Distribution. Holarctic; in North America: British Columbia (Costello 1982), Washington, Oregon, Idaho (Blaine, Bonneville, Custer counties, **new state record**), California (**new state record** [Monarch 2021]), Utah (Garfield, Grand, San Juan, Sanpete, Summit counties), Colorado, Arizona.

Larval ecology. McMullen (1978) found Travisi group (likely *C. kibunensis*) immatures, along with *C. palmerae* James, in slightly acid to neutral semi-aquatic to aquatic habitats with "high organic content of plant origin" in British Columbia.

Vector potential. All of the reported host, parasite, and vector competency studies on *C. kibunensis* have been Eurasian, and much evidence has been accumulated to show *C. kibunensis*' ability to transmit avian protozoans. Bernotienė et al. (2019) found sporozoites of *Haemoproteus pallidus* Valkiūnas and Iezhova (hPFC1) (Aconoidasida: Haemoproteidae), which is a parasite common in birds of the family Muscicapidae, in wild-caught *C. kibunensis*—confirming vector competency for the parasite. Furthermore, Žiegytė et al. (2021) found *Haemoproteus minutus* Valkiūnas and Iezhova (hTURDUS2, hTUPHI01) (Aconoidasida: Haemoproteidae) sporozoites in the salivary glands of and DNA in the thoraxes of *C. kibunensis* collected using UVLTs and bird-baited traps during 19–28 June in Lithuania—confirming its vector competency for this parasite known to cause morbidity and mortality in a broad range of birds from South American and Australasian parrots (Ortiz-Catedral 2019) to migratory and non-migratory European passerine birds (Passeriformes), including Eurasian reed warblers (*Acrocephalus scirpaceus* [Hermann]), icterine warblers (*Hippolais icterina* [Vieillot]), Eurasian blue tits (*Parus caeruleus* Linnaeus), bearded reedlings (*Panurus biarmicus* [Linnaeus]), dunnocks (*Prunella modularis* [Linnaeus]), common blackbirds (*Turdus merula* Linnaeus, Turdidae), ring ouzels (*Turdus torquatus* Linnaeus) (Synek et al. 2013), song thrushes (*Turdus philomelos* Brehm), and European robins (*Erithacus rubecula* [Linnaeus], Muscicapidae) (Palinauskas et al. 2013).

Culicoides kibunensis has also been found infected with other protozoan parasites known to have alternate vertebrate hosts but for which vector competency has not been proven. Martínez-de la Puente et al. (2011) collected *C. kibunensis* from Spain infected with three lineages of *Haemoproteus* and the avian malaria *Plasmodium* Marchiafava and Celli (Aconoidasida: Plasmodiidae) lineage CulPlas1; however, *Plasmodium agamae* Wenyon, a parasite of reptiles, is the only *Plasmodium* known to be transmitted by *Culicoides* (Telford 1988). Santiago-Alarcon et al. (2012a) collected *C. kibunensis* from Germany that had fed on blackcaps (*Sylvia atricapilla* [Linnaeus], Sylviidae) and were infected with the *Haemoproteus* lineage SYAT07—a strain known to infect blackcaps. Synek et al. (2013) collected, with bird-baited traps in the Czech Republic, *C. kibunensis* infected with three lineages of *Haemoproteus*, including lineage TURDUS2. Santiago-Alarcon et al. (2013) found *C. kibunensis* naturally infected with *Haemoproteus parabelopolskyi* Kruse (a parasite of blackcaps), and *H. minutus* (Palinauskas et al. 2013). In addition, Bernotienė et al. (2019) detected *Haemoproteus tartakovskyi* Valkiūnas DNA, and Žiegytė et al. (2021) detected *H. tartakovskyi* (hSISKIN1) and *Plasmodium vaughani* Novy and MacNeal (pSYAT05) DNA in *C. kibunensis* collected in Lithuania. Though these findings were from European *C. kibunensis* and do not confirm any ability to transmit these parasites, because the type host for *P. vaughani* is the American robin (*Turdus migratorius* Linnaeus, Turdidae) (Iezhova et al. 2005) and *P. vaughani* is known to infect other species of Nearctic passerine birds (Herman 1944), they suggest that *C. kibunensis* may play an important role in vectoring avian protozoan parasites in North America.

Symbionts. *Culicoides kibunensis* has also been found infected by parasites not known to have alternate vertebrate hosts. Podlipaev et al. (2004) collected from a buzzard (*Buteo buteo* Linnaeus, Accipitridae) nest a female *C. kibunensis* infected with *Herpetomonas ztiplika* Podlipaev et al. (Kinetoplastida: Trypanosomatidae). Callot (1959, as *C. albicans*) and Callot and Kremer (1963, as *C. cubitalis*) described intersexes of *C. kibunensis* naturally parasitized by mermithid nematodes. Rieb et al. (1982) collected from a fluvial mud bank in France, turquois-blue *C. kibunensis* larvae (as *C. cubitalis*) infected with an iridovirus (Iridoviridae) fatal in the last (fourth) larval instar. Pagès et al. (2017) collected *C. kibunensis* in Spain infected with *Wolbachia* endosymbionts, which can alter dipteran reproduction by killing male embryos, inducing gamete incompatibility, or feminizing genetic males (Stouthamer 1999); and Möhlmann (2019) collected *C. kibunensis* in the Netherlands infected with *Wolbachia* and "*Candidatus* Cardinium", another endosymbiont that may alter reproduction in *Culicoides* (Pilgrim et al. 2020).

Adult behavior. Palearctic hosts of *C. kibunensis* include pig, goat, fowl (Nishijima 1964), cow (*Bos taurus*), marsh warbler (*Acrocephalus palustris* [Bechstein], Acrocephalidae), common wood pigeon (*Columba palumbus* Linnaeus, Columbidae), yellowhammer (*Emberiza citrinella* Linnaeus, Emberizidae) (Lassen et al. 2012), blackcap (*Sylvia atricapilla*), human (Santiago-Alarcon et al. 2012a), and European robin (*Erithacus rubecula*) (Santiago-Alarcon et al. 2013). In addition, engorged *C. kibunensis* were collected from great tit (*Parus major* Linnaeus, Paridae) and European pied flycatcher (*Ficedula hypoleuca* [Pallas], Muscicapidae) nest boxes (Žiegytė et al. 2021). The broad range of Palearctic hosts and vector competency for transmission of avian parasites suggest *C. kibunensis* likely plays a similarly important role in North America.

Remarks. James's (1943: 150) description of the aedeagus of a Colorado *Culicoides simulans* Root and Hoffman seems to be that of *C. kibunensis* instead of *C. travisi*, but because I have not seen the specimen, I am not proposing a new synonymy.

Wirth and Blanton (1969a: 562) state *C. kibunensis* is closely related to *C. travisi*, which can be distinguished from *C. kibunensis* "by the usual presence of marginal wing spots and in the male by the much shorter basal arch and long slender median process with parallel sides in the aedeagus". However, the female wing photographs in Wirth et al. (1985: 39) show marginal wing spots in *C. kibunensis* intermediate between the reduced pattern of *C. travisi* on the same page and the more pronounced pattern of *C. travisi* in Blanton and Wirth (1979: 187); Battle and Turner (1971: 84) state for *C. travisi*, "pale spots rarely present along margin"; Jamnback (1965: 106) states for *C. travisi* the distal spots "often not apparent"; and a Virginia specimen lacks the marginal wing spots (Fig. 232). Hence, the wing pattern distinction is not reliable.

Furthermore, critical quantitative characters for the two species overlap (*C. kibunensis* first, *C. travisi* second): antennal ratio (1.13–1.65, 1.39–1.68), palpal ratio (1.57–2.78, 2.09–2.70), proboscis ratio (0.74–0.90, 0.74–0.85) (data compiled from Jamnback 1965, Jorgensen 1969, Battle and Turner 1971); and leg-banding are nearly identical (Table 15).

This leaves the size differential of the spermathecae as the only consistently described distinction for females. However, an Idaho specimen has an antennal ratio of 1.22 but a 1.26× spermathecal size differential, and similar discrepancies exist with other specimens.

For males, the only remaining described distinction is the shape of the aedeagus. Figure 65G for *C. kibunensis* in Arnaud (1956) shows a pair of lateral finlike distally pointed processes at ~0.7 on the median process of the aedeagus not shown or mentioned in any other references for either *C. kibunensis* or *C. travisi*. Only one of the slide-mounted specimens in the present study unambiguously had this characteristic. The others have aedeagi that otherwise are intermediate between those illustrated for the two species or more closely resemble those of *C. kibunensis*. Altogether, these overlapping characteristics may represent either hybridization between *C. kibunensis* and *C. travisi* or intraspecific variation of a single species and suggest the need for clarification of their species status (see also *C. travisi* remarks).

***Culicoides* (*Sensiculicoides*) *travisi* Vargas (new status)**

(Fig. 99, 153, 232, 274)

Culicoides travisi Vargas, 1949: 233, (new name for *Culicoides simulans* Root and Hoffman, preoccupied by Vimmer, 1932). Foote and Pratt 1954: 33 (key; fig. female wing, mesonotum, palpus, male genitalia).

Culicoides (*Oecacta*) *travisi*: Khalaf 1954: 37 (assignment to subgenus *Oecacta*). Fox 1955: 257 (key and diagnoses of subgenera; species key; taxonomy). Jamnback 1965: 106 (female; male genitalia; pupa, larva; biology; fig. male genitalia; female wing, antenna, palpus, eye separation, pupal tubercles; synonym: *Culicoides horneae* Foote and Pratt). Childers and Wingo 1968: 19 (key; biology; fig. female wing, spermathecae). Battle and Turner 1971: 84 (female; male genitalia; larval habitats; feeding habits; seasonal distribution; fig. female eye separation, palpus, wing, spermathecae, male genitalia, parameres). Blanton and Wirth 1979: 159 (key; numerical characters; female; male genitalia; pupa; fig. female antenna, palpus, wing, eye separation, spermathecae, leg, male genitalia, parameres; larval habitat, feeding habits, seasonal distribution). Wirth et al. 1985: 38 (numerical characters; fig. female wing). Murphree and Mullen 1991: 373 (key; larva; numerical characters; fig. head, epipharynx, hypostoma, mandible, caudal segment).

Culicoides simulans Root and Hoffman, 1937: 167 (diagnosis; female, male; fig. male genitalia, parameres, female wing; Maryland). James 1943: 150 (male genitalia; Colorado).

Culicoides horneae Foote and Pratt, 1954: 25 (key; male; fig. male wing, mesonotum, genitalia; New York).

Culicoides (*Beltranmyia*) *travisi*: Vargas 1960: 38 (assignment to subgenus *Beltranmyia*).

Diagnosis. (Tables 14, 15) Wing pattern reduced; r_2 dark; pale spots at tip of costa, on r-m crossvein, absent or faint in apices of r_3, m_1, m_2, cua_1; antennal ratio 1.39–1.68; proboscis ratio 0.74–0.85; palpal ratio 2.09–2.70; spermathecae unequal by 1.15–1.26×, sclerotized necks absent or shorter than wide; sclerotized ring on spermathecal duct; ventral apodeme of gonocoxite simple; gonostylus almost straight, midportion of lateral contour concave; aedeagus Y-shaped, aedeagal ratio ~0.4; median process long, narrow, parallel-sided on distal half; parameres separate, apices simple, pointed, curved ventrally.

Distribution. Eastern North America, at least from Alberta (Lysyk and Galloway 2014), Ontario, Nova Scotia, south through Wyoming to Oklahoma, Florida. Reported distributions west of the Continental Divide are likely confused with *C. kibunensis* (see remarks).

Larval ecology. Immatures have been collected or reared from a shaded stream margin with decaying leaves (Williams 1955), freshwater soil, stream sand and mud bar margins (Jones 1961b), wet meadow depression, cattail swamp, leaves and detritus on sedimentary rock stream margin (Jamnback 1965), shaded stream margin with leaves, sand, and mud (Hair et al. 1966), soil saturated by spring seepage (Childers and Wingo 1968), soil of wet wooded spring-fed bottomland, leafy pools in woodland bottomland, temporary rain pool, and wooded flowing freshwater (Blanton and Wirth 1979).

Adult behavior. Known hosts are cow (Roberts 1965; Zimmerman and Turner 1983), human (Snow 1955; Hair 1966; Hair and Turner 1968; Blanton and Wirth 1979), turkey, rabbit (Humphreys and Turner 1973), grackle (*Quiscalus quiscula*) (Robinson 1971), horse (Blanton and Wirth 1979), and sheep (Zimmerman and Turner 1983). Hair (1966) collected blood-engorged *C. travisi* from drop traps baited with eastern cotton-tail rabbit (*Sylvilagus*), guinea pig (*Cavia porcellus*), rat (*Rattus*), opossum (*Didelphis*), chicken (*Gallus gallus*), turkey (*Meleagris gallopavo*), mallard duck (*Anas boschas*), bobwhite quail (*Colinus virginianus*), and mourning dove.

Snow (1955) reported *C. travisi* to be a crepuscular and nocturnal blood-feeder with a strong preference for the ecotone and shrub-herb layer rather than within the forest or canopy, and Murray (1957) reported it to be most active in and on the edge of forested areas with peak nighttime activity during 0200–0500 hours. These are behaviors consistent with its mostly mammalian and ground-bird host preferences.

Vector potential. Robinson (1971) found *Chandlerella quiscali* in only 7 of 112 *C. travisi* 10 d after feeding on an infected grackle, suggesting it is not a favorable vector for that parasite. However, Bartlett and Anderson (1980) found *C. travisi* naturally infected with *Chandlerella chitwoodae* Anderson (Nematoda: Filarioidea), a parasite of crows (*Corvus brachyrhynchos*) and grouse (*Dendragapus obscurus* [Say], *Bonasa umbellus*[[Linnaeus], Phasianidae).

Remarks. *Culicoides travisi* matches all the diagnostic characters Szadziewski et al. (2016: 420) list for subgenus *Sensiculicoides* Shevchenko by having: gonocoxites with the ventral apodeme triangular, slender, and simple; paramere bare; apicolateral processes of tergite 9 long, slender, and triangular; female SCo on proximal and distal flagellomeres; two functional strongly sclerotized spermathecae; and palpal segment 3 with a distinct sensory pit on both sexes. Based on this and its similarity to *C. kibunensis*, I propose assignment of *C. travisi* to subgenus *Sensiculicoides* (**new status**).

The only Utah record of *C. travisi* I could find is the map Figure 124 in Blanton and Wirth (1979: 161), which shows Utah and Arizona on the western edge of the distribution. Because *C. travisi* and *C. kibunensis* are difficult to distinguish and their reported distributions overlap in Arizona, Utah, and Colorado, their taxonomic status in North America needs clarification. See also *C. kibunensis* remarks.

Subgenus *Silvaticulicoides* Glukhova

The normally important diagnostic characters of a sclerotized ring on the spermathecal duct and the number of hind tibial spines have been inconsistently reported for our three southwestern species of the Spinosus group of subgenus *Silvaticulicoides*: *C. sublettei*, *C. usingeri*, and *C. vetustus* Breidenbaugh and Mullens.

Wirth (1952a: 192) described and Bullock (1952: 23) redescribed *C. usingeri* with a sclerotized ring on the spermathecal duct. However, Grodhaus (no date, key couplet 25) stated *C. usingeri* lacks a ring; Atchley (1967: 997) reexamined type material and found the ring absent; and the specimen I collected in Utah lacks the ring. Furthermore, Atchley (1967: 997) described *C. sublettei* as not having the ring; however, the specimen I examined from Gillespie County, Texas, and the specimen I collected in Arizona both have the ring. Breidenbaugh and Mullens do not mention the presence or absence of a ring in *C. vetustus*. It seems that, contrary to Atchley's (1967: 997) Spinosus group diagnosis, this characteristic is not consistent in this group.

Breidenbaugh and Mullens (1999b: 159) described *C. vetustus* with five spines on the hind tibial comb and state that there are five on *C. sublettei* and four on *C. usingeri* (their p. 161). However, Atchley (1967: 997) describes *C. sublettei* with four spines, and Atchley (1967: 999) and Grodhaus (no date, couplet 25) state that *C. usingeri* has five spines. Furthermore, five of five *C. vetustus* specimens borrowed from Breidenbaugh and Mullens' collection, including a paratype I examined, had four spines on each comb; and the *C. usingeri* female I collected in Utah has five on one comb and four on the other, and the *C. usingeri* male has four on each.

This confusion suggests that either these characteristics are highly variable or there is significant inter-species hybridization. Furthermore, subgenus *Silvaticulicoides* seems to have close affinity with the Palmerae group. See the remarks for each species and the discussion under "Subgenus unplaced, Palmerae group".

***Culicoides* (*Silvaticulicoides*) *sublettei* Atchley**

(Fig. 94, 148, 237)

Culicoides (*Oecacta*) *sublettei* Atchley, 1967: 997 (key; numerical characters; female; male genitalia; fig. female wing, palpus, tibial comb, spermathecae, male genitalia, parameres; New Mexico). Wirth et al. 1985: 34 (numerical characters; fig. female wing). Breidenbaugh and Mullens 1999b: 161 (comparison to *C. vetustus* Breidenbaugh and Mullens).

Culicoides (*Silvaticulicoides*) *sublettei*: Borkent and Grogan 2009: 15 (in Nearctic catalog).

Culicoides spinosus Root and Hoffman, misidentified: Fox 1955: 255 (in part; key and diagnoses of subgenera; species key; taxonomy). Wirth and Bottimer 1956: 263 (Texas ecology). Khalaf 1957: 203 (may be misidentified; diagnosis; seasonal incidence; Oklahoma). Jones 1961b (Texas ecology). Jamnback 1965: 96 (in part; seasonal distribution; larval habitats).

Diagnosis. (Tables 14, 15) Wing pattern reduced and faint; r_2 dark; pale spots at tip of costa, on r-m crossvein, distal in cua_1 and anal cells, absent from r_3, m_1, indistinct in m_2; spermathecae with sclerotized necks about as long as wide; ventral apodeme of gonocoxite simple, about as long as dorsal apodeme; entire lateral contour of gonostylus convex; aedeagus V-shaped, median process tapered, blunt; parameres separate, mostly straight, apex with 3–4 divergent holly leaflike spines.

Distribution. California, Utah, Colorado (USNM), Arizona (Cochise County, **new state record**), New Mexico, Texas. Khalaf's (1957) *C. spinosus* Oklahoma record may be for *C. sublettei*. One female was collected with UVLT on 15 October 2019 at 31.89365°N 109.21416°W and 1708 m elevation in Arizona.

Larval ecology. *Culicoides sublettei* has been reared from mud at pond margins and light-trapped from 9 March to 9 October in south-central Texas (Wirth and Bottimer 1956, as *C. spinosus*). Jones (1961b, as *C. spinosus*) collected immatures from muddy freshwater spring-creek areas and boggy stream margins in Texas.

Adult behavior. Jones et al. (1977) reported burros as hosts.

Remarks. The Arizona specimen I collected differs from Atchley's (1967) description by having a sclerotized ring on the spermathecal duct. It also has the deeper palpal pit of *C. vetustus* and the shorter proboscis of *C. usingeri*. See subgenus *Silvaticulicoides* discussion.

Culicoides (*Silvaticulicoides*) *usingeri* Wirth

(Fig. 95, 149, 238, 270)

Culicoides usingeri Wirth, 1952a: 192 (key; female; male genitalia; fig. female wing, spermathecae, palpus, male genitalia; California). Bullock 1952: 23 (female; male genitalia; Utah: Salt Lake County). Rees and Bullock 1954 (Utah: Salt Lake County).

Culicoides (*Oecacta*) *usingeri*: Khalaf 1954: 38 (assignment to subgenus *Oecacta*). Fox 1955: 258 (key and diagnoses of subgenera; species key; taxonomy). Wirth et al. 1985: 34 (numerical characters; fig. female wing). Breidenbaugh and Mullens 1999b: 161 (comparison to *C. vetustus*).

Culicoides (*Silvaticulicoides*) *usingeri*: Borkent and Grogan 2009: 15 (in Nearctic catalog).

Diagnosis. (Tables 14, 15) Wing pattern reduced; r_2 dark; pale spots at tip of costa, on r-m crossvein, absent from r_3, m_1, m_2, cua_1, anal cell; spermathecae with sclerotized necks about as long as wide; ventral apodeme of gonocoxite slender, ~2× longer than dorsal apodeme; entire lateral contour of gonostylus convex; aedeagus V-shaped; parameres separate, mostly straight, apex with five or six divergent holly leaflike spines.

Distribution. Oregon, California, Nevada, Utah (Garfield, Salt Lake counties). Though rare or absent from Grand County, this species may be abundant elsewhere in the Canyonlands. *Culicoides usingeri* was reported from Salt Lake County by Bullock (1952) and Rees and Bullock (1954); however, it seems likely the reason these early records were not included in later catalogs or other records is their obscurity. Because *C. usingeri* was collected from Garfield County in the present study, it is likely the Salt Lake County records are valid, and *C. usingeri* is here confirmed as a **Utah record**.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; however, its hosts are unknown. Besides the Garfield County collection, the only other record of *C. usingeri* in Utah is from Bullock (1952) who collected adults during June in Salt Lake County.

Remarks. The female specimen I collected in Utah lacks the sclerotized ring on the spermathecal duct and has five spines on one hind tibial comb and four on the other. The male has four spines on each. The wing patterns are distinct from *C. sublettei* (Fig. 148–150, 237–239), and the *C. usingeri* have apical spines on the hind tarsomeres, whereas the *C. sublettei* and *C. vetustus* specimens I have examined do not. See subgenus *Silvaticulicoides* discussion.

Culicoides (*Silvaticulicoides*) *vetustus* Breidenbaugh and Mullens

(Fig. 96, 150, 239)

Culicoides vetustus Breidenbaugh and Mullens, 1999b: 156 (egg, larva, pupa, adult female; male genitalia; fig. egg, larval head, mouthparts, caudal segment, pupal respiratory trumpet, operculum, caudal segment, chaetotaxy, female eyes, antenna, palpus, leg, wing, spermathecae, male genitalia; comparison to *C. sublettei* and *C. usingeri*; California).

Culicoides (*Silvaticulicoides*) *vetustus*: Borkent and Grogan 2009: 15 (in Nearctic catalog).

Diagnosis. (Tables 14, 15) Wing pattern reduced; r_2 dark; pale spots at tip of costa, on r-m crossvein, absent from r_3, m_1, m_2, cua_1, anal cell; spermathecae with sclerotized necks about as long as wide; male tergite 9 apicolateral processes large: their length ~0.4 the distance between them; ventral apodeme of gonocoxite tapering thornlike, about as long as dorsal apodeme; entire lateral contour of gonostylus convex; aedeagus Y-shaped, arms U-shaped, median process parallel-sided, blunt; parameres separate, mostly straight, apex with four divergent holly leaflike spines.

Distribution. Southern California.

Adult behavior. Breidenbaugh and Mullens (1999b) report collections of females with CO_2-baited traps, and the mandibular and lacinial teeth on the female also indicate it feeds on vertebrate blood; however, its hosts are unknown.

Life cycle. Laboratory studies by Breidenbaugh and Mullens (1999b) found that wild-caught *C. vetustus* laid an average of 86 eggs, of which 67% hatched an average of 7 d later. Average time to pupation was 117 d, with adults emerging ~4 d later at 21 °C, with an overall survivorship of 31%. However, unlike other *Culicoides* they reared, *C. vetustus* larvae would not feed on the nematodes provided. Whether this exceptionally long development time was due to nutritional deficiency is unknown.

Remarks. Willis Wirth referred to this species as new species number 122 (Bradley Mullens, personal communication). Breidenbaugh and Mullens (1999b) describe *C. vetustus* with five spines on the hind tibial comb; however, five of five specimens I examined, including a paratype, had four spines on each. See subgenus *Silvaticulicoides* discussion.

Subgenus *Silvicola* Mirzaeva and Isaev

Using morphological cluster analysis, Mirzaeva and Isaev (1990) placed the Palearctic Grisescens and Nearctic Cockerellii groups of subgenus *Culicoides* into their new subgenus *Silvicola* Mirzaeva and Isaev, retaining the Holarctic Pulicaris group in the subgenus *Culicoides* sensu stricto. More recently, Meiswinkel et al. (2004) and Gomulski et al. (2006) supported this taxonomy using genetic analysis. Western North American members of subgenus *Silvicola* are readily distinguished from subgenus *Culicoides* sensu stricto by lacking a dark spot in the middle of cua$_1$ and by having, in the male, the midportion of tergite 9 convex and extending more caudally than the relatively small apicolateral processes. In contrast with North American authors, I am following their taxonomy here.

Wirth and Blanton (1969b: 207) state in their paper on Nearctic species of subgenus *Culicoides*, "Caution must be exercised in using the key because of variability in many species. A series of specimens is preferred, and the most representative specimens should be selected and keyed. Confirmation by reference to the table of numerical characters, to the illustrations, and finally to the descriptions, is nearly always necessary." Furthermore, Meiswinkel et al. (2004) and Gomulski et al. (2006) reported many Palearctic specimens of this group could not be reliably identified morphologically using published keys.

In his seminal work on subgenus *Selfia*, Atchley (1970) was the first author to use the presence or absence of apical hind tarsal spines as a diagnostic character. Likewise, the presence or absence of spines on the fore and hind tarsomeres seems to clearly separate the southwestern species of *Silvicola* into three groups: those with spines on both fore and hind tarsomeres include *C. cockerellii*, *C. neomontanus*, and *C. sierrensis*; those with spines on only the fore tarsomeres include *C. freeborni*; and, those without spines on either include *C. lahontan*, *C. neofagineus*, and *C. saltonensis* (*C. tristriatulus* Hoffman was not characterized because no specimens were examined). This characteristic is reliable for all the specimens examined; however, further identification of the species relies on the fairly variable characteristics of eye separation, palpal segment 3 sensorial arrangement, and antennal SCo pattern in females, genitalia details in males, and leg-banding and wing pattern. This is especially difficult with the *C. cockerellii* subgroup where there are a considerable number of intermediate forms of the three species collected from similar habitats—suggesting that there is considerable interbreeding or the possibility that *C. cockerellii* is a highly variable species to include the currently recognized *C. neomontanus* and *C. sierrensis*. The three specimens of *Silvicola* representing possible species D and E further complicate this. See also the specific remarks in the following species accounts.

***Culicoides* (*Silvicola*) *cockerellii* (Coquillett)**

(Fig. 66, 119, 178, 287)

Ceratopogon cockerellii Coquillett, 1901: 603 (key; female; Colorado).

Culicoides cockerellii (Coquillett): Kieffer 1906: 54 (combination). Hoffman 1925: 293 (key; female; fig. wing, mesonotum). Root and Hoffman 1937: 157 (key). James 1943: 149 (seasonal distribution; male genitalia; Colorado). Knowlton and Fronk 1950: 114 (Utah: Cache, Duchesne, Kane, Uintah counties). Wirth 1951: 81 (male key, genitalia from Wyoming material; female misidentified, not *C. cockerellii*). Wirth 1952a: 171 (in part; key; female, male; fig. dorsal thoracic patterns, female palpus, wing, male genitalia). Bullock 1952: 19 (female; male genitalia; Utah: Salt Lake County). Rees and Bullock 1954 (Utah: Salt Lake County). Foote and Pratt 1954: 18 (key; diagnosis; fig. female wing, mesonotum, palpus, male genitalia).

Culicoides (*Culicoides*) *cockerellii*: Khalaf 1954: 39 (assignment to subgenus *Culicoides*). Fox 1955: 232 (key and diagnoses of subgenera; species key; taxonomy). Atchley 1967: 966 (in part; key; numerical characters; female; male genitalia; variation; fig. female wing, palpus, tibial comb, male genitalia, parameres). Wirth and Blanton 1969b: 214 (key; numerical characters; female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, male genitalia, parameres). Wirth et al. 1985: 10 (numerical characters; fig. female wing).

Culicoides cockerellii variety b: Wirth 1952a: 172 (female; male genitalia).

Culicoides (*Anilomyia*) *cockerellii*: Vargas 1960: 37 (assignment to subgenus *Anilomyia* Vargas). Atchley 1967: 968 (rejection of assignment to *Anilomyia*).

Culicoides (*Silvicola*) *cockerellii*: Mirzaeva and Isaev 1990: 156 in English translation (as part of Cockerellii group, assignment to new subgenus *Silvicola*).

Diagnosis. (Tables 14, 15) Wing pattern extensive, with distal stripes and pale spots; pale spot over at least distal half of r_2; cua_1 without central dark spot; dark spot over r_1–r_2 merged with spot over M fork; dark spot in distal half of r_3 barely medially constricted; eyes contiguous only at a point; superior transverse suture present; palpal segment 3 with scattered sensilla instead of pit; scutum with sub-lateral dark patches; tibiae without pale bands; fore and hind tarsomeres with apical spines; spermathecae subequal; male tergite 9 apicolateral processes tiny and not projecting beyond median lobe; ventral apodeme of gonocoxite shorter than dorsal apodeme, strongly tapered, pointed, 1–2× as long as basal width; gonocoxite with fine setae on mesal surface; aedeagus V-shaped, median process triangular, tapering, aedeagal ratio ~0.45; parameres separate, apices slender, posteriorly directed, with fringe of tiny hairs at tip.

Distribution. British Columbia, Alberta, Quebec, south through Washington, Idaho (Blaine, Bonneville, Custer counties, **new state record**), Montana, North Dakota (Anderson and Holloway 1993), Oregon, Nevada, Utah (Summit, Uintah counties), Wyoming, South Dakota, Colorado, to California, Arizona, New Mexico. Distribution records for *C. cockerellii* preceding Wirth and Blanton 1969b refer instead—at least in part—to *C. freeborni*, *C. neofagineus*, *C. neomontanus*, and *C. sierrensis* in the southwestern United States. It has been reported from the Needles District of Canyonlands National Park, San Juan County, Utah (Boris Kondratieff, personal communication); however, the habitat characteristics of that area of the park suggest possible confusion with *C. lahontan*, and no specimens could be found for confirmation.

Adult behavior and vector potential. Known hosts are sheep (Jones and Luedke 1969) and human (Wirth and Blanton 1969b). Kramer et al. (1990) found *C. cockerellii* infected with bluetongue virus (BTV).

Remarks. Wirth and Blanton (1969b) redescribed *C. cockerellii* and five other species and described nine new Nearctic species of (then) subgenus *Culicoides*, five of which had been variants of *C. cockerellii*. In addition, they suggested *C. cockerellii* may be a synonym or part of a species complex with the Palearctic *Culicoides grisescens* Edwards.

Culicoides cockerellii is closely similar to *C. sierrensis*, differing mainly by not having a distinct basal pale band on the hind tibia. However, some Idaho and northern Utah specimens are ambiguous with regard to this character, suggesting the character is variable or the species interbreed. See also subgenus *Silvicola* discussion and *C. neomontanus* and *C. sierrensis* remarks.

The three female specimens collected 15 July 2019 in Custer County, Idaho, had eyes contiguous for 0.3 ommatidium diameter, contiguous at a point, and separated by 0.2 ommatidium diameter but were otherwise consistent with the morphology of *C. cockerellii*.

Culicoides (*Silvicola*) *freeborni* Wirth and Blanton

(Fig. 67, 120, 179, 243)

Culicoides (*Culicoides*) *freeborni* Wirth and Blanton, 1969b: 217 (key; numerical characters; female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, male genitalia, parameres; California). Jorgensen 1969 (as species 43): 33 (quantitative characters; key; female, male; seasonal distribution; fig. female wing, spermathecae, palpus, antenna, male parameres, genitalia). Wirth et al. 1985: 10 (numerical characters; fig. female wing). Breidenbaugh and Mullens 1999a: 843 (egg, larva, pupa; fig. egg, larval head, mouthparts, thorax, caudal segment, pupal respiratory trumpet, operculum, caudal segment, chaetotaxy).

Culicoides (*Silvicola*) *freeborni*: Mirzaeva and Isaev 1990: 156 in English translation (as part of Cockerellii group, assignment to new subgenus *Silvicola*).

Culicoides luteovenus Root and Hoffman, misidentified: Root and Hoffman 1937: 156 (in part; female, male; fig. female wing, male genitalia; Federal District, Mexico). Wirth 1952a: 175 (key; female; male genitalia; fig. female wing, mesonotum, palpus). Fox 1955: 245 (in part; key and diagnoses of subgenera; species key; taxonomy).

Diagnosis. (Tables 14, 15) Wing pattern extensive, with distinct distal stripes and pale spots; pale spot over at least distal half of r_2; cua_1 without central dark spot; dark spot over r_1–r_2 not connected or only narrowly connected to spot over M fork; dark spot in distal half of r_3 narrowly hourglass-shaped; eyes contiguous for ~1 ommatidium diameter; superior transverse suture present; palpal segment 3 with wide area of scattered sensilla, sometimes organized into irregular pitlike patches; scutum with prominent pattern; tibiae without pale bands; fore tarsomeres 1 or 2 with, hind tarsomeres without apical spines; spermathecae subequal; male tergite 9 with tiny apicolateral processes not projecting beyond median lobe; ventral apodeme of gonocoxite shorter than dorsal apodeme, strongly tapered, pointed, 1–2× as long as basal width; gonocoxite with short fine black setae on mesal surface; aedeagus V-shaped, median process tapered triangular, aedeagal ratio ~0.4; parameres separate, apices slender, curved hooklike, with fringe of tiny hairs at tip.

Distribution. Washington, Oregon, California.

Larval ecology and adult behavior. Wirth and Blanton (1969b) reported immatures reared from mud, moss, and soil and adult females collected from the ears of deer and jackrabbits. Using truck traps in Kern County, California, Nelson and Bellamy (1971) found *C. freeborni* more abundant in the fall than in the summer, with flight activity peaking near dusk and diminishing through the night without a peak at dawn.

Life cycle. Further studies by Breidenbaugh and Mullens (1999a) found that wild-caught females laid an average of 67 eggs, of which 35% hatched in ~4 d at 21–25 °C, and the larvae fed on the bacterial-feeding nematode *Panagrellus redivivus* in the laboratory.

Symbionts. Mullens et al. (1997b) experimented with the potential biocontrol parasitic nematode, *Heleidomermis magnapapula* in the laboratory and found it readily penetrated but did not develop or emerge from *C. freeborni* larvae, which continued to develop to adults with no sign of the nematodes.

Culicoides* (*Silvicola*) *lahontan **Wirth and Blanton**

(Fig. 68, 121, 180, 241, 242)

Culicoides (*Culicoides*) *lahontan* Wirth and Blanton, 1969b: 223 (key; numerical characters; female, male; fig. female antenna, palpus, wing, spermathecae, eye separation, male genitalia, parameres; California). Wirth et al. 1985: 10 (numerical characters; fig. female wing). Breidenbaugh and Mullens 1999a: 845 (egg, larva, pupa; fig. egg, larval head, mouthparts, thorax, pupal respiratory trumpet, operculum, caudal segment, chaetotaxy).

Culicoides (*Silvicola*) *lahontan*: Mirzaeva and Isaev 1990: 156 in English translation (as part of Cockerellii group, assignment to new subgenus *Silvicola*).

Culicoides luteovenus Root and Hoffman, misidentified: Root and Hoffman 1937: 156 (in part; female, male; fig. female wing, male genitalia; Federal District, Mexico). Knowlton and Fronk 1950: 114 (Utah: Uintah County). Wirth 1952a: 175 (key; female; male genitalia; fig. female wing, mesonotum, palpus). Bullock 1952: 10 (key). Fox 1955: 245 (in part; key and diagnoses of subgenera; species key; taxonomy). Spinelli and Huerta 2015: 818 (mistaken as to presence of *C. luteovenus* in United States; compared with *Culicoides rulfoi* Spinelli and Huerta).

Diagnosis. (Tables 14, 15) Wing pattern extensive, with distal stripes and pale spots; pale spot over at least distal half of r_2; cua_1 without central dark spot; eyes contiguous for 1–2 ommatidium diameters; superior transverse suture nearly always present; palpal segment 3 with distinct wide shallow sensory pit on female, small distinct on male, scattered sensilla lacking; scutum with trace of faint pattern; scutellum often with 6–8 setae on female, 4–6 on male; tibiae without pale bands; fore and hind tarsomeres without apical spines; spermathecae subequal; male tergite 9 with tiny apicolateral processes not projecting beyond median lobe; ventral apodeme of gonocoxite shorter than dorsal apodeme, strongly tapered, pointed, 1–2× as long as basal width; gonocoxite with short fine black setae on mesal surface; aedeagus somewhat Y-shaped, median process abruptly narrowing on distal half to slender fingerlike tip, aedeagal ratio ~0.4; parameres separate, apices slender, posteriorly directed, with fringe of tiny hairs at tip.

Distribution. Alberta (Lysyk and Galloway 2014), Montana, south through Oregon, to California, Utah (Grand, Salt Lake, Uintah, Washington counties). See remarks.

Larval ecology and life cycle. Breidenbaugh and Mullens (1999a) collected *C. lahontan* adults with emergence traps from soil margins of an ephemeral creek at 300–350 m elevation in San Bernardino County, California. They also conducted laboratory studies and found that wild-caught females laid an average of 89 eggs, of which 55% hatched in ~7 d at 21–25 °C. The larvae fed on the bacterial-feeding nematode *Panagrellus redivivus*, pupated ~60 d after hatch, and eclosed ~4 d later.

Adult behavior. Mullens and Dada (1992a) reported bighorn sheep (*Ovis canadensis nelsoni*) as a host. They also reported (1992b) moderate parity rates of 13% to 25% for females collected using CO_2-with-light-baited traps, suggesting a moderate vector potential. Their finding (1992b) of a single activity peak of May–June in the Santa Rosa Mountains of Southern California sharply contrasts with the double peaks of March–April (week 14) and October (week 43) I found in Grand County, Utah (Table 5).

Symbionts. Mullens et al. (1997b) experimented with the potential biocontrol parasitic nematode, *Heleidomermis magnapapula* in the laboratory and found it readily entered, infected, developed, but did not emerge from *C. lahontan* larvae, which continued to develop to adults with no sign of the nematode.

Atypical biology. A *C. lahontan* collected in Grand County and another collected by Xinmi Zhang in Riverside County, California, have three fully developed spermathecae instead of two with a vestigial third (Table 12).

Remarks. Knowlton and Fronk (1950), Wirth (1952a), Bullock (1952), and Wirth and Blanton (1959) reported the (now only Neotropical) *C. luteovenus* from Utah. However, upon examining the redescriptions of *C. luteovenus* in Wirth (1952a: 175) and Wirth and Blanton (1959: 297), the wing photographs in Wirth et al. (1985) and Wirth et al. (1988), and the key characters in Bullock (1952: 10–11), it seems Wirth in part, Bullock, and probably Knowlton and Fronk are referring to *C. lahontan* instead. The broad shallow sensory pit on palpal segment 3, mesonotal pattern, and narrow median process of the aedeagus are distinctive. Wirth and Blanton (1969b) state *C. freeborni* was often mistaken for *C. luteovenus* but do not offer *C. lahontan* as mistaken for *C. luteovenus*, which seems more likely.

Culicoides (*Silvicola*) *neofagineus* Wirth and Blanton

(Fig. 69, 122, 181, 244)

Culicoides (*Culicoides*) *neofagineus* Wirth and Blanton, 1969b: 227 (key; numerical characters; female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, male genitalia, parameres; Arizona). Wirth et al. 1985: 10 (numerical characters; fig. female wing). Murphree and Mullen 1991: 312 (key; larva; numerical characters; fig. head, thorax, epipharynx, hypostoma, mandible, caudal segment).

Culicoides (*Silvicola*) *neofagineus*: Mirzaeva and Isaev 1990: 156 in English translation (as part of Cockerellii group, assignment to new subgenus *Silvicola*).

Diagnosis. (Tables 14, 15) Wing pattern extensive, with distinct distal stripes and pale spots; pale spot over at least distal half of r_2; cua_1 without central dark spot; eyes contiguous for ~2 ommatidium diameters; superior transverse suture present; palpal segment 3 with wide shallow, irregular, often subdivided sensory pit, often with scattered sensilla; scutum with prominent pattern; scutellum with ~17 setae on female, 10–13 on male; hind tibiae with basal pale band ~2× longer than wide; fore and hind tarsomeres without apical spines; spermathecae subequal to unequal by 1.2×; male tergite 9 with tiny apicolateral processes not projecting beyond median lobe; ventral apodeme of gonocoxite shorter than dorsal apodeme, strongly tapered, pointed, 1–2× as long as basal width; gonocoxite with strong black spines on mesal surface; aedeagus somewhat Y-shaped, median process abruptly narrowing on distal half to slender fingerlike tip, aedeagal ratio ~0.6; parameres separate, apices slender, posteriorly directed, with fringe of tiny hairs at tip.

Distribution. Oregon, California, southeastern Arizona, New Mexico (**new state record** [Monarch 2021]).

Larval ecology. William C. Reeves reared *C. neofagineus* from a sycamore treehole (Wirth and Blanton 1969b), and E. S. Tikasingh reared it from treehole "humus". Woodward et al. (1988) collected adults from emergence traps over treeholes in oaks (*Quercus kelloggii* Newberry and *Q. wislizenii* Candolle, Fagaceae) from early April through August in Northern California.

Adult behavior. Adult females have been collected from the ear of a deer, from a quail-baited drop trap (Wirth and Blanton 1969b), and while biting a human (Wirth 1977).

Culicoides (*Silvicola*) *neomontanus* Wirth

(Fig. 70, 123, 182, 245, 288)

Culicoides (*Culicoides*) *neomontanus* Wirth, 1976 (new name for *Culicoides montanus* Wirth and Blanton, preoccupied by Shakirzjanova, 1962). Wirth et al. 1985: 10 (numerical characters; fig. female wing).

Culicoides cockerellii variety c: Wirth 1952a: 172 (female; male genitalia; California). Atchley 1967: 968 (comparison of female with *C. cockerellii* sensu stricto; New Mexico).

Culicoides (*Culicoides*) *montanus* Wirth and Blanton, 1969b: 225 (key; numerical characters; female, male; fig. female antenna, palpus, wing, spermathecae, eye separation, male genitalia, parameres; Utah: Beaver, Cache, Duchesne, Uintah counties). Jorgensen 1969 (as species 44): 34 (key; quantitative characters; female; male genitalia; fig. female wing, spermathecae, palpus, antenna, male genitalia, parameres; seasonal distribution; Washington).

Culicoides (*Silvicola*) *montanus*: Mirzaeva and Isaev 1990: 156 in English translation (as part of Cockerellii group, assignment to new subgenus *Silvicola*).

Diagnosis. (Tables 14, 15) Wing pattern extensive, but with distal stripes and pale spots indistinct; pale spot over at least distal half of r_2; cua_1 without central dark spot; hourglass-shaped distal dark spot in r_3 usually not darker than other distal dark patches; eyes contiguous for 1–2 ommatidium diameters; superior transverse suture present; palpal segment 3 with scattered sensilla instead of pit; scutum sometimes with faint pattern; tibiae without pale bands; fore and hind tarsomeres with apical spines; spermathecae subequal; male tergite 9 with tiny apicolateral processes not projecting beyond median lobe; ventral apodeme of gonocoxite shorter than dorsal apodeme, strongly tapered, pointed, 1–2× as long as basal width; gonocoxite with moderately strong black setae on mesal surface; aedeagus V-shaped, median process triangular, tapering, aedeagal ratio ~0.3; parameres separate, apices slender, posteriorly directed, with fringe of tiny hairs at tip.

Egg morphology. One female I collected from Montrose County, Colorado, contained a single 617 µm × 80 µm egg (Fig. 288), which is considerably larger than the range of 285–515 µm × 41–75 µm reported for some other *Culicoides* species (Breidenbaugh and Mullens 1991a, 1991b; Day et al. 1997; Cribb and Chitra 1998; Abubekerov and Mullens 2018).

Distribution. British Columbia, Alberta, Manitoba, south through Washington, Idaho (Blaine and Custer counties, **new state record**), Montana, Oregon, Nevada, Utah (Beaver, Cache, Duchesne, San Juan, Sanpete, Summit, Uintah, Wasatch counties), Wyoming, Colorado (Montrose County, **new state record**), to California, Arizona, New Mexico. The Colorado record is of 50 males and 32 females collected with UVLT on 30 July 2020 at 38.32234°W and 108.18359°W and 2934 m elevation on the Uncompahgre Plateau in Colorado.

Larval ecology. McMullen (1978) found *C. neomontanus* (as *C. montanus*) to be univoltine, with peak adult abundance from late June until mid-July, and reared it in greatest abundance from pH 6.8–8.2 pond water-saturated and heavily cattle-manured soil ~1 m from the water's edge in British Columbia.

Adult behavior. Known hosts are human, jackrabbit (Wirth and Blanton 1969b, as *C. montanus*), cow, and horse (Jorgensen 1969, as species 44; however, the horse record in his Table 6 is contradicted in the text).

Remarks. Some of the specimens of female *C. neomontanus* collected in San Juan County, Utah, and Montrose County, Colorado—identified by having SCo on some of flagellomeres 3–8 and eyes contiguous for >0.4 ommatidium diameter—had relatively distinct wing patterns typical for *C. cockerellii* or *C. sierrensis* or indistinct to distinct pale basal hind tibial banding typical for *C. sierrensis*. This caused some uncertainty for the several *C. neomontanus* males with similar wing pattern variations or pale hind tibial banding in the same collection. This suggests these diagnostic characters have considerable variability and throws into doubt the status of these species. See also subgenus *Silvicola* discussion and *C. cockerellii* and *C. sierrensis* remarks.

Culicoides (*Silvicola*) *saltonensis* Wirth

(Fig. 71, 124, 183)

Culicoides cockerellii saltonensis Wirth, 1952a: 173 (key; female, male; fig. female palpus, male genitalia; California).

Culicoides (*Culicoides*) *cockerellii saltonensis*: Khalaf 1954: 39 (assignment to subgenus *Culicoides*). Fox 1955: 232 (key and diagnoses of subgenera; species key; taxonomy).

Culicoides (*Culicoides*) *saltonensis* Wirth, 1965: 128 (status). Wirth and Blanton 1969b: 231 (key; numerical characters; female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, male genitalia, parameres). Wirth et al. 1985: 10 (numerical characters; fig. female wing).

Culicoides (*Silvicola*) *saltonensis*: Mirzaeva and Isaev 1990: 156 in English translation (as part of Cockerellii group, assignment to new subgenus *Silvicola*).

Diagnosis. (Tables 14, 15) Wing pattern extensive, with distinct distal stripes and pale spots; pale spot over at least distal half of r_2; cua_1 without central dark spot; dark spot in distal half of r_3 barely medially constricted; eyes contiguous for ~1 ommatidium diameter; superior transverse suture distinct to barely discernable; palpal segment 3 ratio 2.2, with wide area of scattered sensilla; scutum without pattern; tibiae without pale bands; fore and hind tarsomeres without apical spines; spermathecae subequal; male tergite 9 apicolateral processes tiny or absent; ventral apodeme of gonocoxite shorter than dorsal apodeme, strongly tapered, pointed, 1–2× as long as basal width; gonocoxite with stout black spinose setae on mesal surface; aedeagus V-shaped, median process triangular, tapering to broad blunt tip, aedeagal ratio ~0.5; parameres separate, apices slender, with fringe of tiny hairs at tip.

Distribution. Known only from the low deserts of Southern California and southern Nevada (Clark County, **new state record**). Six females were collected with UVLT on 2 April 2019 at 36.14032°N 114.72704°W and 384 m elevation in Nevada.

Adult behavior and atypical biology. Along with a normal male *C. saltonensis*, a female collected "near mud from saline thermal springs" in Imperial County, California, by John Einmo, had two fully developed and one half-size, but apparently functional, spermathecae instead of two with a vestigial third (Table 12). However, little else is known about the biology of this species other than that the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Remarks. Contrasting with Wirth and Blanton's (1969b) statement that *C. saltonensis* has contiguous eyes and SCo only on flagellomeres 1 and 9–13, five of the six female specimens I collected in Nevada had SCo irregularly on flagellomeres 5, 7, and 8, in addition to 1, 9–13, and two had narrowly separated eyes—good examples of how variable some important diagnostic characters can be.

Culicoides (*Silvicola*) *sierrensis* Wirth and Blanton

(Fig. 72, 125, 184, 282, 286)

Culicoides (*Culicoides*) *sierrensis* Wirth and Blanton, 1969b: 232 (key; numerical characters; female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, male genitalia, parameres; California). Wirth et al. 1985: 10 (numerical characters; fig. female wing).

Culicoides (*Silvicola*) *sierrensis*: Mirzaeva and Isaev 1990: 156 in English translation (as part of Cockerellii group, assignment to new subgenus *Silvicola*).

Culicoides cockerellii variety a: Wirth 1952a: 172 (female; male genitalia; California).

Diagnosis. (Tables 14, 15) Wing pattern extensive, with distinct distal stripes and pale spots; pale spot over at least distal half of r_2; cua_1 without central dark spot; dark spot over r_1–r_2 merged with spot over M fork; eyes contiguous; superior transverse suture present; palpal segment 3 with scattered sensilla instead of pit; scutum with sub-lateral dark patches; hind tibiae with basal pale band ~2× longer than wide; fore and hind tarsomeres with apical spines; spermathecae subequal to unequal by 1.2×; male tergite 9 with tiny apicolateral processes not projecting beyond median lobe; ventral apodeme of gonocoxite shorter than dorsal apodeme, strongly tapered, pointed, 1–2× as long as basal width; gonocoxite with fine setae on mesal surface; aedeagus V-shaped, median process tapered triangular, aedeagal ratio ~0.4; parameres separate, apices slender, posteriorly directed, with fringe of tiny hairs at tip.

Distribution. northern California, Idaho (Blaine County, **new state record**), Nevada, Utah (San Juan, Summit, Uintah counties, **new state record**). New records, all collected with UVLT: two females on 16 July 2019 at 43.73340°N 114.27168°W and 1974 m elevation along Corral Creek in the Pioneer Mountains of central Idaho; two females on 11 July 2019 at 40.80841°N 110.87270°W and 2752 m elevation along the Bear River in the Uinta Mountains in Utah; one female during June 2017 at 39.4639°N 109.2869°W and 2436 m elevation on the Tavaputs Plateau in Utah; and two females on August 2019 at 38.41373°N 109.22369°W and 2894 m elevation in the La Sal Mountains in Utah.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; however, its hosts are unknown.

Remarks. The two females collected in San Juan County, Utah, had the eyes contiguous at a point, distinct wing pattern, and basal pale band on the hind tibia characteristic of *C. sierrensis*, but had SCo patterns 1, (3), (5), (6), 7, (8), 9–13 more characteristic of *C. neomontanus*. See also subgenus *Silvicola* discussion and *C. cockerellii* and *C. neomontanus* remarks.

Culicoides (*Silvicola*) *tristriatulus* Hoffman

Culicoides cockerellii, var. *tristriatulus* Hoffman, 1925: 294 (key; female; fig. wing, mesonotum; California).

Culicoides tristriatulus Hoffman: Williams 1951a: 431 (egg, larva, pupa; 18 fig.). Wirth 1951: 78 (key; female, male; fig. wing, eye separation, palpus, spermathecae, mesonotum, male genitalia). Wirth 1952a: 173 (key; female, male; fig. dorsal thoracic pattern, eye separation, female palpus, male genitalia).

Culicoides (*Culicoides*) *tristriatulus*: Khalaf 1954: 39 (assignment to subgenus *Culicoides*). Fox 1955: 257 (key and diagnoses of subgenera; species key; taxonomy). Wirth and Blanton 1969b: 238 (key; numerical characters; female, male; fig. female antenna, palpus, wing, spermathecae, eye separation, male genitalia, parameres). Wirth et al. 1985: 12 (numerical characters; fig. female wing). Murphree and Mullen 1991: 314 (key; larva; numerical characters; fig. labium, epipharynx, mandible, hypostoma).

Culicoides (*Silvicola*) *tristriatulus*: Mirzaeva and Isaev 1990: 156 in English translation (as part of Cockerellii group, assignment to new subgenus *Silvicola*).

Culicoides sordidellus (Zetterstedt), misidentified: Jenkins 1948: 154 (Alaska).

Diagnosis. (Tables 14, 15) Wing pattern extensive, with distal stripes and pale spots (as in Fig. 119, 178 *C. cockerellii*); pale spot over at least distal half of r_2; cua_1 without central dark spot; female eyes separated 1–2 ommatidium diameters; superior transverse suture present; palpal segment 3 with scattered sensilla instead of pit; legs without pale bands; fore and hind tarsomeres with apical spines; spermathecae subequal; male tergite 9 apicolateral processes tiny and not projecting beyond median lobe; ventral apodeme of gonocoxite shorter than dorsal apodeme, strongly tapered, pointed, 2× as long as basal width; gonocoxite with fine setae on mesal surface; aedeagus V-shaped, median process triangular, tapering, aedeagal ratio ~0.3; parameres separate, major bend at close to middle of paramere, apex slender, posteriorly directed, with fringe of tiny hairs at tip. (Male genitalia most similar to Fig. 66 *C. cockerellii*.)

Distribution. Coastal Alaska, British Columbia, Washington, Oregon, California.

Larval ecology and life cycle. Williams (1951b) studied *C. tristriatulus* in Alaska and found the larval habitats to be tidally inundated marshes and stream banks characterized by sedge (*Carex* Linnaeus [Cyperaceae]), with an average soil temperature of 13 °C, a pH of 6.2–6.6, and a larval density of up to ~1000/m^2. In the laboratory, ~15 d after blood-feeding, females laid 41–81 eggs, which hatched within 10 h to 3 d at 18 °C. The species in univoltine, and larvae overwinter in the soil and pupate in the early summer. In the laboratory at 16–18 °C, the pupal stage lasts 7.5–9.5 d.

Adult behavior. Sailer et al. (1954) also studied *C. tristriatulus* in Alaska and found adult emergence in late July, with peak activity and formation of male swarms in the evening. *Culicoides tristriatulus* is a severe diurnal biting pest of humans (Jenkins 1948; Williams 1951b; Sailer et al. 1956), with peak activity during low-light conditions in the morning and evening and a flight range of up to 8 km (Williams 1951b).

Remarks. The Fish Creek Flats records reported by Wirth (1951) and larval habitat reports by Sailer et al. (1954) for *C. tristriatulus* are actually for *Culicoides sommermanae* Wirth and Blanton (Wirth and Blanton 1969). I did not examine any *C. tristriatulus*.

Culicoides (*Silvicola*) species D

(Fig. 185, 246, 267)

Diagnosis. (Tables 14, 15) (n = 2, numeric data presented here as Nevada specimen first, Utah specimen second). Large, wing length 1.95–2.17 mm; wing pattern extensive, with distinct distal stripes and pale spots; pale spot over at least distal half of r_2; cua_1 without central dark spot; eyes contiguous for ~1 ommatidium diameter; superior transverse suture present; antennal ratio 0.90–0.88; SCo patterns 1, (7), 9–13 and 1, 5–13; palpal segment 3 with wide shallow, irregular sensory pit and scattered sensilla, ratio 2.75–2.82; proboscis ratio 0.91–0.83; 16–15 mandibular teeth; apical spines single on fore tarsomeres, paired on hind tarsomeres; spermathecae unequal by 1.15–1.20; male unknown.

Distribution. One female was collected with a CO_2-baited trap on 13 May 2003 at 38.5286°N 109.48156°W and 1389 m elevation 8 km southeast of Moab in Grand County, Utah; and one female was collected with UVLT on 2 April 2019 at 36.14032°N 114.72704°W and 384 m elevation in Clark County, Nevada.

Adult behavior. The mandibular and lacinial teeth and collection in a CO_2-baited trap indicate it feeds on vertebrate blood; however, its hosts are unknown.

Remarks. The combination of diagnostic characters places this species in the Cockerellii group of subgenus *Silvicola* and distinguishes it from all other described species of the group. The specimens have the SCo patterns of *C. neomontanus*, *C. freeborni*, or *C. saltonensis*, irregular palpal sensorial pits of *C. neofagineus*, apical fore and hind tarsal spines of *C. cockerellii*, *C. neomontanus*, or *C. sierrensis*, unequal spermathecae of *C. neofagineus* or *C. sierrensis*, and distinct wing patterns similar to that of *C. freeborni* or *C. neofagineus*. However, all of these characters are somewhat variable; and with only two specimens, this species will not be formally described at this time. See subgenus *Silvicola* discussion.

***Culicoides* (*Silvicola*) species E**

(Fig. 186)

Diagnosis. (Tables 14, 15) Wing pattern extensive, with distal stripes and pale spots; pale spot over at least distal half of r_2; cua_1 without central dark spot; eyes contiguous for 1 ommatidium diameter; superior transverse suture present; palpal segment 3 with distinct wide shallow sensory pit, scattered sensilla lacking; scutum without evident pattern; scutellum with 14 setae; tibiae without pale bands; fore and hind tarsomeres with apical spines; three developed spermathecae, unequal; male unknown.

Distribution. A single female was collected with a CO_2-baited trap on 22 April 2003 in northwest Moab at 38.58296°N 109.56663°W and 1214 m elevation in Grand County, Utah.

Adult behavior. The mandibular and lacinial teeth and collection in a CO_2-baited trap indicate it feeds on vertebrate blood; however, its hosts are unknown.

Remarks. Were it not for the apical fore and hind tarsal spines, which are not present on any *C. lahontan* examined (including another specimen with three developed spermathecae), the specimen would be identified as an aberrant *C. lahontan*. This suggests it may be another species not matching others in North America; however, the third spermatheca suggests the possibility that the tarsomere spines are also abnormally developed and it is not a new species. See subgenus *Silvicola* discussion.

Subgenus *Wirthomyia* Vargas

***Culicoides* (*Wirthomyia*) *bottimeri* Wirth**

(Fig. 43, 44, 293)

Culicoides bottimeri Wirth, 1955: 356 (female; male genitalia; female palpus, wing, male genitalia, parameres; Texas). Wirth and Bottimer 1956: 261 (seasonal distribution).

Culicoides (*Wirthomyia*) *bottimeri*: Vargas 1973: 112 (assignment to subgenus *Wirthomyia*). Wirth et al. 1985: 34 (numerical characters; fig. female wing). Phillips et al. 2006: 48 (diagnosis, female, male; fig. female sternite 8, spermathecae, head, male tergite 9, genitalia; seasonal activity; Utah: Garfield, Grand counties; synonym: *C. multidentatus*).

Culicoides multidentatus Atchley and Wirth, 1975: 1421 (female; fig. female eye separation, spermathecae, antenna, palpus; California). Wirth et al. 1985: 38 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing without pattern of pale spots; two sclerotized ovoid unequal spermathecae, with vestigial third spherical or pyriform; posterior portion of female sternite 8 medially concave but not cleft, with pair of pointed submedian posterior projections; ventro-posterior membrane of male sternite 9 spiculate; gonocoxal ventral apodeme simple thin sinuous; aedeagus broadly U-shaped with median process only ~0.2 length of basal arms; parameres separate, apices are long curved heavily sclerotized serrated saberform blades.

Distribution. California, Idaho (Bonneville County, **new state record**), Utah (Garfield, Grand, Washington counties), Arizona, New Mexico, Texas. The Idaho collection of one female with UVLT on 14 July 2019 at 43.52974°N 111.18504°W and 2002 m elevation in the Snake River Range, is the northernmost record for this southwestern species.

Adult behavior and vector potential. Atchley and Wirth (1975) collected female *C. bottimeri* (as *C. multidentatus*) from California quail (*Callipepla californica*). In addition, Weinmann et al. (1979) observed *C. bottimeri* (as *C. multidentatus*) feeding on California quail primarily from 1–2 h after sunset until ~2400–0100 hours and collected and found them naturally infected with fully developed and infective *Splendidofilaria californiensis*, implicating *C. bottimeri* as the primary vector of this quail heartworm. Furthermore, Mullens et al. (2006) reported bobwhite quail (*Colinus virginianus*) as a likely host and provided experimental evidence for *C. bottimeri* also being the primary vector for the California quail malarial parasite, *Haemoproteus lophortyx* O'Roke.

Symbionts. The larval habitat for *C. bottimeri* is unknown; however, a female specimen collected in Grand County, Utah, was parasitized by a larval mite (Table 10), which species may indicate its pupal habitat or oviposition site.

Remarks. The simultaneous Grand County collections of males identified as *C. bottimeri* and females initially identified as *C. multidentatus* provided the initial evidence for demoting *C. multidentatus* to junior synonym of *C. bottimeri* (Phillips et al. 2006).

Subgenus unplaced, Daedalus group

Culicoides daedalus Macfie

(Fig. 116, 195)

Culicoides daedalus Macfie, 1948: 83 (key; male; fig. wing, tergite 9, gonocoxal apodemes, paramere; Chiapas).

Culicoides (*Oecacta*) *daedalus*: Khalaf 1954: 37 (assignment to subgenus *Oecacta*). Forattini 1957: 401 (key; female; male genitalia; fig. female wing, flagellomeres 8–9, palpus, male wing, genitalia, paramere; distribution map). Wirth and Blanton 1959: 319 (key; quantitative characters; female; male genitalia; fig. female wing, mesonotum, palpus, tibial comb, spermathecae, male genitalia, parameres). Wirth et al. 1985: 18 (numerical characters; fig. female wing). Wirth et al. 1988: 28 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 38 (in Neotropical catalog). Huerta et al. 2012: 15 (Veracruz).

Culicoides (*Beltranmyia*) *daedalus*: Vargas 1960: 38 (assignment to subgenus *Beltranmyia*).

Diagnosis. (Tables 14, 15) Cell r_2 dark; distal pale spot in r_3 irregular, equidistant between r_2 and wing tip, quadrate to slightly C-shaped, sometimes thinly connected along posterior margin of cell with a smaller faint spot at apex of cell to form a U; M_1 dark; isolated pale spot at ~0.5 on M_2; distal pale spot in m_1 not extending to wing margin; two distal pale spots in anal cell; sensory pit on palpal segment 3 about as deep as wide, widening internally, pore ~0.3 as wide as segment (as in Fig. 249 *C. hinmani*); ventral apodeme of gonocoxite simple, similar in length and breadth to dorsal apodeme; aedeagus simple, strongly Y-shaped, median process with moderately narrow nearly parallel-sided truncate tip, aedeagal ratio ~0.6; parameres separate, apical portion simple curved filiform.

Distribution. Arizona, Veracruz, Chiapas, Guatemala, Honduras, Costa Rica, Panama, Columbia, Venezuela. The New Mexico distribution reported in Wirth et al. (1985), Borkent and Spinelli (2000), and Huerta et al. (2012) is doubtful. See *Culicoides pampoikilus* Macfie remarks.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; however, its hosts are unknown.

Remarks. No *C. daedalus* were examined.

Culicoides pampoikilus Macfie

(Fig. 103, 157, 196)

Culicoides pampoikilus Macfie, 1948: 79 (key; female; fig. wing; Chiapas). Forattini 1957: 398 (key; female; male genitalia; fig. female wing, flagellomeres 8–9, palpus, male genitalia, paramere; distribution map). Wirth and Blanton 1959:

324 (key; quantitative characters; female; male genitalia; fig. female wing, mesonotum, palpus, tibial comb, spermathecae, male genitalia, parameres). Atchley 1967: 999 (key; numerical characters; female, male; fig. female wing, palpus, tibial comb, spermathecae, male genitalia, parameres). Wirth et al. 1985: 18 (numerical characters; fig. female wing). Wirth et al. 1988: 30 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 38 (in Neotropical catalog). Huerta et al. 2012: 15 (Veracruz).

Culicoides dominicii Ortiz, 1951: 7 (male; fig. palpus, wing, genitalia; Venezuela). Mirsa and Ortiz 1952: 476 (female; fig. wing, mesonotum, antenna, palpus, spermathecae).

Culicoides (*Beltranmyia*) *pampoikilus*: Vargas 1960: 38 (assignment to subgenus *Beltranmyia*).

Diagnosis. (Tables 14, 15) Cell r_2 dark; distal pale spot in r_3 irregular, equidistant between r_2 and wing tip, slightly C-shaped, thinly connected along posterior margin of cell with small spot at apex of cell to form a U; M_1 dark on female; pale spot at ~0.5 on M_2 isolated on female, enlarged and merged with pale bands on M_1 and CuA_1 on male; distal pale spot in m_1 at wing margin; two distal pale spots in anal cell, merged on male to form a broad 8-shape; sensory pit on palpal segment 3 about as deep as wide, widening internally, pore ~0.3 as wide as segment (as in Fig. 249 *C. hinmani*); ventro-posterior membrane of male sternite 9 not spiculate; ventral apodeme of gonocoxite simple; aedeagus Y-shaped, median process broad, tapering abruptly at ~0.6 to slender blunt fingerlike tip; parameres separate, apical portion simple curved filiform.

Distribution. Arizona, New Mexico, Veracruz, Oaxaca, Chiapas, Costa Rica, Panama, Venezuela.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; however, its hosts are unknown.

Remarks. Atchley collected a single female at light at 2160 m 16 June 1965 (erroneously reported in Atchley [1967] as 16 July 1965) in Lincoln County, New Mexico. Wirth et al. (1985) does not report *C. pampoikilus* from New Mexico but instead reports *C. daedalus*, calling into question the identification. However, I examined Atchley's female (still labeled as *C. pampoikilus*) and a *C. pampoikilus* male collected by Frommer in Cochise County, Arizona, 1 August 1967 (misidentified as *C. cochisensis*), and found they match the *C. pampoikilus* redescriptions by Wirth and Blanton (1959) from Panama specimens—and more so for the male than Atchley's (1967) redescription from a Costa Rican specimen.

Subgenus unplaced, Leoni group

Culicoides reevesi Wirth

(Fig. 56–62, 292)

Culicoides reevesi Wirth, 1952a: 193 (key; female; fig. female wing; California). Fox 1955: 253 (key and diagnoses of subgenera; species key; taxonomy). Wirth and Blanton 1956: 51 (female; fig. female wing, palpus, hind tibial comb, spermatheca, mesonotum; assignment to Leoni Group of subgenus *Oecacta*). Atchley 1967: 1002 (key; numerical characters; female; fig. female wing, palpus, tibial comb, spermatheca, antennal segments). Grogan et al. 2004: 433 (diagnosis, female, male; fig. female, antenna, palpus, wing, spermatheca, sternite 8, male antenna, wing, genitalia, parameres; seasonal abundance; biting records; reassignment to Leoni group, subgenus unplaced).

Culicoides (*Haematomyidium*) *reevesi*: Wirth et al. 1985: 28 (numerical characters; fig. female wing; placement in subgenus *Haematomyidium*).

Diagnosis. (Tables 14, 15) Wing pattern distinct; r_2 dark; distal pale spot in r_3, ovoid, not reaching wing margin; eyes with interommatidial pubescence; flagellomeres 9–10 on both sexes much shorter and narrower than any others; one ovoid spermatheca with sclerotized neck longer than wide; male tergite 9 apicolateral processes prominent; ventral apodeme of gonocoxite with two widely divergent processes, footlike; aedeagus broadly V-shaped, arm spread wider than aedeagus length, median process short tapered blunt, with pair of pointed clawlike lateral subapical processes that extend past apex; parameres separate, each with submedian lobe and subapical fringe of spines.

Distribution. California, Utah (Grand County), Arizona, New Mexico.

Larval ecology. Immatures and their habitats are unknown despite intensive efforts to locate them in Lake County, California (Dave Woodward, personal communication). Collections in California and Utah were associated with oak (*Quercus* Linnaeus, Fagaceae) woodlands (Grogan et al. 2004). However, the females I collected in Grant County, New Mexico, were in a Gila River riparian woodland with silty soil, surrounded by upper Chihuahuan Desert, and dominated by Arizona sycamore (*Platanus wrightii* S. Watson, Platanaceae), Fremont poplar (*Populus fremontii* S. Watson, Salicaceae), and willows (*Salix* Linnaeus, Salicaceae), with *Juniperus* Linnaeus (Cupressaceae), mesquite (*Prosopis* Linnaeus, Fabaceae), catclaw (*Senegalia greggii* [A. Gray] Britton and Rose, Fabaceae), and few if any oaks. Because *C. reevesi* is not photophilic (Table 4), the New Mexico collections with UVLT and while biting suggest a high population; and there seemed to be an unusually large number of nearby mouse-size rodent burrows, which may be adult harborage or a rather novel larval habitat.

Experiments have shown that inter-ommatidial pubescence helps protect insect eyes by reducing impact and deposition of airborne particles onto ommatidia (Amador et al. 2015). Similarly, *C. reevesi*'s eye hairs may help prevent soil particles from lodging between or damaging ommatidia, suggesting a relatively dry or deep soil larval habitat such as that of *L. carteri*—the only other southwestern species of biting midge with abundant inter-ommatidial pubescence for which the larval habitat is known. Furthermore, the relatively small adult body size of *C. reevesi* may facilitate egress from a coarsely granular soil habitat.

Adult behavior. Wirth (1952a), Atchley (1967), and Grogan et al. (2004) reported *C. reevesi* can be a significant human-biting pest. Though none were found biting in Utah, I collected a female biting the back of my hand at ~1630 on 15 October 2019 at 32.84753°N 108.59258°W and 1332 m elevation in the New Mexico habitat described above. The sensation was that of a minute burning-hot needle. The bite itself lasted about a minute until I was able to collect the midge and left a painless erythematous 1 cm spot that later resembled a bruise. The only other reported host is black-tailed deer (*Odocoileus hemionus*) (Hopken et al. 2017).

Symbionts. Two nematode-parasitized female intersex specimens were collected (Fig. 292, Table 11). Both lacked spermathecae but otherwise seemed to be normal females. The specific worms may indicate *C. reevesi*'s pupal habitat or oviposition site.

Remarks. Partial gene sequences were determined for a *C. reevesi* specimen by Hopkin et al. (2017) for comparison with *C. occidentalis* and *C. sonorensis* and their blood-meal analyses.

Subgenus unplaced, Limai group

Culicoides luglani Jones and Wirth

(Fig. 88, 141, 206)

Culicoides luglani Jones and Wirth, 1958: 89 (female, male; fig. female wing, mesonotum, spermathecae, palpus, male genitalia, parameres; Texas). Atchley 1967: 990 (key; numerical characters; female; male genitalia; variation; fig. female wing, palpus, spermathecae, male genitalia, parameres). Wirth et al. 1985: 18 (numerical characters; fig. female wing). Wirth et al. 1988: 30 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 38 (in Neotropical catalog).

Culicoides new species near *haematopotus*: Wirth and Bottimer 1956: 265 (biology).

Culicoides tenuilobus Wirth and Blanton, 1959: 354 (key; quantitative characters; female; male genitalia; fig. female wing, mesonotum, palpus, tibial comb, spermathecae, male genitalia, parameres; Panama). Wirth 1963: 68 (synonym). Atchley 1967: 990 (not synonym; see remarks). Wirth et al. 1988: 36 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 40 (in Neotropical catalog).

Diagnosis. (Tables 14, 15) Wing pattern distinct; r_2 dark; pale spot in r_3 nearly filling distal third of cell; M_1 dark; spot pattern on M_2 distinctive: dark spot on basal 0.4, symmetric dart-shaped pale spot on 0.4–0.8, dark 0.8 to end; all femora with prominent subapical pale band; ventral apodeme of gonocoxite simple; median process of aedeagus with pair of pointed elongate parallel lateral subapical processes (these often difficult to see); parameres separate, each with submedian elongate curved pointed thornlike process and subapical fringe of spines.

Distribution. California, Utah (Garfield, Grand counties), Arizona, New Mexico, Texas, Baja California, Sonora. The report for Florida in Wirth et al. 1985 was an error corrected in Wirth et al. 1988—possibly from the similarity of the name of *Culicoides loughnani* Edwards, which is an unrelated Florida, Texas, and West Indies species. If *C. tenuilobus* is a synonym, *C. luglani* would also have an El Salvador, Guatemala, Honduras, and Panama distribution (see remarks).

Adult behavior. The mandibular and lacinial teeth on the female and collection in CO_2-baited traps indicate it feeds on vertebrate blood; and though its hosts are unknown, the SCo presence on only the proximal flagellomeres suggests it is mammalophilic. Furthermore, the relatively high proportion of males collected with CO_2-baited traps (Table 4) suggests they seek hosts to find females for mating.

Remarks. Wirth (1963) demoted *C. tenuilobus* to junior synonym of *C. luglani*; however, Atchley (1967) both contradicts and cites Wirth (1963) on this synonymy, and none of the catalogs (Borkent and Wirth 1997; Borkent and Spinelli 2000; Borkent and Grogan 2009; Borkent and Dominiak 2020) list these species as synonyms or reference Wirth (1963). Indeed, these catalogs place *C. luglani* in the Daedalus group and *C. tenuilobus* in the Limai group. Comparisons of the descriptions and wing photographs of these two species indicate they should be placed in the same species group and suggest their status needs clarification. The similarity of wing pattern, SCo pattern, lateral processes on the median process of the aedeagus, and submedian process and fringe of spines on the parameres support Atchley's (1967) tentative placement of *C. luglani* with *C. tenuilobus* in the Limai group, which is followed here (**new status**).

Subgenus unplaced, Mohave group

Culicoides hoguei Wirth and Moraes

Culicoides hoguei Wirth and Moraes, 1979: 293 (female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, male genitalia, parameres, leg; California). Wirth et al. 1985: 38 (numerical characters; fig. female wing). Wirth et al. 1988: 56 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 40 (in Neotropical catalog).

Culicoides mohave Wirth, misidentified: Wirth 1952a: 187 (in part).

Diagnosis. (Tables 14, 15) Brown; wing similar to *C. mohave* (Fig. 131, 207), pattern faint on distal half; r_2 dark; distal pale spot in r_3 distinct, centered at ~0.6 the distance from apex of costa to apex of M_1, not extending into distal 0.2 of cell; one pale spot in distal half of anal cell; two ovoid subequal spermathecae, with necks ~2× longer than wide; sclerotized ring on spermathecal duct; male tergite 9 apicolateral processes long: their length ~0.5 the distance between them; ventral apodeme of gonocoxite with two widely divergent processes, footlike; aedeagal arms simple V-shaped, median process tapering triangular to rounded tip; paramere with bulbous submedian lobe and subapical fringe of spines.

Distribution. Coastal Southern California, Baja California, Baja California Sur.

Adult behavior. Ryckman and Ryckman (1963) reported *C. hoguei* biting humans, sometimes after dark and suggested *C. hoguei*'s larval habitat is likely the rotting organic material on the beaches surrounding the Baja California islands where the midges were collected.

Remarks. Wirth and Moraes (1979) found some Baja California specimens to have smaller proboscis ratios and more mandibular teeth than those of the California types. I include these variations within parenthesis in Table 14; however, no *C. hoguei* were examined.

Culicoides mohave Wirth

(Fig. 79, 131, 132, 207–210)

Culicoides mohave Wirth, 1952a: 187 (key; female; male genitalia; fig. female palpus, wing, male genitalia; California).

Culicoides (*Oecacta*) *mohave*: Khalaf 1954: 37 (assignment to subgenus *Oecacta*). Fox 1955: 247 (key and diagnoses of subgenera; species key; taxonomy). Wirth and Moraes 1979: 288 (female, male; fig. female antenna, wing, palpus, eye separation, spermathecae, male genitalia, parameres, leg). Wirth et al. 1985: 38 (numerical characters; fig. female wing). Wirth et al. 1988: 58 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 40 (in Neotropical catalog).

Diagnosis. (Tables 14, 15) Brown; wing pattern faint on distal half; r_2 dark; distal pale spot in r_3 distinct, sometimes irregular, centered at ~0.6 the distance from apex of costa to apex of M_1, not extending into distal 0.2 of cell; one pale spot in distal half of anal cell; two ovoid subequal spermathecae, with necks ~2× longer than wide; sclerotized ring on spermathecal duct; male tergite 9 apicolateral processes small: their length ~0.1 the distance between them; ventral apodeme of gonocoxite with two widely divergent processes, footlike; aedeagal arms simple V-shaped, median process tapering triangular to a truncated tip having two black apicolateral spines; paramere with bulbous submedian lobe and subapical fringe of spines.

Distribution. California, Arizona, Baja California, Baja California Sur.

Larval ecology. A habitat adjacent to a small stream near the Salton Sea in Southern California characterized by scattered iodinebush (*Allenrolfea occidentalis*) and desert holly (*Atriplex hymenelytra*) and sandy alkali or saline soil with 10–13% moisture produced *C. mohave* and larval *L. knowltoni* and *Dasyhelea festiva* (Foulk 1966).

Adult behavior. Mullens and Dada (1992a) reported collecting unfed females from bighorn sheep (*Ovis canadensis nelsoni*) and Japanese quail (*Coturnix japonica*). Breidenbaugh and Mullens (1999b) reported collecting females with CO_2-baited traps, and also observed laboratory-reared larvae would not feed on the nematodes provided.

Mullens and Dada (1992b) reported *C. mohave* to be most abundant in the summer at lower elevations in Southern California. Brenner et al. (1984b) observed *C. mohave* had evening and morning crepuscular host-seeking peaks. In addition, they used a capture-mark-release-recapture method to determine a mean 1.2 km flight distance over the first 12 h and a cumulative 1.9 km flight distance over 30 h after release.

Vector potential. Rosenstock et al. (2003) detected epizootic hemorrhagic disease virus (EHDV) in *C. mohave* in Arizona, suggesting it may be a vector of that virus.

Remarks. *Culicoides mohave* has been confused with *C. inyoensis* where their populations overlap in the Mojave Desert. See *C.* (*Diphaomyia*) *inyoensis* remarks.

Subgenus unplaced, Palmerae group

The species of this group rely heavily on male characters for differentiation. Even when slide-mounted, some females can be only tentatively identified.

Diagnoses for the Palmerae group are presented by Atchley (1967) and Wirth and Rowley (1971). In addition, apical spines on fore and hind tarsomeres would also be a diagnostic character for the group (Table 14) if they were also on the Palmerae group species not examined in the present study.

The sclerotized ring on the spermathecal duct in the members of the Palmerae group has been inconsistently reported: Wirth (1952a) reported it present in *C. utahensis*; Bullock (1952) reported it present in *C. palmerae*; Atchley (1967) reported it present in *C. palmerae* and *C. utahensis*; Jorgensen (1969) reported it present in 3 of 27 *C. palmerae*; however, Wirth and Rowley (1971: 161) state, "In *hawsi*, the sclerotized ring…persists, a generalized feature found in no other species of this group". Hence, this character is apparently variable in the Palmerae group and may not be reliable in some other groups as well (see subgenus *Silvaticulicoides* discussion).

Some males of the Palmerae group (one of one *C. calexicanus* and four of ten *C. palmerae* in the present study) have minute divergent spines on the apices of the parameres (Fig. 90). This characteristic is less pronounced but similar to that of subgenus *Silvaticulicoides* and has been reported by Jorgensen (1969) for *C. palmerae* as "apex with a few microscopic hairs". Together with the apical spines on hind tarsomeres of the Palmerae group and *C.* (*Silvaticulicoides*) *usingeri*, the prominent apicolateral processes, the simple gonocoxal apodemes, the strongly convex lateral contours of the gonostyli, the simple aedeagus of both groups except for *C. palmerae* and *Culicoides davisi* Wirth and Rowley, the otherwise simple parameres, the usual absence of a sclerotized ring on the spermathecal duct of both groups except for *Culicoides hawsi* Wirth and Rowley, and the similarity of wing patterns of subgenus *Silvaticulicoides* species variously with the Palmerae group species *C. hawsi*, *Culicoides leechi* Wirth, *Culicoides oregonensis* Wirth and Rowley, and *Culicoides wirthi* Foote and Pratt suggest a close relationship of the Palmerae group to the subgenus *Silvaticulicoides*.

Culicoides calexicanus Wirth and Rowley

(Fig. 90, 144, 221, 223, 275, 285)

Culicoides calexicanus Wirth and Rowley, 1971: 156 (numerical characters; key; female, male; fig. female antenna, palpus, eye separation, spermathecae, male genitalia, parameres; California). Wirth et al. 1985: 26 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing pattern distinct and extensive; r_2 dark; prominent distal pale spots in r_3, m_1, m_2; scutellum yellowish, lighter than the brown scutum; fore and often hind tarsomeres with apical spines; spermathecae unequal by ~1.1, necks shorter than wide; ventral apodeme of gonocoxite simple; gonostylus about evenly curved, not abruptly bent, entire lateral contour convex; aedeagus V-shaped, median process tapering to tip ~0.2 as wide as basal arm spread; parameres separate, with abrupt ventro-lateral bend at ~0.8 and sharp tip often with divergent apical spines.

Distribution. California, Nevada, Utah (Grand, Washington counties, **new state record**). Evidently, *C. calexicanus* is an uncommon but wide-ranging species, having been reported by Wirth and Rowley (1971) from near sea level in Imperial County, California, and from ~2300 m elevation in the Humboldt Mountains of Elko County, Nevada.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; and the CO_2-baited trap collection of the male suggests that males may seek hosts to find females for mating. Its week 14 collection datum in Table 5 is from Imperial County, California, a much warmer climate, representing much earlier activity than in Utah or Nevada.

Remarks. Some of the Palmerae group females that were not identified to species may be *C. calexicanus*. See *C. palmerae* and species C remarks.

Culicoides hawsi Wirth and Rowley

(Fig. 91, 145, 224, 276)

Culicoides hawsi Wirth and Rowley, 1971: 159 (numerical characters; key; female, male; fig. female antenna, palpus, eye separation, spermathecae, male genitalia, parameres; Washington, Utah: Cache, Uintah counties). Wirth et al. 1985: 26 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing pattern reduced; r_2 dark; distal pale spots faint or absent from r_3, m_1, m_2; scutellum about same brown as scutum; faint pale band apical on fore femora; fore and hind tarsomeres with apical spines; spermathecae unequal by ≥1.3; elongate, sometimes faint; sclerotized ring on spermathecal duct; ventral apodeme of gonocoxite simple; gonostylus about evenly curved, not abruptly bent, entire lateral contour convex; aedeagus V-shaped, median process tapering to tip ~0.4 as wide as basal arm spread; parameres separate, apices abruptly bent ventro-laterally with simple sharp tip.

Distribution. Washington, Oregon, California, Utah (Cache, Grand, Uintah counties).

Adult behavior. The mandibular and lacinial teeth on the female and collection in CO_2-baited traps indicate it feeds on vertebrate blood; however, its hosts are unknown.

Culicoides leechi Wirth

Culicoides leechi Wirth, 1977: 53 (female, male; fig. female antenna, wing, palpus, eye separation, spermathecae, male antenna, palpus, parameres, genitalia; California). Wirth et al. 1985: 26 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing pattern reduced; r_2 dark; pale spots only at tip of costa, on r-m crossvein; spermathecae subequal with short necks; sclerotized ring absent from spermathecal duct; male antenna, palpus, and wing feminized, flagellomeres 9–10 lengthened similar to 11–13, lacking dense whorls of sensilla chaeticae on 1–10, palpal ratio ~2, with large sensory pit (as in Fig. 251 *C. utahensis*); tergite 9 apicolateral processes stout, ~2× longer than wide, broadly flaring laterally at ~30°; ventral apodeme of gonocoxite simple; gonostylus about evenly curved, not abruptly bent, entire lateral contour convex; aedeagus V-shaped, median process tapering to tip ~0.3 as wide as basal arm spread; parameres separate, apices abruptly bent ventro-laterally with simple stout sharp tip.

Distribution. California (Napa, San Luis Obispo counties).

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood, and it is likely the feminization of the males facilitates finding females at a host—despite that reported *C. leechi* mating-pair collections have only been at light (Wirth 1977). See *C. utahensis* adult behavior.

Remarks. No *C. leechi* were examined.

Culicoides novamexicanus Atchley

Culicoides (*Oecacta*) *novamexicanus* Atchley, 1967: 1012 (key; numerical characters; female; male genitalia; fig. female wing, palpus, tibial comb, spermathecae, male genitalia, parameres; New Mexico). Wirth and Rowley 1971: 161 (numerical characters; key; female, male; fig. female antenna, palpus, eye separation, spermathecae, male genitalia, parameres). Wirth et al. 1985: 26 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing pattern distinct and extensive; r_2 dark; prominent distal pale spots in r_3, m_1, m_2 (as in Fig. 144, 223 *C. calexicanus*); spermathecae subequal, with sclerotized necks shorter than wide (as in Fig. 275 *C. calexicanus*); ventral apodeme of gonocoxite simple; basal portion of gonostylus abruptly bent ~90°, L-shaped (as in Fig. 92 *C. palmerae*); aedeagus V-shaped, median process tapering to tip ~0.2 as wide as basal arm spread (as in Fig. 90 *C. calexicanus*); parameres separate, apices abruptly bent ventro-laterally with simple sharp tip.

Distribution. The only report of this species is of five specimens collected by W. R. Atchley on 14 June 1965 (week 24) from Chavez County on the High Plains of southeastern New Mexico.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; however, its hosts are unknown.

Remarks. No *C. novamexicanus* were examined. See *C. palmerae* remarks.

Culicoides oregonensis Wirth and Rowley

Culicoides oregonensis Wirth and Rowley, 1971: 162 (numerical characters; key; female, male; fig. female antenna, palpus, eye separation, spermathecae, male genitalia, parameres; Oregon). Wirth et al. 1985: 26 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing pattern reduced; r_2 dark; pale spots only at tip of costa, on r-m crossvein; scutellum about same brown as scutum; spermathecae ovoid, subequal, without sclerotized necks (as in Fig. 277 *C. palmerae*); ventral apodeme of gonocoxite simple; gonostylus not abruptly bent to an L-shape, entire lateral contour convex; aedeagus broadly Y-shaped, median process narrow, nearly parallel-sided, <0.1 as wide as basal arm spread, ~5× longer than median width; parameres separate, with hooklike bend at ~0.8 and sharp tip.

Distribution. Oregon, Northern California.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; however, its hosts are unknown.

Remarks. No *C. oregonensis* were examined.

Culicoides palmerae James

(Fig. 92, 146, 225, 277, 283)

Culicoides palmerae James, 1943: 151 (female, male; fig. male genitalia, seasonal abundance; Colorado). Knowlton and Fronk 1950: 114 (Utah: Cache County). Wirth 1952a: 191 (diagnosis; fig. female lateral view, palpus). Bullock 1952: 15 (female; male genitalia; fig. male genitalia; Utah: Salt Lake County). Rees and Bullock 1954 (Utah: Salt Lake County). Foote and Pratt 1954: 30 (female wing, male genitalia; fig. female wing, mesonotum, palpus, male genitalia).

Culicoides (*Oecacta*) *palmerae*: Khalaf 1954: 38 (assignment to subgenus *Oecacta*). Fox 1955: 250 (key and diagnoses of subgenera; species key; taxonomy). Atchley 1967: 1008 (key; numerical characters; female; male genitalia; fig. female wing, palpus, male genitalia, parameres). Jorgensen 1969: 22 (key; quantitative characters; female; male genitalia; seasonal distribution; fig. female antenna, spermathecae, palpus, wing, male genitalia, parameres). Wirth and Rowley 1971: 164 (numerical characters; key; female, male; fig. female antenna, palpus, eye separation, spermathecae, male genitalia, parameres; Utah: Cache, Uintah counties). Wirth et al. 1985: 26 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing pattern extensive; r_2 dark; large distal pale spots in r_3, m_1, m_2, sometimes indistinct; scutellum about same brown as scutum; fore and hind tarsomeres with apical spines; spermathecae subequal, without sclerotized necks; ventral apodeme of gonocoxite simple; basal portion of gonostylus abruptly bent ~90°, L-shaped; aedeagus not V-shaped, median process broad, with wide shoulders abruptly constricting to a narrow tip; parameres separate, apices strongly curved back anteriorly with sharp 90° elbowlike bend or protuberance at ~0.8 and sharp tip sometimes with tiny divergent apical spines.

Distribution. British Columbia, Alberta (Lysyk 2006), Montana, North Dakota (Anderson and Holloway 1993), south through Washington, Oregon, Wyoming, Colorado, Nebraska, to California, Nevada, Utah (Cache, Grand, Salt Lake, Summit, Uintah counties), New Mexico.

Adult behavior. Bullock (1952) collected *C. palmerae* adults May–August in Salt Lake County; and Barnard and Jones (1980b) reported that adults were active May–September and mostly during daylight hours in Weld County, Colorado. However, little else is known about the biology of this species other than that the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Remarks. The Palmerae group females that were not slide-mounted, and thus not identified to species, are listed as "unidentified", though they have the typical *C. palmerae* wing pattern. In addition, all but 2 of the 94 Palmerae group males collected were identified as *C. palmerae*, thus it is likely most of these unidentified females are also *C. palmerae*.

Culicoides utahensis Fox

(Fig. 93, 147, 221, 251)

Culicoides utahensis Fox, 1946: 246 (male; fig. male genitalia; Utah: Cache County). Knowlton and Fronk 1950: 114 (Utah: Sanpete County, from jackrabbit ear). Wirth 1952a: 189 (key; female; male genitalia; fig. female wing, palpus, male genitalia). Bullock 1952: 14 (female; male genitalia; Utah: Salt Lake County). Rees and Bullock 1954 (Utah: Salt Lake County).

Culicoides (*Oecacta*) *utahensis*: Khalaf 1954: 38 (assignment to subgenus *Oecacta*). Fox 1955: 258 (key and diagnoses of subgenera; species key; taxonomy). Atchley 1967: 1010 (key; numerical characters; female; male genitalia; fig. female palpus, male genitalia, parameres). Wirth and Rowley 1971: 166 (numerical characters; key; female, male; fig. female antenna, eye separation, palpus, spermathecae, male antenna, palpus, genitalia, parameres; Utah: Beaver, Iron, Kane, Millard, Salt Lake counties). Wirth et al. 1985: 26 (numerical characters; fig. female wing). Breidenbaugh and Mullens 1999a: 862 (egg; fig.).

Diagnosis. (Tables 14, 15) Wing pattern extensive; r_2 dark; distal pale spots large, often diffuse in r_3, m_1, m_2; scutellum about same brown as scutum; fore and hind tarsomeres with apical spines (not evident on the one male collected); spermathecae subequal, with sclerotized necks shorter than wide; male antenna and palpus feminized, flagellomeres 9–10 lengthened similar to 11–13, lacking dense whorls of sensilla chaeticae on 1–10, palpal ratio ~2, with large sensory pit; ventral apodeme of gonocoxite simple; gonostylus about evenly curved, not abruptly bent, entire lateral contour convex; aedeagus V-shaped, median process tapering to broad tip ~0.4 as wide as basal arm spread; parameres separate, apices abruptly bent ventro-laterally with simple sharp tip.

Distribution. Washington, Idaho, Montana, south through Oregon, to California, Nevada, Utah (Beaver, Cache, Grand, Iron, Kane, Millard, Salt Lake, Sanpete counties), New Mexico.

Adult behavior. Known hosts are jackrabbit, black-tailed jackrabbit (Knowlton and Fronk 1950; Wirth 1952a; Wirth and Rowley 1971), ground squirrel (*Spermophilus* Cuvier sp., Sciuridae) (Wirth 1952a), rabbit, sheep, deer (Wirth and Rowley 1971), and black-tailed deer (*Odocoileus hemionus*) (Hopken et al. 2017).

Culicoides utahensis has been found mating within the ears of jackrabbits, sheep, and deer in California (Wirth 1977) and from jackrabbit ears in Idaho, Nevada, and Utah (Wirth and Rowley 1971). The feminization of the antennae and palpi of the males was originally thought to be an abnormality; however, it is now known to be normal for this species and correlates with the ability to find and mate with females on their hosts (Wirth and Rowley 1971).

Breidenbaugh and Mullens (1999a) found *C. utahensis* eggs failed to hatch in the laboratory even though the embryos seemed to develop normally and survive, suggesting they overwinter in diapause and need cold conditioning or interaction with photoperiod to continue development. Bullock (1952) collected adults during June in Salt Lake County, which has a much colder winter climate. Bradley Mullens (personal communication) observed that wild-caught adults were unusually willing to feed through chick skin membranes on bovine blood in the laboratory, and much mating occurred in the feeding apparatus or aspirator tubes. This likely reflects a considerable degree of stenogamy, as are the reports of mating within the ears of its hosts; thus, if the apparent egg diapause could be investigated and managed and the larvae reared on laboratory substrates, this species might be easily colonized.

Remarks. *Culicoides leechi*, a closely related species of the Palmerae group, also has males normally with feminized antennae and palpi; however, collections of *C. leechi* mating-pairs have been only at light (Wirth 1977).

Culicoides Palmerae group species C

(Fig. 222, 253, 254, 278)

Diagnosis. (Tables 14, 15) Wing pattern extensive; r_2 dark; distal pale spots in r_3, m_1, m_2 small; eight mandibular teeth; scutellum yellowish brown, lighter than the brown scutum; fore tarsomeres with apical spines, hind tarsomeres without; spermathecae unequal by ~1.1, necks shorter than wide.

Distribution. One female was collected with a CO_2-baited trap on 25 June 1999 in west Moab at 38.57239°N 109.56754°W and 1217 m elevation in Grand County, Utah.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; however, its hosts are unknown.

Remarks. The specimen is similar to *C. calexicanus* except for being smaller, having only eight mandibular teeth, and having smaller distal wing spots. Thus, it may be a *C. calexicanus* variant and is not being recognized as a new species at this time.

Subgenus unplaced, Piliferus group

The large and diverse Piliferus group is readily distinguished from all other *Culicoides* known from the southwestern United States by the males having the combination of broadly bifurcate footlike ventral gonocoxal apodemes, simple Y-shaped aedeagi, and parameres without submedian lobes but with a subapical fringe of spines. However, the females as a group are not so sharply defined because they only usually have pale spots straddling the midportions of M_1 and M_2, unequal spermathecae, and basic odd-numbered SCo patterns.

It is perhaps the most difficult group of *Culicoides* in the western United States to reliably identify to species. Their male genitalia offer only a few somewhat variable characters; and wing and SCo patterns and quantitative characters vary enough among the females to overlap more than what Table 14 suggests with its listed average values. Furthermore, descriptive literature for four of the five species that are known to occur west of the Continental Divide has been limited to only one species at a time in widely separate geographic locations: California for *C. cavaticus* and *C. lophortygis*, Maryland and Alabama for *C. chewaclae*, and New Mexico and Arizona for *C. doeringae*. The other, *C. unicolor*, was described from California in 1905 and is now considered a composite of four species.

Culicoides unicolor sensu stricto has never been differentially redescribed since its original description, despite the more recent descriptions of its currently recognized sisters, *C. cavaticus* (1956) and the eastern species, *Culicoides denticulatus* Wirth and Hubert (1962) and *Culicoides franclemonti* Cochrane (1974) (see *C. unicolor* remarks). Furthermore, two western species (*C. doeringae* and *C. lophortygis*) are similar enough to call into question their distinction (see *C. doeringae* remarks); and at least six species known from the western United States are undescribed: species 10, 25, 58, 73, 76 (Wayne Kramer, personal communication), and species B herein.

Culicoides cavaticus Wirth and Jones

(Fig. 81–83, 136, 137, 228, 263)

Culicoides cavaticus Wirth and Jones, 1956: 166 (key; female, male; fig. female wing, mesonotum, palpus, spermathecae, male genitalia; California). Wirth et al. 1985: 22 (numerical characters; fig. female wing). Murphree and Mullen 1991: 338 (key; larva; numerical characters; fig. head, epipharynx, hypostoma, mandible, caudal segment).

Culicoides unicolor (Coquillett), misidentified: Wirth 1952a: 185, 253 (in part as "well-marked treehole phase"; key; female; male genitalia; pupa; larva; fig. female wing, palpus, male genitalia, pupal respiratory horn, caudal segment, larval head, caudal segment; larval habitat). Fox 1955: 258 (in part; keys).

Diagnosis. (Tables 14, 15) Wing pattern distinct; r_2 dark; isolated pale spots straddling midportions of M_1 and M_2; distal pale spots in r_3, m_1, m_2; distinct to barely visible pale band or patch along posteromedian margin of anal cell; flagellomeres 9–10 normal, each larger than 8; SCo pattern 1–13; palpus with broad shallow sensory pit almost as wide as segment; labrum without apical median projection; scutellum with 28–30 setae on female; fore and hind tarsomeres without apical spines; spermathecae unequal by ~1.1, sclerotized necks absent; sclerotized ring on spermathecal duct; male tergite 9 posterior margin concave, with distinct apicolateral processes extending beyond medial portion; sternite 9 caudomedian excavation moderate, about evenly curved; ventral apodeme of gonocoxite broad with two short widely divergent processes, stoutly footlike; aedeagus Y-shaped, basal arms with basal ends sharply bent laterally, arms without submedian fingerlike lobes, arms posteromedially connected only by unsclerotized or barely sclerotized membrane, median process simple, aedeagal ratio ~0.7; parameres separate with basal heads clublike, with fringe of spines on apical third, without submedian lobe.

Distribution. Oregon, California, Utah (Grand County, **new state record**), Arizona. A male was collected using a CDC incandescent light trap on 5 July 2001 at 38.54491°N 109.51000°W and 1331 m elevation, a riparian habitat with abundant cottonwoods (*Populus fremontii*) and oaks (*Quercus* sp.).

Larval ecology. *Culicoides cavaticus* have been collected and reared from treeholes in black walnut, walnut, sycamore, and cottonwood (Wirth and Jones 1956) and collected from emergence traps over treeholes in Pacific madrone (*Arbutus menziesii* Pursh, Ericaceae), and oaks (Fagaceae: *Quercus kelloggii*, *Q. lobata* Nee, and *Q. wislizenii*) with strong emergence peaks in April and July in Northern California (Woodward et al. 1988). Clark and Fukuda (1967) collected *C. cavaticus* larvae and *Aedes sierrensis* (Ludlow) (Culicidae) larvae from an oak treehole and observed some of the *C. cavaticus* killing and feeding on the mosquitos, indicating a predatory role on macroinvertebrates in its treehole habitat.

Adult behavior. Weinmann et al. (1979) collected blood-engorged *C. cavaticus* from California quail (*Callipepla californica*)-baited traps; however, they found no *C. cavaticus* infected with quail heartworm (*Splendidofilaria californiensis*) or other evidence it can transmit the parasite.

Culicoides chewaclae Glick and Mullen

(Fig. 234)

Culicoides chewaclae Glick and Mullen, 1983: 378 (female; fig. antenna, palpus, eye separation, mandible, legs, tibial comb, spermathecae, wing; Alabama). Wirth et al. 1985: 22 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Dark Brown; wing pattern indistinct; r_2 dark; isolated pale spots straddling midportions of M_1 and M_2; distal pale spots faint in r_3, m_1, m_2; flagellomeres 9–10 normal, each larger than 8; SCo pattern 1, 3, 5, 7, (8), (9), (10), 11–13; combined length of flagellomeres 7+8 greater than 9; proboscis short, ratio 0.61; labrum without apical median projection; scutellum with 12 setae on female; fore and hind tarsomeres without apical spines; spermathecae unequal by ~1.3, sclerotized necks absent; sclerotized ring on spermathecal duct; male unknown, but genitalia should be similar to those of other Piliferus group species.

Distribution. California, Oregon, Utah (San Juan County, **new state record**), Maryland, South Carolina (Swanson 2012), Alabama, Florida (Quaglia et al. 2020). Apparently an uncommon but widely distributed species across temperate North America. A single female was collected with UVLT on 15 August 2019 in the La Sal Mountains in San Juan County, Utah, at 38.41373°N 109.22369°W at 2894 m elevation.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; and though its hosts are unknown, *C. chewaclae* is a member of the Piliferus group, generally considered ornithophilic (Wirth and Hubert 1962). Quaglia et al. (2020) report collecting *C. chewaclae* with UVLTs only during weeks 15–19 in Florida; whereas, collections in other states at higher latitudes and elevations have been made during weeks 17, 18, 25, 29, and 33 (Table 5).

Remarks. *Culicoides chewaclae* is most similar to *Culicoides* Piliferus group species A and B but has smaller antennal and proboscis ratios (Table 14). See also Piliferus group species A, B, and unplaced species F remarks.

Culicoides doeringae Atchley

(Fig. 84, 85, 138, 139, 229, 230, 264)

Culicoides (*Oecacta*) *doeringae* Atchley, 1967: 1014 (key; numerical characters; female; male genitalia; fig. female wing, palpus, tibial comb, eye separation, spermathecae, antennal segments, male genitalia, parameres; New Mexico). Atchley and Wirth 1975: 1423 (comparison with *C. lophortygis*). Wirth et al. 1985: 22 (numerical characters; fig. female wing).

Culicoides piliferus No. 2: Jorgensen 1969: 24 (key; quantitative characters; female; male genitalia; fig. wing, spermathecae, palpus, antenna, male parameres, genitalia; eastern Washington).

Diagnosis. (Tables 14–16) Brown. Wing pattern distinct; r_2 dark; isolated pale spots straddling midportions of M_1 and M_2; distal pale spot in r_3 filling most of distal half, but may be indistinct; distal pale spots in m_1, m_2; no pale band or patch on posteromedian margin of anal cell; flagellomeres 9–10 normal, each larger than 8; SCo pattern 1, 3, 5, 7, 9, (10), 11–13, rarely absent from 9; eyes narrowly separated 0.1–1.0 ommatidium diameter; labrum without apical median projection; scutellum with 8–10 setae on female; fore and hind tarsomeres without apical spines; spermathecae unequal by ~1.4, sclerotized necks <0.5 as long as wide or absent; sclerotized ring on spermathecal duct; male tergite 9 posterior margin concave, with distinct apicolateral processes extending beyond medial portion; sternite 9 caudomedian excavation deep and about three-sided; ventral apodeme of gonocoxite with two widely divergent processes, footlike; aedeagus Y-shaped, basal arms with basal ends slightly curved laterally, arms without submedian fingerlike lobes, arms posteromedially fused by moderate sclerotization, median process simple, aedeagal ratio 0.45–0.6; parameres separate with basal heads broad anvillike, with fringe of spines on apical third, without submedian lobe.

Distribution. Washington (Jorgensen 1969), Oregon, Idaho (Bonneville County **new state record**), Montana, south through Utah (Garfield, Grand, Summit counties), Colorado, to California, Arizona, New Mexico.

Larval ecology. Jorgensen (1969) collected "*C. piliferus* No. 2" (which I think is synonymous with *C. doeringae*, see remarks) with an emergence trap over a freshwater seepage spring in a cattle pasture; however, he conflates the seasonal distribution and abundance data for "*C. piliferus* No. 2" with that of his distinctly different "*C. piliferus* No. 1", making it uncertain as to which species these data apply.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; and though its hosts are unknown, it is a member of the Piliferus group, generally considered ornithophilic (Wirth and Hubert 1962). Furthermore, like Piliferus group species A, *C. doeringae* was moderately common in light traps but nearly absent from CO_2-baited traps (Table 4).

Symbionts. Male and female *C. doeringae* were parasitized by larval mites (Table 10), which species may indicate *C. doeringae*'s pupal habitat or oviposition site.

Remarks. Because Jorgensen's (1969: 24) descriptions of the female and of the male genitalia of his "*C. piliferus* No. 2" (including his Fig. 8B1) are so similar to *C. doeringae* in all respects, I think they are conspecific.

Culicoides doeringae specimens collected in Grand County have considerable variation of wing pattern intensity (Fig. 138, 139, 229, 230); however, the range of variations were clustered together in the same peaks of seasonal distribution (Table 5), indicating they represent variation within a single species. Furthermore several *C. doeringae* specimens collected in Grand County had smaller antennal ratios (down to 1.29), and males often had a greater aedeagal arch height (aedeagal ratio 0.59 in Fig. 84) than described by Atchley (1967) (~0.45 in text, 0.5 in his Fig. 129) for New Mexico and Arizona specimens; and one of the two females collected in the same trap on 11 July 2019 in Summit County, despite being otherwise completely similar, had equal-sized spermathecae (1.00 versus 1.30 differential of the other specimen), indicating spermathecae may be somewhat variable.

Culicoides doeringae and *C. lophortygis* may be conspecific. From the descriptions by Atchley (1967) and Atchley and Wirth (1975), the following characters overlap (*C. doeringae* first, *C. lophortygis* second): female wing length (1.13–1.34, 1.09–1.23), antennal ratio (1.48–1.73, 1.38–1.62), ratio of the lengths of flagellomeres

7+8 to flagellomere 9 (1.00–1.27, 0.97–1.15), palpal ratio (2.30–2.87, 2.82–2.88), and proboscis ratio (1.03–1.20, 0.89.–1.03). This leaves the intensity of the wing pattern ("more prominent", "rather indistinct" [Atchley and Wirth 1975]) and eye separation ("width of median hair socket" [Atchley 1967], "greater than width of an ommatidial facet" [Atchley and Wirth 1975]) as the only stated distinctions. However, their differing described SCo patterns (1, 3, 5, 7, 9, (10), 11–13 and 1, 3, (5), (7), 11-13) are not cited as a distinction in Atchley and Wirth (1975: 1423).

Table 16 shows the six different SCo patterns of 27 *C. doeringae* specimens and compares their wing pattern intensities and eye separations. These data fail to show a correlation between these characteristics—calling into question the species distinction between *C. doeringae* and *C. lophortygis*. That *C. lophortygis* is known to bite California valley quail (*Lophortyx californicus*) (Atchley and Wirth 1975) has implications for *C. doeringae* being a possible vector of avian parasites.

Culicoides lophortygis Atchley and Wirth

Culicoides lophortygis Atchley and Wirth, 1975: 1422 (female; fig. antenna, wing, palpus, eye separation, spermathecae, leg; comparison with *C. doeringae*; California). Wirth et al. 1985: 24 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing pattern distinct; r_2 dark; isolated pale spots straddling midportions of M_1 and M_2; distal pale spot in r_3 filling most of distal half of cell; distal pale spots in m_1, m_2; flagellomeres 9–10 normal, each larger than 8; SCo pattern 1, 3, (5), (7), 11–13; eyes separated >1 ommatidium diameter; spermathecae unequal by ~1.3, with short, sclerotized necks <0.5 as long as wide; sclerotized ring on spermathecal duct. Male unknown, but genitalia likely similar to that of *C. doeringae*.

Distribution. California (Mendocino, Monterey counties).

Adult behavior and vector potential. *Culicoides lophortygis* has been collected from California quail (*Lophortyx californicus*) and while biting a human at dusk in California (Atchley and Wirth 1975). In addition, Weinmann et al. (1979) collected blood-engorged *C. lophortygis* from California quail-baited traps, found development of quail heartworm (*Splendidofilaria californiensis*) to the first-juvenile non-infective stage in several specimens, but found no other evidence *C. lophortygis* can transmit the parasite.

Remarks. Based on data collected in this study, *C. lophortygis* and *C. doeringae* may be conspecific. However, no *C. lophortygis* were examined. See *C. doeringae* remarks.

Culicoides unicolor (Coquillett)

(Fig. 227, 279)

Ceratopogon unicolor Coquillett, 1905: 65 (key; female, male; California).

Culicoides unicolor (Coquillett): Hoffman 1925: 279 (combination; key; female; fig. wing, mesonotum). Root and Hoffman 1937: 152 (key). Wirth 1951: 85 (in part; keys; fig. male genitalia from California type). Wirth 1952a: 185 (in part as "poorly marked coastal phase"; female, male genitalia [all figures, larval and pupal descriptions, and larval habitats are for *C. cavaticus* as the "well-marked tree hole phase"]).

Culicoides (*Oecacta*) *unicolor*: Khalaf 1954: 36 (assignment to subgenus *Oecacta*). Fox 1955: 258 (in part; keys). Jones 1956: 26 (misidentified). Wirth and Jones 1956: 167 (misidentified in key). Wirth and Hubert 1962: 193 (the eastern *C. unicolor* of Wirth and Jones [1956] is actually *C. denticulatus*). Cochrane 1974: 128 (*C. franclemonti* is part of *C. denticulatus*, thus part of eastern *C. unicolor*). Wirth et al. 1985: 24 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Wing pattern greatly reduced and faint; r_2 dark; pale spots at tip of costa, on r-m crossvein extending to CuA fork, absent from midportions of M_1 and M_2, distal portions of r_3, m_1, m_2, cua_1, anal cell; eyes contiguous; flagellomeres 9–10 normal, each larger than 8; SCo pattern 1, 11–13; palpus with deep sensory pit ~0.4 diameter of segment; 11 mandibular teeth; apex of labrum with small distinct median lightly sclerotized grayish tonguelike projection; scutellum with nine setae on female; hind tibial comb with five spines; fore tarsomeres without apical spines; legs without pale banding; spermathecae subequal, with tapering sclerotized necks shorter than wide; sclerotized ring on spermathecal duct; male tergite 9 posterior margin concave, with distinct apicolateral processes extending beyond medial portion; ventral apodeme of gonocoxite broad with two short widely divergent processes, stoutly footlike; aedeagus Y-shaped, heavily sclerotized basal arms without submedian fingerlike lobes, median process simple, pointed, aedeagal ratio ~0.6; parameres separate, with fringe of spines on apical third, without submedian lobe.

Distribution. Alaska (USNM), British Columbia, Washington, Oregon, Idaho (Bonneville County, **new state record**), California, Colorado. One female was collected with UVLT on 14 July 2019 at 43.52974°N 111.18504°W and 2002 m elevation in the Snake River Range, Idaho.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; and though its hosts are unknown, it is a member of the Piliferus group, generally considered ornithophilic (Wirth and Hubert 1962).

Remarks. My Idaho specimen matches the Wirth et al. (1985) data and the above diagnosis, which is a composite from the specimen and relevant items from Wirth 1951 (male genitalia figure from a type) and 1952a (items related to "poorly marked coastal phase"). Furthermore, despite being unable to see an entire wing (Fig. 227), the projection at the tip of the labrum (Fig. 279) is distinctive.

Culicoides unicolor originally encompassed the currently recognized species *C. unicolor* sensu stricto, *C. cavaticus*, *C. denticulatus*, and *C. franclemonti*. I have been unable to find descriptions of *C. unicolor* sensu stricto newer than that of the portions from Wirth (1951, 1952a).

In addition, the keys of Jones (1956), Wirth and Jones (1956), Grodhaus (no date), and Kramer and Wirth (no date) that say *C. unicolor* has 4–6 mandibular teeth seem to be conflating *C. unicolor* sensu stricto with *C. denticulatus* and the more recently described *C. franclemonti*, which are closely related eastern Piliferus group species with 3–6 teeth. Indeed, Wirth and Hubert (1962: 194) state in their discussion of *C. denticulatus*, "the remarkable reduction of the mandibular teeth, from whence comes the name *denticulatus*, is so far unique in these groups", implying that *C. unicolor* sensu stricto has the greater number of teeth more normal for the Piliferus group.

Culicoides Piliferus group species A (likely USNM species 25)

(Fig. 86, 87, 140, 235, 265)

Culicoides piliferus No. 1: Jorgensen 1969: 24 (key; quantitative characters; female, male genitalia; fig. female wing, spermathecae, palpus, antenna, male parameres, genitalia; geographic distribution; Washington).

Diagnosis. (Tables 14, 15) Pale to medium yellowish brown when fresh in alcohol. Wing pattern faint; r_2 dark; pale spots at ~0.5 on M_2, faint at ~0.3 on M_1 (pale spots on M_1 and M_2 of male wings sometimes so faint as to be inapparent); pale spots absent from r_3, absent from or faint in m_1, m_2; flagellomeres 9–10 normal, each larger than 8; SCo pattern 1, 3, 5, 7, 9, (10), 11–13; combined length of flagellomeres 7+8 less than 9; palpal sensory pit small, round, ~0.2 as deep as opening is wide, not enlarged internally; labrum without apical median projection; fore and hind tarsomeres without apical spines; scutellum with 8–10 setae on female, 7–9 on male; two ovoid spermathecae unequal by ~1.4, with sclerotized necks <0.5 as long as wide; sclerotized ring on spermathecal duct; male tergite 9 posterior margin concave, with distinct apicolateral processes extending beyond medial portion; ventral apodeme of gonocoxite with two widely divergent processes, footlike; aedeagus Y-shaped, heavily sclerotized basal arms without submedian fingerlike lobes, arms posteromedially fused by moderate sclerotization, median process simple, aedeagal ratio ~0.6; parameres separate, each with fringe of four or five spines on apical third, without submedian lobe.

Distribution. Utah (Garfield, Grand counties). Wayne Kramer (personal communication) reports this species (as "n sp 25") is present in Washington, Montana, Oregon, California, Utah, Wyoming, Colorado, Arizona.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; and though its hosts are unknown, it is a member of the Piliferus group, generally considered ornithophilic (Wirth and Hubert 1962). Like *C. doeringae*, this species was moderately common in light traps but nearly absent from CO_2-baited traps (Table 4).

Remarks. The SCo pattern, pale spots on midportions of M_1 and M_2, unequal spermathecae, footlike gonocoxal roots, simple aedeagus, and distal fringe of spines on the parameres place this species in the Piliferus group. The combination of reduced wing pattern, pale yellowish-brown color, SCo pattern, and antennal and proboscis ratios readily distinguish it from the other Piliferus group species collected. Because Jorgensen's (1969: 24) descriptions of the female and of the male genitalia of his "*C. piliferus* No. 1" (including his Fig. 8B2) are so similar to Piliferus group species A in all aspects, I think they are conspecific. However, without examining material from the USNM (as species 25 [Wayne Kramer, personal communication]) and other collections to consider wider geographic variation, I think to formally describe this species now would be premature.

Four females—one in each of Blaine and Bonneville counties, Idaho, and Sanpete and San Juan counties, Utah—were similar except for being dark brown and with relatively faint wing pattern are listed in data Tables 7 and 9 as "near species A". All were collected in higher altitude montane habitats. See the remarks for unplaced species F and for *C. chewaclae* and species B, the other Piliferus group species in this study with a reduced wing pattern and basic odd-numbered SCo pattern.

Culicoides Piliferus group species B

(Fig. 233, 266)

Diagnosis. (Tables 14, 15, data from eight specimens) Dark brown. Wing pattern faint; r_2 dark; faint pale spots at ~0.3 on M_1, at ~0.5 on M_2, distal in r_3, m_1, m_2 (difficult to see without digital camera); flagellomeres 9–10 normal, each larger than 8; SCo pattern 1, 3, 5, 7–13, occasionally also on 2, 4, or 6 of one antenna; combined length of flagellomeres 7+8 less than 9; palpal sensory pit broad, round, shallow, not enlarged internally; labrum without apical median projection; fore and hind tarsomeres without apical spines; scutellum with 13–14 setae; two ovoid spermathecae unequal by ~1.5, with sclerotized necks <0.2 as long as wide; sclerotized ring on spermathecal duct. Male unknown.

Distribution. Idaho (Blaine County), Utah (San Juan, Sanpete counties), Colorado (Montrose County). Thirty-six females were collected in Colorado at Antone Spring on the Uncompahgre Plateau at 2934 m elevation on 30 July 2020, and three females were collected in the La Sal Mountains of Utah at 2894 m elevation on 16 August 2019. Both sites were montane conifer forest habitats.

Adult behavior. The mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood; and though its hosts are unknown, it is a member of the Piliferus group, generally considered ornithophilic (Wirth and Hubert 1962). The Colorado collection environment was a marshy spring and creek within Engelmann spruce (*Picea engelmannii* Parry ex Engelmann, Pinaceae) and aspen (*Populus tremuloides* Michaux, Salicaceae) forest. The Utah environment was a similar conifer-aspen forest with a nearby marshy spring.

Remarks. The SCo pattern, pale spots on midportions of M_1 and M_2, unequal spermathecae, and basic odd-numbered SCo pattern place this species in the Piliferus group. However, it does not key to or match any species in the unpublished key and data table of Kramer and Wirth (no date), which includes 27 Nearctic Piliferus group species. The combination of extensive but faint wing pattern, dark brown color, SCo pattern, close eye separation, and antennal and proboscis ratios readily distinguish it from the other species collected.

In addition, three females collected at 2658 m elevation on 19 July 2019 in the Wasatch Plateau in Sanpete County, Utah, and one female collected at 1974 m elevation on 16 July 2019 along Corral Creek in the Pioneer Mountains in Blaine County, Idaho, in similar conifer-aspen forests were similar in all aspects but differed in having an unusual SCo pattern of 1, (2), 3, (4), 5, (6), 7–13, where the missing SCo were from only one antenna. Furthermore, two other specimens from the same Blaine County collection had 1–13 SCo patterns but were otherwise identical. Because of this anomaly, though included in the collection data Tables 5, 7, and 9, their morphological data are not included in Tables 14 and 15.

Subgenus unplaced, Saundersi group

Culicoides atchleyi Wirth and Blanton

(Fig. 4)

Culicoides atchleyi Wirth and Blanton, 1969a: 559 (female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, male genitalia, parameres; Alaska). Wirth et al. 1985: 36 (numerical characters; fig. female wing; placement in Chaetophthalmus group). Borkent and Dominiak 2020: 22 (rename Chaetophthalmus group as Saundersi group).

Diagnosis. (Tables 14, 15) Brown; wing without pattern of pale spots, veins thicker and darker than normal, nearly obliterating cell r_2; eyes with prominent interommatidial pubescence; mandibular teeth vestigial; two sclerotized ovoid spermathecae, vestigial third fingerlike; ventro-posterior membrane of male sternite 9 bare; aedeagus Y-shaped, median process simple, moderately slender, blunt, aedeagal ratio ~0.45; parameres separate, apex simple, straight, not extending beyond tip of aedeagus.

Distribution. Alaska, New Brunswick, Nova Scotia, Idaho (Bonneville County, **new state record**), New Mexico. A widely distributed, but apparently rare species. The week 27 collection record (x) in the seasonal distribution (Table 5) is by a light trap in a pinyon-juniper-Douglas fir forest area, 6 July 1953 at ~2280 m elevation in Taos County, New Mexico. This record, and my collection of one female with UVLT on 14 July 2019 at 43.52974°N 111.18504°W and 2002 m elevation in the Snake River Range of Idaho, indicate it may be present in similar montane habitats in Utah and other western states during July. The other Xs in Table 5 are from Alaska records.

Adult behavior. The absence of mandibular teeth on the female indicates it does not blood-feed.

Larval ecology. *Culicoides atchleyi*'s larval habitat is unknown. However, experiments have shown that inter-ommatidial pubescence helps protect insect eyes by reducing impact and deposition of airborne particles onto ommatidia (Amador et al. 2015). Similarly, *C. atchleyi*'s eye hairs may help prevent soil particles from lodging between or damaging ommatidia, suggesting a relatively dry or deep soil larval habitat such as that of *L. carteri*—the only other southwestern species of biting midge with abundant inter-ommatidial pubescence for which the larval habitat is known.

Remarks. The female collected in Idaho more closely matches the Wirth and Blanton (1969a) description of *C. atchleyi* rather than that of *C. saundersi* in having a 2.3 palpal ratio, 0.67 proboscis ratio, 0.9 ommatidium diameter eye separation, 4 tibial comb spines, the same position of SCo on flagellomeres 12 and 13 as in their figure 2a, and smaller (0.52 mm) rounder spermathecae with narrower necks. However, its 1.04 antennal ratio is like that of *C. saundersi*; and having seven teeth on one mandible, but none on the other or on the laciniae is ambiguous—other examples of the variability of diagnostic characters.

Culicoides saundersi Wirth and Blanton

Culicoides saundersi Wirth and Blanton, 1969a: 557 (female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, male genitalia, parameres; Washington). Wirth et al. 1985: 36 (numerical characters; fig. female wing; placement in Chaetophthalmus group). Borkent and Dominiak 2020: 22 (rename Chaetophthalmus group as Saundersi group).

Diagnosis. (Tables 14, 15) Brown; wing without pattern of pale spots, veins thicker and darker than normal (as in Fig. 4 *C. atchleyi*); eyes with prominent interommatidial pubescence; mandible with 14–18 teeth; two sclerotized ovoid spermathecae, vestigial third fingerlike; ventro-posterior membrane of male sternite 9 bare; aedeagus Y-shaped, median process simple, moderately slender, blunt, aedeagal ratio ~0.45; parameres fused at base by a narrow bridge, apex simple, slightly curved, extending beyond tip of aedeagus.

Distribution. Alaska, British Columbia, Washington, Montana, Oregon, California.

Adult behavior. This species has been collected while biting humans and from a magpie nest (Wirth and Blanton 1969a), suggesting it may also feed on birds.

Larval ecology. *Culicoides saundersi*'s larval habitat is unknown. However, the eye pubescence suggests a relatively dry soil habitat. See the discussion in the larval ecology section of *C. atchleyi*.

Remarks. No specimens of *C. saundersi* were examined.

Subgenus unplaced, Stonei group

Jones and Wirth (1978) state that males of the four recognized western species of the Stonei group (*C. stonei*, *C. mortivallis*, *C. owyheensis*, and *C. werneri*) are morphologically indistinguishable; however, *C. werneri* seems to be distinguishable—at least in part—by body and leg color and by the shape of the median process of the aedeagus. The females can be distinguished morphologically only by the combination of SCo pattern, antennal, palpal, and proboscis ratios, and mean wing length (Jones and Wirth 1978). The ranges of these measurements and ratios have considerable overlap between species, with mean values differing by 13% for the antennal ratio, 19% for the palpal ratio, 9% for the proboscis ratio, and 13% for the wing length.

Furthermore, I found 20 different combinations of SCo patterns among 85 Stonei group females (Table 17). SCo patterns ranged from the 1–12 of *C. stonei*, to the 1, 5–12 of both *C. mortivallis* and *C. owyheensis*, to the 1, 8–12 pattern of *C. werneri*, with some specimens possessing different SCo patterns on their antennae. Though the seasonal distributions for the *mortivallis-owyheensis* and unidentified Stonei group collections have peaks in late May (weeks 21, 22) and September (weeks 36, 37) (Table 5), no significant seasonal difference of SCo patterns was evident.

Such variability in SCo patterns and ratios casts doubt over the status of several of these species. In particular, the only way to distinguish *C. owyheensis* from *C. mortivallis* in Jones and Wirth's (1978: 57) key is to compare wing lengths and to compare the ratios of the length of flagellomeres 7+8, the length of palpal segment 3, and the length of the proboscis to the length of flagellomere 9.

I did this with 10 randomly selected Stonei group specimens from Grand County having SCo patterns of 1, 5–12 on both antennae; however, though wing length was tabulated, the final determinations did not use wing length because of its variability depending on food availability and other environmental conditions during larval development (Akey et al. 1978; Mullens 1987; Mullens and Rodriguez 1988; Smith and Mullens 2003). Using the medians between the published average values of the three ratio variables for the two species (Jones and Wirth 1978), whereby values less than the median indicate *C. mortivallis* and values greater indicate *C. owyheensis*, seven of the specimens met all three criteria for *C. mortivallis*, one was intermediate within ~1% for all criteria, and one met two criteria and another met all three criteria for *C. owyheensis* (Table 18).

Further study is needed to determine the status of species in this group and consider the possibility *C. owyheensis* and *C. mortivallis* are synonymous. Incidentally, Grand County, Utah, is ~660 km from the Inyo County, California, *C. mortivallis* type locality and ~710 km from the Owyhee County, Idaho, *C. owyheensis* type locality, and all are arid to semi-arid habitats.

Specimens not so evaluated and with SCo pattern 1, 5–12 are listed in the tables as "*mortivallis-owyheensis*"; and all males and those females of the Stonei group that have not been identified to species or as "*mortivallis-owyheensis*" are listed as "unidentified" in the data tables.

Biology. Records and descriptions of *C. stonei* prior to Atchley (1967) do not mention SCo pattern, or antennal, palpal, or proboscis ratios and, thus, are conflated with *C. mortivallis* and *C. owyheensis* records from California, Idaho, Utah, and western Colorado.

Jones's (1961a: 741) description of the *C. stonei* pupa variant from Grand County, Utah, is likely of *C. mortivallis*. He collected these immatures from the nonvegetated sunlit margin of an alkaline stream near Cisco (47 km north-northeast of Moab), along with immatures of *C. jamesi*, *C. occidentalis* or *C. sonorensis* (as *C. variipennis australis*), *C. haematopotus* (may be *C. defoliarti*), *C. grandensis* (as "n. sp."), and *C. crepuscularis* (Jones 1961b). I was able to rear *C. mortivallis* along with *C. crepuscularis*, *C. occidentalis*, and *C. sonorensis* from mud collected from nonvegetated sunlit alkaline pools in the same stream bed on 10 September 2020 in Grand County at 38.96339°N 109.33585°W and 1315 m elevation.

Jones (1961c, as *C. stonei*) also collected blood-engorged Stonei group females from a domestic sheep near Grand Junction, Colorado. Based on my Grand County collection data, these specimens are also likely to be *C. mortivallis*.

One Stonei group female collected in Grand County, identified as intermediate between *C. mortivallis* and *C. owyheensis* (Table 18), has dark starburst infections inside abdominal segments 6–8 (Fig. 290, Table 11).

Culicoides mortivallis Wirth and Blanton

(Fig. 41, 280, 289, 290, 294)

> *Culicoides mortivallis* Wirth and Blanton, 1971: 465 (key; female, male; fig. female antenna, palpus, eye separation, hind tibial comb, wing, spermathecae, legs, male genitalia, parameres; California). Jones and Wirth 1978: 57 (key). Wirth et al. 1985: 36 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15, 17, 18) Yellowish brown; wing without pattern of pale spots (as in Fig. 3 *C. stonei*); legs straw-colored; two sclerotized ovoid spermathecae and fingerlike vestigial third (as in Fig. 45 *C. stonei*);

posterior portion of female sternite 8 cleft, with blunt submedian posterior projections (as in Fig. 45 *C. stonei*); ventro-posterior membrane of male sternite 9 spiculate; aedeagus Y-shaped, median process stout, short, blunt, half as long as basal arms; parameres separate, simple, apex curved hooklike. To distinguish from *C. owyheensis*, ratios to length of flagellomere 9: <1.50 for flagellomeres 7+8, <3.95 for proboscis, <1.90 for palpal segment 3.

Distribution. California (Inyo, Monterey, San Bernardino counties), Utah (Grand County, **new state record**), Arizona (Greenlee County, **new state record**). The Arizona specimen was collected with UVLT on 10 October 2019 at 32.96215°N 109.30566°W and 1056 m elevation near the Gila River.

Larval ecology. I reared one female and two presumptive male *C. mortivallis* along with *C. crepuscularis*, *C. occidentalis*, and *C. sonorensis* from mud collected on 10 September 2020 from nonvegetated sunlit alkaline pools in a stream bed in Grand County at 38.96339°N 109.33585°W and 1315 m elevation. One of the males emerged on 2 October, indicating a development period of at least 22 d at ~25°C.

Adult behavior. *Culicoides mortivallis* has been collected biting a human at dusk in California (Wirth and Blanton 1971). In addition, Jones's sheep host record (Jones 1961c), description of the Grand County, Utah, pupa variant (1961a: 741), Grand County larval habitat record (Jones 1961b), and Mesa County, Colorado, record for *C. stonei* are likely for *C. mortivallis*. Furthermore, if *C. mortivallis* and *C. owyheensis* are synonymous, then reports of *C. owyheensis* females collected from the ear of a sheep prostrate with bluetongue in Idaho (Jones and Wirth 1978) are for *C. mortivallis*. See also Stonei group discussion.

Symbionts. A female with SCo pattern 1, 6–12 collected in Grand County was parasitized by a larval mite (Fig. 294, Table 10); and specimens with SCo patterns 1, 5–12 and 1, (3), 4–12 collected in Grand County were parasitized by what seem to be ciliate protozoans (possibly *Tetrahymena* sp. [Ciliophora: Oligohymenophorea] [Mullens and Schmidtmann 1982]) and possibly mermithid nematodes (Fig. 289, Table 11).

Atypical biology. A female with SCo patterns 1, 3–12 and 1, 5–12 and collected in Grand County had three developed spermathecae instead of two with a vestigial third (Table 12).

Remarks. Using the measurement ratios from Wirth and Jones (1978: 57), 12 of 16 Grand County specimens and an Arizona specimen recognized as either *C. owyheensis* or *C. mortivallis* based on SCo pattern were identified as *C. mortivallis* (Table 18). See also Stonei group discussion.

Culicoides owyheensis Jones and Wirth

Culicoides owyheensis Jones and Wirth, 1978: 57 (misspelled as *owyheenis*; key; female; Idaho). Wirth et al. 1985: 36 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15, 17, 18) Brown with some yellow; wing without pattern of pale spots (as in Fig. 3 *C. stonei*); two sclerotized ovoid spermathecae and fingerlike vestigial third (as in Fig. 45 *C. stonei*); posterior portion of female sternite 8 cleft, with blunt submedian posterior projections (as in Fig. 45 *C. stonei*); ventro-posterior membrane of male sternite 9 spiculate; aedeagus Y-shaped, median process stout, short, blunt, half as long as basal arms; parameres separate, simple, apex curved hooklike (as in Fig. 41 *C. mortivallis*). To distinguish from *C. mortivallis*, ratios to length of flagellomere 9: >1.50 for flagellomeres 7+8, >3.95 for proboscis, >1.90 for palpal segment 3.

Distribution. Idaho (Owyhee County), Utah (Grand County).

Adult behavior. R. H. Jones and H. W. Potter Jr. collected females from the ear of a sheep prostrate with bluetongue in Idaho (Jones and Wirth 1978). However, I think that *C. owyheensis* may be a junior synonym of *C. mortivallis*, and the record may be for that species.

Remarks. Using the measurement ratios from Wirth and Jones (1978: 57), 2 of 17 specimens recognized as either *C. owyheensis* or *C. mortivallis* based on SCo pattern were identified as *C. owyheensis* (Table 18). See also Stonei group discussion.

Culicoides stonei James

(Fig. 3, 7, 45)

Culicoides stonei James, 1943: 149 (female, male; fig. male genitalia, seasonal abundance; Colorado). Foote and Pratt 1954: 33 (key; diagnosis; fig. female wing, mesonotum, male genitalia).

Culicoides (*Oecacta*) *stonei*: Khalaf 1954: 38 (assignment to subgenus *Oecacta*). Fox 1955: 256 (key and diagnoses of subgenera; species key; taxonomy). Jones and Wirth 1958: 91 (synonym: *Culicoides weesei* Khalaf). Jones 1961a: 741 (in part; key; pupa; fig. respiratory trumpet, operculum; Texas; Utah variant, misidentified). Atchley 1967: 995 (key; numerical characters; female; male genitalia; fig. female wing, palpus, spermathecae, male genitalia, parameres). Wirth and Blanton 1971: 461 (key; Stonei group diagnosis; female, male; fig. female eye separation, antenna, palpus, spermathecae, wing, legs, male genitalia, parameres). Jones and Wirth 1978: 57 (key). Wirth et al. 1985: 36 (numerical characters; fig. female wing).

Culicoides weesei Khalaf, 1952b: 65 (male; fig. genitalia; Oklahoma). Khalaf 1952a: 351 (female; fig. female antenna, palpus, seasonal incidence). Fox 1955: 260 (key and diagnoses of subgenera; species key; taxonomy). Wirth and Bottimer 1956: 264 (Texas ecology). Khalaf 1957: 205 (diagnosis; seasonal incidence).

Diagnosis. (Tables 14, 15, 17) Brown; wing without pattern of pale spots; legs yellowish; two sclerotized ovoid spermathecae and fingerlike vestigial third; posterior portion of female sternite 8 cleft, with blunt submedian posterior projections; ventro-posterior membrane of male sternite 9 spiculate; aedeagus Y-shaped, median process stout, short, blunt, half as long as basal arms; parameres separate, simple, apex curved hooklike (as in Fig. 41 *C. mortivallis*).

Distribution. Alberta (Lysyk and Galloway 2014), South Dakota, south through Utah (Grand, Tooele counties), Colorado, Nebraska, Kansas (Swanson et al. 2018), Oklahoma, to New Mexico, Texas.

Larval ecology and adult behavior. In Texas, immatures have been collected from salt-water and alkaline-water soil and grassy saline pools (Jones 1961b), and adult females have been collected from white-tailed and unidentified deer (Wirth and Blanton 1971).

Remarks. Jones's description of the Grand County, Utah, pupa variant (1961a: 741), Grand County larval habitat record (Jones 1961b), and Mesa County, Colorado, sheep host record (Jones 1961c) for *C. stonei* are likely for *C. mortivallis*. See also Stonei group discussion.

Culicoides werneri Wirth and Blanton

(Fig. 42)

Culicoides werneri Wirth and Blanton, 1971: 46 (key; female, male; fig. female antenna, palpus, eye separation, hind tibial comb, wing, spermathecae, legs, male genitalia, parameres; Arizona). Jones and Wirth 1978: 57 (key). Wirth et al. 1985: 36 (numerical characters; fig. female wing). Borkent and Spinelli 2000: 42 (in Neotropical catalog).

Diagnosis. (Tables 14, 15, 17) Dark brown; wing without pattern of pale spots (as in Fig. 3 *C. stonei*); legs brown; two unequal sclerotized ovoid spermathecae and fingerlike vestigial third (as in Fig. 45 *C. stonei*); posterior portion of female sternite 8 cleft, with blunt submedian posterior projections (as in Fig. 45 *C. stonei*); ventro-posterior membrane of male sternite 9 spiculate; aedeagus Y-shaped, median process stout, short, truncate, half as long as basal arms; parameres separate, simple, apex curved hooklike.

Distribution. California, Arizona, Texas, Sonora.

Adult behavior. A female has been collected from a jackrabbit (Wirth and Blanton 1971).

Remarks. The specimens I collected in Greenlee County, Arizona, have 1, 8–12 and 1, (5), 8–12 SCo patterns. See also Stonei group discussion.

Unplaced species

Culicoides monoensis Wirth

Culicoides monoensis Wirth, 1952a: 193 (female, male; fig. female wing, palpus, male genitalia; California).

Culicoides (*Oecacta*) *monoensis*: Khalaf 1954: 38 (assignment to subgenus *Oecacta*). Fox 1955: 247 (key and diagnoses of subgenera; species key; taxonomy). Wirth et al. 1985: 38 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Black; wing without pattern of pale spots; legs brown; female palpal segment 3 not swollen, palpal ratio 3.0, sensory pit small, ~0.4 diameter of segment; two sclerotized subspherical spermathecae with vestigial third; sclerotized ring on spermathecal duct; ventro-posterior membrane of male sternite 9 bare; ventral apodeme of gonocoxite simple, longer than dorsal apodeme, thin, >5× longer than wide; aedeagus V-shaped, apex bifurcate as deeply as wide; parameres separate, posterior portion with conspicuous submedian lateral bump and truncate tip.

Distribution. California (Mono, Plumas, San Benito counties).

Adult behavior. *Culicoides monoensis* has been collected by sweeping stream and lake margins (Wirth 1952a). The greatly reduced SCo pattern (1, 12, 13), unswollen palpal segment 3 with small sensory pit, and short proboscis of the female are more typical of male *Culicoides*, suggesting this species either has an atypical host or does not blood feed. I have not examined any specimens, and there is no mention of mandibular teeth in the limited literature.

Culicoides nanellus Wirth and Blanton

Culicoides nanellus Wirth and Blanton, 1969a: 565 (female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, hind leg, male genitalia, parameres; California). Wirth et al. 1985: 38 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Pale brown; wing pattern reduced, distal pale spots absent from or barely discernable in r_3, m_1, m_2 (similar to Fig. 145, 224 *C. hawsi* or 148, 237 *C. sublettei*); tibiae with basal pale band; female palpus fusiform, with a deep sensory pit ~0.4 as wide as segment (pit similar to Fig. 249 *C. hinmani*); two unequal ovoid spermathecae (ratio 1.06) with fingerlike vestigial third; sclerotized ring on spermathecal duct; ventro-posterior membrane of male sternite 9 bare; gonocoxal apodemes simple, ventral apodeme thin, ~5× longer than wide; midportion of lateral contour of gonostylus slightly concave; aedeagus almost V-shaped, basal arms relatively slender and only slightly curved, each ~10× longer than wide, median process simple, tapering to narrow blunt tip, aedeagal ratio ~0.55; parameres separate, apical half simple thin sinuous.

Distribution. California (Mendocino County).

Larval ecology. *Culicoides nanellus* was collected by F.K. Murphy in a treehole trap 1 July 1965 (Wirth and Blanton 1969a).

Adult behavior. The mandibular teeth on the female indicate it feeds on vertebrate blood; however, its hosts are unknown.

Remarks. Male *C. nanellus* would most likely be confused with those *C. kibunensis* that occasionally have five spines in the hind tibial comb; however, *C. kibunensis* has a more robust aedeagus with thicker basal arms and a broader distal process (Fig. 98). Females are readily distinguished by SCo pattern, antennal ratio, and the distinctive palpal segment 3. No *C. nanellus* specimens were examined.

Culicoides posoensis Wirth and Blanton

(Fig. 97, 151, 236, 272)

Culicoides posoensis Wirth and Blanton, 1969a: 562 (female, male; fig. female antenna, palpus, wing, eye separation, spermathecae, male genitalia, parameres; California). Wirth et al. 1985: 38 (numerical characters; fig. female wing).

Diagnosis. (Tables 14, 15) Brown; wing pattern reduced, with pale spots only on wing base, at tip of costa, on r-m crossvein; tibiae with faint basal pale band; two subequal ovoid spermathecae with fingerlike vestigial third; sclerotized ring on spermathecal duct; ventro-posterior membrane of male sternite 9 bare; gonocoxal apodemes simple, ventral apodeme thin, >5× longer than wide; aedeagus Y-shaped, basal arms curved, median process simple with truncate tip ~0.2 as wide as basal arch, aedeagal ratio ~0.5; parameres separate, apical half simple thin sinuous.

Distribution. California (Kern County).

Adult behavior. Using truck traps in Kern County, California, Nelson and Bellamy (1971) found *C. posoensis* was more abundant in the summer than in the fall, with flight activity through the night with peaks near dusk and dawn. However, little else is known about the biology of this species other than that the mandibular and lacinial teeth on the female indicate it feeds on vertebrate blood.

Culicoides unplaced species F

(Fig. 226, 284)

Diagnosis. (Tables 14, 15) Dark brown; r_2 dark; wing pattern relatively faint; pale spots over bases of m_2 and anal cells, on r-m crossvein extending from costa into m_2 above CuA fork, at tip of costa in r_3, on midportions of M_1 and M_2, distally in anal cell, faint in cua_1, faint distally in m_1 and m_2, barely discernable distally in r_3; flagellomeres 9–10 normal, each larger than 8; SCo pattern 1, 3, 5, 7, (8), 9, 11–13; labrum without apical median projection; scutellum with 12 setae; fore and hind tarsomeres with apical spines; two ovoid spermathecae unequal by ~1.4, sclerotized necks <0.5 as long as wide; sclerotized ring on spermathecal duct. Male unknown.

Distribution. Idaho (Bonneville County). One female was collected with UVLT on 14 July 2019 at 43.52974°N 111.18504°W and 2002 m elevation in the Snake River Range, Idaho.

Adult behavior. The mandibular and lacinial teeth indicate it feeds on vertebrate blood; however, its hosts are unknown.

Remarks. This species shares characteristics with *C. chewaclae* and species A of the Piliferus group and *C. hawsi* of the Palmerae group. It is similar to species of the Piliferus group in having pale spots straddling veins M_1 and M_2, no bilobed distal pale spot in r_3, a broadly open palpal sensory pit, and very unequal spermathecae. It seems close to *C. chewaclae* in having an extremely short proboscis and a similar SCo pattern but differs by being larger and having a larger antennal ratio. It shares with *C. hawsi* apical spines on the fore and hind tarsomeres, a similar SCo pattern, a broadly open palpal sensory pit, and very unequal spermathecae; however, it differs from *C. hawsi* by having a more extensive wing pattern with pale spots on M_1 and M_2, a shorter proboscis, no SCo on flagellomere 10, and narrower eye separation. If the species F specimen is not an aberration, the male should be easy to associate by having apical spines on the fore and hind tarsomeres and pale spots straddling the midportions of M_1 and M_2—a combination unique among the known *Culicoides* of the southwestern United States.

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Table 1. Grand County, Utah, collection sites. Latitude and longitude coordinates are WGS 84. Only CDC traps were used unless otherwise stated. Descriptions are for correlation with some specimen labels.

°N	°W	Description
38.96339	109.33585	wash near Cisco, no trap, immatures collected
38.83484	109.55360	Yellow Cat area, bite
38.799	109.181	Entrada Ranch, Rio Mesa, CDCT + bite
38.64	109.41	Castle Valley, bite
38.6052	109.58395	N of Colorado River, W of highway 191 bridge
38.5937	109.5722	NW Moab, Ferrell Gas
38.59009	109.57025	NW Moab, Portal RV-N
38.58900	109.56295	NW Moab, SW of Motel 6
38.5889	109.5692	NW Moab, Portal RV-S old
38.58867	109.56890	NW Moab, Portal RV-S new
38.5886	109.5639	NW Moab, property S of Motel 6
38.58786	109.57059	NW Moab, W of N pastures
38.58775	109.56551	NW Moab, W end of Westwood Av
38.58529	109.56196	W Moab, barn on N 500 West, NJT + CDCT
38.58296	109.56663	W Moab, N Riversands Rd
38.58144	109.56495	W Moab, Orchard SE
38.58112	109.57401	NW Moab, N Higgins Ln
38.57965	109.57394	NW Moab, S Higgins Ln
38.57908	109.57136	W 400 North, W of Stewart Ln
38.57881	109.57204	NW Moab, S Berm trail
38.57709	109.56635	S Riversands Rd
38.57698	109.57030	S Stewart Ln
38.57634	109.55916	W Moab, orchard E of Grand Center
38.5757	109.5577	W Moab, Walnut Ln orchard
38.57561	109.54358	Moab, E 100 North
38.5745	109.56611	W Moab, W end of Bartlett Circle
38.5745	109.5620	W Moab, Bartlett Marsh at 500 West
38.5743	109.5633	W Moab, Bartlett Circle
38.57239	109.56754	W Moab, Kane Cr Rd, TNC headquarters
38.57047	109.55684	W Moab, W 200 South, NJT + CDCT
38.56217	109.52447	E Moab, 1100 Sand Flats Rd, spring near creek
38.56149	109.54583	S Moab, Mill Cr Parkway, behind La Quinta Inn
38.56143	109.54324	S Moab, S 400 East at Pack Creek
38.5601	109.5256	SE Moab, Powerhouse Ln orchard
38.55893	109.53922	S Moab, Antiquity Ln NW
38.55852	109.53792	S Moab, Antiquity Ln SE
38.55740	109.58207	3 km SW Moab, box canyon S of Rim Trail parking
38.54970	109.59165	4 km SW Moab, residence, NJT + CDCT
38.54606	109.59159	4 km SW Moab, drive-up canyon
38.54491	109.51000	4 km SE Moab, Spanish Valley Dr
38.54458	109.59424	5 km SW Moab, canyon opposite barn
38.5405	109.5968	5 km SW Moab, canyon at S campgound entrance
38.5347	109.5992	6 km SW Moab, Pritchett Canyon
38.52860	109.48156	8 km SE Moab, E Bench Rd
38.52764	109.49960	7 km SE Moab, Desert Rd
38.5274	109.4997	7 km SE Moab, Desert Rd, bite
38.504	109.5828	8 km SSW Moab, Hunter Canyon, bite
38.5068	109.5890	8 km SSW Moab, Hunter Canyon, UVLT

Table 2. Utah collection sites outside Grand County. Latitude and longitude coordinates are WGS 84. "B" indicates a bite-only collection site. "+B" indicates a UVLT and bite collection site. Others are UVLT-only sites.

County	°N	°W	m	Date	Bite
Box Elder	41.95409	113.32065	1922	18 Jul 2019	-
Garfield	37.795	111.413	1632	7–8 Jul 2003	-
San Juan	38.4990	109.5843	1297	30 Mar 2003	B
	38.41373	109.22369	2894	15–16 Aug 2019	-
	38.40182	109.21042	2722	13 Aug 2019	-
	38.15339	109.82893	1598	12 Nov 2017	B
Sanpete	39.52538	111.25375	2658	19 Jul 2019	-
Summit	40.80841	110.87270	2752	11 Jul 2019	-
	40.63037	111.17363	2201	2 Jul 2018	-
	40.59399	110.97655	2529	10 Jul 2019	-
Uintah	39.4639	109.2869	2436	11 Jun 2017	-
	39.46307	109.28427	2450	31 Aug 2017	-
Wasatch	40.55424	111.03065	2621	27 Jun 2018	-
Washington	37.20522	113.24106	1106	2-3 Jun 2019	+B
	37.11312	113.98512	1009	6 Jun 2019	+B
	37.09706	113.91110	1325	5 Jun 2019	+B
	37.03357	113.91521	935	4 Jun 2019	+B

Table 3. Collection sites outside Utah. Latitude and longitude coordinates are WGS 84. "+B" indicates a UVLT and bite collection site. Others are UVLT-only sites.

State	County	°N	°W	m	Date	Bite
Arizona	Mohave	35.03568	114.27928	748	7-8 Apr 2019	-
Arizona	Cochise	31.89365	109.21416	1708	15 Oct 2019	-
Arizona	Cochise	31.96795	109.32022	1743	13 Oct 2019	-
Arizona	Graham	32.64853	109.82030	2038	11 Oct 2019	-
Arizona	Greenlee	32.96215	109.30566	1056	10 Oct 2019	-
California	San Bernardino	34.81440	115.61413	1219	4–5 Apr 2019	-
Colorado	Montrose	38.32234	108.18359	2934	30 Jul 2020	-
Idaho	Blaine	43.79184	114.45986	1955	19–21 Aug 2017	-
Idaho	Blaine	43.73340	114.27168	1974	16 Jul 2019	-
Idaho	Bonneville	43.52974	111.18504	2002	14 Jul 2019	-
Idaho	Custer	43.86294	114.20625	2256	15 Jul 2019	-
Nevada	Clark	36.14032	114.72704	384	2 Apr 2019	-
New Mexico	Grant	32.84743	108.59278	1332	16 Oct 2019	+B
Wyoming	Lincoln	43.14524	110.87651	1822	12 Jul 2019	-

Table 4. Light-trap responses (LTRs). Unmarked data indicate the proportion of each species collected with light traps in Grand County, where both light-baited and CO_2-baited traps were used during 1999–2016, adjusted as LTRs to show the fraction that would have been collected with light traps if equal numbers of the traps had been used. Data with an asterisk (*) are for species or sexes collected in other areas where only UVLTs were used and are only to show that UVLTs can be used for their collection. Data with a dagger (†) are for species D, which was collected under both circumstances, and for *C. mortivallis* and *C. owyheensis*, which were randomly selected for identification, are simple unadjusted fractional LTR calculations.

Species	n ♂	LTR	n ♀	LTR
Leptoconops				
(Holoconops)				
americanus			2	0.000
foulki	1	1.000	3	0.540
knowltoni	19	1.000	17	0.128
sublettei			13	0.299
unidentified *Holoconops*			873	0.089
(Leptoconops)				
torrens			2	0.000
Culicoides				
(Amossovia)				
californiensis	37	0.879	96	0.478
(Beltranmyia)				
crepuscularis	237	0.874	2,218	0.157
(Diphaomyia)				
bergi			16	0.917
defoliarti–haematopotus	1,603	0.985	3,718	0.939
erikae	1	1.000	2	1.000
inyoensis	16	1.000	49	0.973
salihi	1	1.00*	1	1.00*
(Drymodesmyia)				
bakeri			1	1.00*
butleri	3	1.00*	18	1.00*
byersi	8	0.943	10	0.369
cacticola	6	1.00*	34	1.00*
copiosus	3	1.00*	57	1.00*
hinmani	1	1.000	60	0.207
insolatus			1	1.00*
jonesi	10	1.00*	10	1.00*
ryckmani	15	1.00*	106	1.00*
sitiens	17	1.000	31	1.000
torridus	4	1.00*	1	1.00*
(Haematomyidium)				
stellifer	238	0.995	5,696	0.274
(Monoculicoides)				
grandensis			1	1.000
sonorensis	1,269	0.695	11×10^3	0.109
(Selfia)				
brookmani	32	1.000		
denningi	568	1.000		
hieroglyphicus	5,384	0.999		
jacksoni	4	1.000		
jamesi	39	1.000		
moabensis	15	1.000	173	0.397
unidentified *Selfia*			46.5×10^3	0.526
(Sensiculicoides)				
kibunensis	36	1.000	110	0.992
travisi			2	1.00*
(Silvaticulicoides)				
sublettei			1	1.00*
usingeri	1	1.00*	1	1.00*
(Silvicola)				
cockerellii	5	1.00*	13	1.00*
lahontan	2	1.000	51	0.128
neomontanus	59	1.00*	72	1.00*
saltonensis			6	1.00*
sierrensis			7	1.00*
species D			2	0.50†
species E			1	1.000
(Wirthomyia)				
bottimeri	67	0.980	115	0.957
Leoni group				
reevesi	2	1.000	1,944	0.008
Limai group				
luglani	398	0.762	3,496	0.277
Palmerae group				
calexicanus	1	0.000	1	1.000
hawsi			6	0.701
palmerae	90	0.990	19	0.926
utahensis	1	1.000	12	0.766
species C			1	0.000
unidentified Palmerae group			99	0.969
Piliferus group				
cavaticus	1	1.000		
chewaclae			1	1.00*
doeringae	124	1.000	163	0.997
unicolor			1	1.00*
species A	34	0.987	48	1.000
species B			45	1.00*
Saundersi group				
atchleyi			1	1.00*
Stonei group				
mortivallis			11	0.09†
owyheensis			2	0.50†
mortivallis–owyheensis			26	0.163
stonei			6	0.000
werneri			3	1.00*
unidentified Stonei group	1	1.000	25	0.309
unplaced				
species F			1	1.00*

Table 5. Seasonal distributions of species reported from the southwestern United States. Data for species collected in the present study in Grand County, Utah, are expressed as parts-per-thousand of the total for the species adjusted by the number and kind of traps used each week. "#" indicates other week of collection outside Grand County during the present study. "x" indicates additional week and "•" indicates additional month of collection reported by others. The data for *C. sanguisuga* are entirely from Eastern North American records. Data for *C. mortivallis* and *C. owyheensis* (indicated by asterisks) are not related to trap proportions and are indicated by an "O". Boxed entries for species A indicate weeks where "near species A" were also collected.

Week			10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Species collected per week			2	3	3	4	12	10	7	9	8	15	23	28	32	28	30	29	26	27	31	28	18	21	17	27	19	19	18	19	23	13	8	17	12	9	4	3	1
Total species reported per week			6	6	12	12	25	26	20	31	25	26	50	53	46	46	51	56	55	44	47	48	39	39	40	43	34	29	21	24	29	15	15	24	16	14	8	3	1
Species	♂	♀	Mar	Mar	Mar		Apr	Apr	Apr	Apr		May	May	May		Jun	Jun	Jun		Jul	Jul	Jul	Jul		Aug	Aug	Aug		Sep	Sep	Sep	Sep		Oct	Oct	Oct		Nov	Nov
Leptoconops																																							
(Brachyconops)																																							
californiensis						x	x			x		•	•	•																				•	•	•			
(Holoconops)																																							
belkini							x	x	x		x			x																									
Kerteszi group																																							
americanus		2					x	500	x	x	x		x	500			x	x	x																				
andersoni									x				x																										
arnaudi									x				x						x					x		x				x									
asilomar			x	x	x	x					x	x	x			x		x			x		x	x			x	x					x						
atchleyi			x							x																													
foulki	1	5								208	x	x	x	x	125		160		x		169	x		x	337														
knowltoni	19	19					x		x	83	29	44	x	40			x	46		17	50	18	34	167	61	32	165	24	29	46	92	23							
reesi								x	x	x	x		x	x			x																						
sublettei		20				293			69	57	x	96		x		90	38	x	32			x						x		64	38		75		70	78			
whitseli																		x							x						x								
unnamed species										x																													
unidentified *Holoconops*		912				27	6		7	11	2	1	2	4	10			4	5	3	25	11	7	21	27	90	286	55	19	36	325	16							
(Leptoconops)																																							
carteri											x	x	x	x	x	x	x	x	x				x																
freeborni												x					x	x		x																			
mohavensis													x																										

		Week	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Species	♂	♀	Mar	Mar	Mar		Apr	Apr	Apr	Apr		May	May	May		Jun	Jun	Jun		Jul	Jul	Jul	Jul		Aug	Aug	Aug		Sep	Sep	Sep	Sep		Oct	Oct	Oct		Nov	Nov
torrens		16					x					217	x		68	650	66	x	x	x	x	x	x	x	x	x													
(Proleptoconops)																																							
werneri					x		x		x	x	x		x	x		x		x	x	x		x	x	x	x		x												
Culicoides																																							
(Amossovia)																																							
californiensis	44	161											6	5	36	63	52	67	39	31	93	72	67	160	95	88	47	21	23	9	10	6				10			
cochisensis								x											x			x		x	x	x		x	x	x									
oklahomensis						x						x		x				x					x	x	x	x	x	x	x	x	x	x		x					
pecosensis										x														x															
(Avaritia)																																							
boydi								x					x		x			x	x							x	x		x		x			•	•	•			
chiopterus																					x																		
obsoletus																		x		x		x				x	x			x			x						
sanguisuga													•	•	•	•	•	•	•	•	•	•	•	•	•	•	•												
(Beltranmyia)																																							
crepuscularis	244	2,427					5	13	28	14	14	21	24	38	35	48	37	95	56	98	97	64	36	44	53	53	31	26	19	22	15	5	5	3	1	1			
(Diphaomyia)																																							
bergi		16						x						255	412		225	63	x	46	#	#																	
defoliarti–haematopotus	1,620	3,960					1	1	2	4	13	16	29	278	184	45	22	37	32	34	78	21	17	43	20	31	15	21	17	17	10	2	1	2	3	1			
erikae	2	12											333	x	667		#	x			x	#				x													
inyoensis	16	49												79	390	58	215	184	41		33																		
salihi	1	1								x									x	#			x													x			
(Drymodesmyia)																																							
arizonensis								x			x								x						x												x		
bakeri		1																	#																				
butleri	3	18									x						x		x		x				x									#					
byersi	8	32											50	28	25	165	24	129	47	30	247	55	17		20	82	40			21	18								
cacticola	6	34					#	x	x		x	x		x	x	#			x	x					x		x							#			x		
copiosus	3	57					x	x		x			x	x	x	#			x			x			x								x	#			x		

		Week	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Species	♂	♀	Mar	Mar	Mar		Apr	Apr	Apr	Apr		May	May	May		Jun	Jun	Jun		Jul	Jul	Jul	Jul		Aug	Aug	Aug		Sep	Sep	Sep	Sep		Oct	Oct	Oct		Nov	Nov
hinmani	1	102											11	11	11	13		114	44	61	34	23	120	188	111	83	64	57	37	9	11								
insolatus		1					#	x																									x						
jonesi	10	10																																#	x				
ryckmani	15	106	x			x	#	x		x		x		x	#	#	x								x									x			x		
sitiens	17	31						25					123	45	221		212	112	x	45		21	17	19	15	48	13	12	14		15				45				
torridus	4	1					#	x		x			x	x																			x	#					
(Haematomyidium)																																							
kettlei					x			x			x		x	x			x	x	x	x											x			x					
stellifer	238	5,806										1	26	17	116	157	170	149	44	94	17	15	18	16	55	46	29	16	4	3	4	1							
(Monoculicoides)																																							
grandensis		1																x													1000								
occidentalis	1+	+							•	•	•	•	•	•	•	•	•	•	•	•	•	•	•							500	500								
sonorensis	1,455	15,200	1	9	2	12	11	5	5	7	3	5	6	12	55	12	12	15	14	19	24	23	74	71	45	55	46	68	25	18	31	32	72	39	80	68	8	18	
(Selfia)																																							
brookmani	48		•	•	•	•	•	•	x		x		80	365	80	#	31	73	31		40		27	31			219		23	•	•	•	•	•	•	•			
denningi	566	6											13	163	66	4	84	124	13	50	71	188	82	92	5	10	22	4	6	1	1								
hieroglyphicus	5,404						1	1	1	1	32	18	108	77	70	4	28	56	12	39	67	161	93	118	15	25	42	6	11	2	4	1	1	2	3	1			
jacksoni	4							274					274		274						x					177								#					
jamesi	41							28			88	31	28	154	112	#	110	180			56	24	x	44		18		13	32	14	17				51				
moabensis	15	175						15		13		22	60	109	52	15	38	34	12	19	23	13	12	4	4	10	53	22	57	36	45	109		134	49	19	21		
tenuistylus									x	x			x	x		x	x	x	x				x																
unidentified *Selfia*		51,700	1	1	1	5	3	10	17	12	25	17	74	25	23	9	32	98	43	46	39	77	45	44	28	28	39	27	24	13	14	49	15	39	21	23	26	10	3
(Sensiculicoides)																																							
kibunensis	36	123											20	261	471	46	42	92	50	12	6	#	x	x	x	#													
travisi		2																			#																		
(Silvaticulicoides)																																							
sublettei		1														x	x	x		x															#				
usingeri	1	1																		#																			
vetustus													x	x	x	x	x	x	x	x																			

		Week	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Species	♂	♀	Mar	Mar	Mar		Apr	Apr	Apr	Apr		May	May	May		Jun	Jun	Jun		Jul	Jul	Jul	Jul		Aug	Aug	Aug		Sep	Sep	Sep	Sep		Oct	Oct	Oct		Nov	Nov
(Silvicola)																																							
cockerellii	5	13			x								x					x	x	#	#	#		x	x	#													
freeborni							x			x			x	x	x	x		x	x	x	x	x	x	x	x	x	x	x						x					
lahontan	7	85		28	136	24	84	84	60	28	12	9	19	46	#	#	4	47	12	21						6					4	6	52	80	59	112	29	38	
neofagineus					x	x				x			x			x		x	x	x	x	x			x														
neomontanus	59	72															#		#	#	#	#	x	#	x	#	#												
saltonensis		6			x	x	#								x																								
sierrensis		7														•	#	•			#	#		x		#													
tristriatulus																x	x	x	x	x	x	x	x	x	x	x	x	x											
species D		2					#					1000																											
species E		1							1000																														
(Wirthomyia)																																							
bottimeri	68	124												18	59	22	72	279	52	93	51	191	41	15	32	13	4	16	4	7	4	5		22					
Daedalus group																																							
daedalus																x																							
pampoikilus																	x							x															
Leoni group																																							
reevesi	2	2,362												4	10	12	17	70	71	44	38	32	43	67	112	57	73	148	77	60	47	14	3	1	#				
Limai group																																							
luglani	453	4,320												1	1	5	13	70	108	227	183	115	132	93	25	13	8	2	2	1	1	1		#		1			
Mohave group																																							
hoguei										x				x												x													
mohave					x		x	x		x				x	x				x		x	x	x		x	x	x				x								
Palmerae group																																							
calexicanus	1	6					x							733	267		x																						
hawsi		10											116	97	103	189		185	116	x	99	95																	
leechi										x			x																										
novamexicanus																	x																						

		Week	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Species	♂	♀	Mar	Mar	Mar		Apr	Apr	Apr	Apr		May	May	May		Jun	Jun	Jun		Jul	Jul	Jul	Jul		Aug	Aug	Aug		Sep	Sep	Sep	Sep		Oct	Oct	Oct		Nov	Nov
oregonensis										x			x	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•											
palmerae	92	28									12		34	199	491	87	66	85	6	5		7		6															
utahensis	1	12											59		264		91	96	42										45								404		
species C		1																1000																					
unidentified Palmerae group		101												241	565	45	84	29	8	12		9		7															
Piliferus group																																							
cavaticus	1			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	1000	x	x	x	x	x	x	x												
chewaclae		1						x	x	x	x	x						x				x				#													
doeringae	125	167										12		243	370	10	71	150	18	23	49	32	8	9	2		2	2											
lophortygis																							x				x												
unicolor		1												x	x	x					#																		
species A	34	48											26	146	452	11	167	135	21	16	$\boxed{13}$	$\boxed{11}$				$\boxed{\#}$													
species B		45																				#		#		#													
Saundersi group																																							
atchleyi		1																		x	#	x			x	x		x											
saundersi													x			x	x		x	x	x	x	x				x	x											
Stonei group																																							
mortivallis *	2	12										O		O	x			O					x					O	O	O	O		O	#					
owyheensis *		2																										O			O								
mortivallis–owyheensis		33										90	40	62	154	37	31		26	60		31	53	58		39	49	56	29	80	64	41							
stonei		6										124						90								125		240		316	105								
werneri		3								x				x							x	x			x									#		x			
unidentified Stonei group	1	28											45	70	37	82		33	29		35		99			26	102	53	159	116		50			64				
unplaced																																							
monoensis										x						x	x																						
nanellus																			x																				
posoensis							x															x	x	x	x	x	x	x											
species F		1																			#																		

Table 6. Collections from University of Utah Rio Mesa Field Station, Grand County, Utah. Collections are from 38.799°N 109.181°W, 1280 m elevation, during 1999–2002. ILT = CDC incandescent light trap, CO_2T = CDC CO_2-baited trap without light, bite = human-biting.

Week	20		20		23	25		27		28	
Method	ILT		ILT		bite	ILT		CO_2T		ILT	
Species	♂	♀	♂	♀	♀	♂	♀	♂	♀	♂	♀
Leptoconops											
(Holoconops)											
knowltoni						1					
(Leptoconops)											
torrens					10						
Culicoides											
(Amossovia)											
californiensis								1			
(Beltranmyia)											
crepuscularis							1				
(Diphaomyia)											
defoliarti						1	4				
defoliarti–haematopotus	1	1	7	5						1	
inyoensis							8				
(Drymodesmyia)											
byersi				1							
hinmani						1			1		
sitiens			1								
(Monoculicoides)											
sonorensis		1							67	1	
(Selfia)											
denningi						4				7	
hieroglyphicus	4		10			74				41	
jamesi			1								
unidentified *Selfia*		20		24			620		13×10^3		103
(Silvicola)											
lahontan							1		2		
Leoni group											
reevesi									1		
Limai group											
luglani						1	1		2		
Palmerae group											
palmerae							2				
Piliferus group											
doeringae							5				
species A							1				
Stonei group											
mortivalis–owyheensis									37		
unidentified Stonei group									15		

Table 7. Utah UVLT collections outside Grand County.

County	Washington				Uinta		Wasatch		Garfield		Summit				Box Elder		Sanpete		San Juan		Uinta	
Week	22		23		24		26		27		27		28		29		29		33		35	
Species	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Leptoconops																						
torrens				1																		
Culicoides																						
(Beltranmyia)																						
crepuscularis						12																
(Diphaomyia)																						
bergi										1						1						
defoliarti					2	6			9	4									1			2
erikae						9									1	1						
inyoensis									1	24												
salihi									1	1												
(Drymodesmyia)																						
cacticola				2																		
copiosus				1																		
ryckmani		1	1	28																		
(Haematomyidium)																						
stellifer									1		1					4						
(Monoculicoides)																						
sonorensis	5	13	27	38		2			1	1												
(Selfia)																						
brookmani			16																			
denningi									1													
hieroglyphicus	11		10		4				75													
jamesi			2		2				1		3				1							
unidentified *Selfia*		50		11		35				761		1				2						
(Sensiculicoides)																						
kibunensis										2		1						5		1		
(Silvaticulicoides)																						
usingeri									1	1												
(Silvicola)																						
cockerellii												3										
lahontan		4	5			1																
neomontanus						2		2				6	1	6				5	3	12		
sierrensis						1								2						2		
unidentified *Silvicola*												8		10				56		49		
(Wirthomyia)																						
bottimeri			1							2												
Limai group																						
luglani									2	3												
Palmerae group																						
calexicanus		5																				
palmerae											1											

County	Washington				Uinta		Wasatch		Garfield		Summit				Box Elder		Sanpete		San Juan		Uinta	
Week	22		23		24		26		27		27		28		29		29		33		35	
Species	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Piliferus group																						
chewaclae																				1		
doeringae										1				2								
species A									2	5												
near species A																		1		1		
species B																		3		3		

Table 8. Checklist of Utah species. Those with an asterisk (*) were reported from Utah by others but were not collected in Utah in the present study. "G" indicates species collected in Grand County. The last column indicates species reported as human-biting, with the number collected in the present study or a "+" for reports by others.

Species		Bite n
Leptoconops Skuse		
subgenus *Holoconops* Kieffer		
L. americanus Carter	G	1
L. foulki Clastrier and Wirth	G	1
L. knowltoni Clastrier and Wirth	G	+
L. reesi Clastrier and Wirth *		+
L. sublettei Clastrier and Wirth	G	7
subgenus *Leptoconops* Skuse		
L. torrens (Townsend)	G	13+
***Culicoides* Latreille**		
subgenus *Amossovia* Glukhova		
C. californiensis Wirth and Blanton	G	
C. cochisensis Wirth and Blanton *		
subgenus *Avaritia* Fox		
C. chiopterus (Meigen) *		+
C. obsoletus (Meigen) *		+
subgenus *Beltranmyia* Vargas		
C. crepuscularis Malloch	G	+
subgenus *Diphaomyia* Vargas		
C. bergi Cochrane	G	
C. defoliarti Atchley and Wirth	G	
C. erikae Atchley and Wirth	G	
C. haematopotus Malloch	G	+
C. inyoensis Wirth and Blanton	G	
C. salihi Khalaf		
subgenus *Drymodesmyia* Vargas		
C. byersi Atchley	G	
C. cacticola Wirth and Hubert		
C. copiosus Root and Hoffman		
C. hinmani Khalaf	G	+
C. ryckmani Wirth and Hubert		
C. sitiens Wirth and Hubert	G	
subgenus *Haematomyidium* Goeldi		
C. stellifer (Coquillett)	G	+
subgenus *Monoculicoides* Khalaf		
C. grandensis Grogan and Phillips	G	
C. occidentalis Wirth and Jones	G	
C. sonorensis Wirth and Jones	G	+
subgenus *Selfia* Khalaf		
C. brookmani Wirth	G	
C. denningi Foote and Pratt	G	4
C. hieroglyphicus Malloch	G	
C. jacksoni Atchley	G	
C. jamesi Fox	G	
C. moabensis Phillips	G	
subgenus *Sensiculicoides* Shevchenko		
C. kibunensis Tokunaga	G	+
C. travisi Vargas *		+
subgenus *Silvaticulicoides* Glukhova		
C. sublettei Atchley *		
C. usingeri Wirth		
subgenus *Silvicola* Mirzaeva & Isaev		
C. cockerellii (Coquillett)		+
C. lahontan Wirth and Blanton	G	
C. neomontanus Wirth		+
C. sierrensis Wirth and Blanton		
C. species D	G	
C. species E	G	
subgenus *Wirthomyia* Vargas		
C. bottimeri Wirth	G	
Leoni species group		
C. reevesi Wirth	G	1
Limai species group		
C. luglani Jones and Wirth	G	
Palmerae species group		
C. calexicanus Wirth and Rowley	G	
C. hawsi Wirth and Rowley	G	
C. palmerae James	G	
C. utahensis Fox	G	
C. Palmerae group species C	G	
Piliferus species group		
C. cavaticus Wirth and Junes	G	
C. chewaclae Glick and Mullen		
C. doeringae Atchley	G	
C. Piliferus group species A	G	
C. Piliferus group species B		
Stonei species group		
C. mortivallis Wirth and Blanton	G	
C. owyheensis Jones and Wirth	G	
C. stonei James	G	

Table 9. UVLT collections outside Utah. Numbers with exponents indicate a crude estimate: 10^2 = in the hundreds, 10^3 = in the low thousands.

State	AZ		CA		NV		WY		ID		ID		CO		ID		ID		AZ		AZ		NM	
Week	14		14		14		28		28		29		31		33		34		41		42		42	
Culicoides	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
(Beltranmyia)																								
crepuscularis						1				2	1	1	1	1			1							
(Diphaomyia)																								
bergi								1																
defoliarti														1						3			1	5
(Drymodesmyia)																								
butleri																			3	18				
cacticola		1			1														5	31				
copiosus																			3	56				
insolatus				1																				
jonesi																			10	10				
ryckmani	14	62		16																				
torridus					1														3	1				
unidentified *Drymodesmyia*																			11					
(Haematomyidium)																								
stellifer										3														
(Monoculicoides)																								
sonorensis	4	5							1										10^2	10^2				2
(Selfia)																								
denningi								3		4														
hieroglyphicus										1									10^2				10^2	
jacksoni																			1					
jamesi											3				1									
unidentified *Selfia*		3				1				12		34								10^3				10^3
(Sensiculicoides)																								
kibunensis										2		5												
travisi								2																
(Silvaticulicoides)																								
sublettei																						1		
(Silvicola)																								
cockerellii									2	10	3													
neomontanus								3	1				53	32	1	2		2						
saltonensis						6																		
sierrensis												2												
species D						1																		
unidentified *Silvicola*												150												
(Wirthomyia)																								
bottimeri										1														
Leoni group																								
reevesi																								1
Limai group																								
luglani																			1	1				
Palmerae group																								
palmerae														1										
Piliferus group																								
doeringae										4	1													
unicolor										1														
near species A										1		1												
species B												3		36										
Saundersi group																								
atchleyi										1														
Stonei group																								
mortivallis																				1				
werneri																				3				

Table 10. Mite-parasitized Ceratopogonidae. CO$_2$T = CO$_2$-baited trap without light. ILT = incandescent light trap. UVLT = ultraviolet light trap. When collections were combined from nearby traps, geographic coordinates are rounded and will not match those of Table 1. "n" is the number of specimens with the same collection data. Specimens with an asterisk (*) were identified by males in the same collection.

Host	Sex	Date	Trap	State	°N	°W	n	Parasites on each
Forcipomyia sp.	♀	1 Aug 2006	CO$_2$T	Utah	38.589	109.570	1	2 mite larvae
F. frutetorum (Winnertz)	♀	1 Aug 2006	CO$_2$T	Utah	38.589	109.570	1	1 mite larva
Dasyhelea sp.	♀	28 Jul 2009	CO$_2$T	Utah	38.584	109.571	1	1 mite larva
D. ryckmani Wirth and Hubert	♀	10 Oct 2019	UVLT	Arizona	32.96215	109.30566	2	2 mite larvae
Stilobezzia (Acanthohelea) sp.	?	17 Jun 2003	UVLT	Utah	38.54606	109.59159	1	1 mite larva (loose with ♂ & ♀)
C. crepuscularis	♂	16 May 2002	UVLT	Utah	38.52860	109.48156	3	2 mite larvae
C. crepuscularis	♂	16 May 2002	UVLT	Utah	38.52860	109.48156	5	1 mite larva
C. crepuscularis	♀	30 May 2001	CO$_2$T	Utah	38.54606	109.59159	1	1 mite larva
C. defoliarti	♀	6 Jun 2002	UVLT	Utah	38.52860	109.48156	2	1 mite larva
C. defoliarti	♀	22 Jun 2003	UVLT	Utah	38.5068	109.5890	1	2 mite larvae
C. defoliarti	♀	4 Jul 2002	UVLT	Utah	38.52860	109.48156	1	2 mite larvae
C. defoliarti	♀	2 Aug 2000	ILT	Utah	38.57047	109.55684	2	1 mite larva
C. defoliarti	♀	2 Aug 2000	ILT	Utah	38.57047	109.55684	1	4 mite larvae
C. defoliarti	♂	28 Aug 2001	ILT	Utah	38.54491	109.51000	1	1 mite larva
C. defoliarti–haematopotus	♂	1 May 2002	UVLT	Utah	38.54491	109.51000	1	1 mite larva
C. defoliarti–haematopotus	♂	22 Jun 2003	UVLT	Utah	38.5068	109.5890	1	1 mite larva
C. defoliarti–haematopotus	♂♀	4 Jul 2002	UVLT	Utah	38.52860	109.48156	1	1 mite larva + nematodes
C. defoliarti–haematopotus	♂	4 Jul 2002	UVLT	Utah	38.52860	109.48156	1	1 mite larva
C. defoliarti–haematopotus	♂	2 Aug 2000	ILT	Utah	38.57047	109.55684	2	1 mite larva
C. haematopotus	♀	6 Jun 2002	UVLT	Utah	38.52860	109.48156	1	1 mite larva
C. inyoensis	♀	28 May 2017	UVLT	Utah	38.52764	109.49960	1	1 mite larva
C. inyoensis	♂	27 Jun 2002	UVLT	Utah	38.52860	109.48156	1	2 mite larvae
C. inyoensis	♂	27 Jun 2002	UVLT	Utah	38.52860	109.48156	1	1 mite larva
C. ryckmani	♂	8 Apr 2019	UVLT	Arizona	35.03568	114.27928	1	1 mite larva
C. sonorensis	♀	23 May 2002	CO$_2$T	Utah	38.52860	109.48156	1	1 mite larva
C. denningi	♀	30 May 2001	CO$_2$T	Utah	38.54606	109.59159	1	1 mite larva
C. denningi	♂	10 Aug 2000	ILT	Utah	38.5405	109.5968	1	3 mite larvae
C. hieroglyphicus	♂	10 Oct 2019	UVLT	Arizona	32.96215	109.30566	20	1 mite larva
C. hieroglyphicus	♂	10 Oct 2019	UVLT	Arizona	32.96215	109.30566	5	2 mite larvae
C. hieroglyphicus	♂	10 Oct 2019	UVLT	Arizona	32.96215	109.30566	1	3 mite larvae
C. hieroglyphicus	♂	10 Oct 2019	UVLT	Arizona	32.96215	109.30566	1	4 mite larvae
C. hieroglyphicus *	♀	10 Oct 2019	UVLT	Arizona	32.96215	109.30566	26	1 mite larva
C. hieroglyphicus *	♀	10 Oct 2019	UVLT	Arizona	32.96215	109.30566	14	2 mite larvae
C. hieroglyphicus *	♀	10 Oct 2019	UVLT	Arizona	32.96215	109.30566	1	4 mite larvae
C. hieroglyphicus	♂	16 Oct 2019	UVLT	New Mexico	32.84743	108.59278	1	1 mite larva
C. hieroglyphicus *	♀	16 Oct 2019	UVLT	New Mexico	32.84743	108.59278	11+	1 mite larva
C. hieroglyphicus *	♀	16 Oct 2019	UVLT	New Mexico	32.84743	108.59278	1+	2 mite larvae
C. hieroglyphicus *	♀	16 Oct 2019	UVLT	New Mexico	32.84743	108.59278	1	3 mite larvae
C. bottimeri	♀	9 Jun 2004	CO$_2$T	Utah	38.52860	109.48156	1	1 mite larva
C. doeringae	♀	27 May 2003	UVLT	Utah	38.52860	109.48156	2	1 mite larva
C. doeringae	♂	30 May 2002	UVLT	Utah	38.54491	109.51000	1	1 mite larva
C. doeringae	♂	31 May 2002	UVLT	Utah	38.52860	109.48156	1	1 mite larva
C. doeringae	♀	1 Jun 2003	UVLT	Utah	38.52764	109.49960	3	1 mite larva
C. doeringae	♀	6 Jul 2001	ILT	Utah	38.54491	109.51000	1	1 mite larva
C. mortivallis	♀	23 Jun 2004	CO$_2$T	Utah	38.52860	109.48156	1	1 mite larva

Table 11. Intersex and internally parasitized Ceratopogonidae. Intersexes marked ♂♀ have male genitalia and a feminized head and ♀♂ have female genitalia and androgenized head. CO$_2$T = CO$_2$-baited trap without light. ILT = incandescent light trap. UVLT = ultraviolet light trap. ET = emergence trap. When collections were combined from nearby traps, geographic coordinates are rounded and will not match those of Table 1. “n” is the number with the same collection data. Specimens with (*) were identified by males in the same collection; (**) are either *C. hieroglyphicus*, *C. jacksoni*, or *C. jamesi*; (***) is either *C. denningi*, *C. hieroglyphicus*, *C. jacksoni*, or *C. jamesi*.

Host	Sex	Date	Method	State	°N	°W	n	Parasites or notes
F. tenuichela Dow and Wirth	♂♀	10 Sep 2002	CO$_2$T	Utah	38.5889	109.5692	1	nematode
F. tenuichela Dow and Wirth	♀	4 Aug 2009	CO$_2$T	Utah	38.5745	109.562	1	4 infuscated eggs (infected?)
C. californiensis	♂	6 Sep 2002	UVLT	Utah	38.52764	109.49960	1	disseminated granular infection
C. defoliarti–haematopotus	♂♀	21 May 2003	UVLT	Utah	38.54606	109.59159	1	nematode
C. defoliarti–haematopotus	♂♀	6 Jun 2002	UVLT	Utah	38.52860	109.48156	3	nematode
C. defoliarti–haematopotus	♀♂	13 Jun 2002	UVLT	Utah	38.52860	109.48156	1	apparently not parasitized
C. defoliarti–haematopotus	♂♀	4 Jul 2002	UVLT	Utah	38.52860	109.48156	5	nematode (1 also with mite larva)
C. sonorensis	♂	12–17 Sep 2020	reared	Utah	38.96339	109.33585	4	nematode, dead
C. sonorensis	♀♂	15 Sep 2020	reared	Utah	38.96339	109.33585	1	male antennae; not parasitized
C. sonorensis	1♀, 1♂	10 Oct 2019	UVLT	Arizona	32.96215	109.30566	2	nematode
C. hieroglyphicus *	♀	19 Jun 2002	CO$_2$T	Utah	38.54491	109.51000	1	melanized nematode
C. hieroglyphicus *	3♀, 1♂♀	10 Oct 2019	UVLT	Arizona	32.96215	109.30566	4	nematode
C. (Selfia) sp. **	♀♂	20 Jun 2001	ILT	Utah	38.54606	109.59159	1	♀♂ palpi, melanized nematode
C. (Selfia) sp. ***	♀♂	7-8 Jul 2003	UVLT	Utah	37.795	111.413	1	nematode
C. (Selfia) sp. **	♀♂	22 Aug 2003	UVLT	Utah	38.55893	109.53922	2	♂ head, no ♂ genitalia
C. reevesi	♀♂	13 Aug 2002	CO$_2$T	Utah	38.58296	109.56663	1	nematode, no spermatheca
C. reevesi	♀♂	23 Aug 2016	CO$_2$T	Utah	38.57965	109.57394	1	nematode, no spermatheca
C. mortivallis	♀	20 Jun 2002	CO$_2$T	Utah	38.52860	109.48156	1	protozoan (*Tetrahymena* ?)
C. mortivallis	♀	7 May 2002	CO$_2$T	Utah	38.54606	109.59159	1	protozoan (*Tetrahymena* ?)
Stonei group undetermined	♀	2 Jul 2002	CO$_2$T	Utah	38.54606	109.59159	1	starburst-like infection

Other’s reports of intersex or internal parasites (references and more details are in the species accounts)

Host	Sex		Method	Location	n	Parasites
L. americanus	?	(as *L. kerteszi*)	ET	Utah	-	nematode
L. knowltoni	♀	(as *L. kerteszi*)	-	Baja California Sur	1	nematode
C. crepuscularis	♂♀		NJLT	Florida	8	nematode
C. crepuscularis	♂♀		LT	Washington	44	nematode
C. crepuscularis	♂♀		LT	New Mexico	2	(not reported)
C. crepuscularis	♂♀		UVLT±CO$_2$	Louisiana	110	(not reported)
C. defoliarti–haematopotus	♂♀	(as *C. haematopotus*)	LT	New Mexico	1	(not reported)
C. haematopotus	♂♀		ET, NJLT	Florida	123+	nematode
C. stellifer	♂♀		ET, NJLT	Florida	44+	nematode
C. stellifer	♂♀		UVLT±CO$_2$	Louisiana	31	(not reported)
C. sonorensis	♂♀	(as *C. variipennis*)	UVLT±CO$_2$	Louisiana	1	(not reported)
C. sonorensis	♂, ♀	(as *C. variipennis sonorensis*)	ET, UVLT, CO$_2$T	California	-	*Heleidomermis*
C. hieroglyphicus	♂♀		LT	New Mexico	-	nematode
C. kibunensis	♂♀	(as *C. albicans* and *C. cubitalis*)	-	Eurasia	-	nematode

Table 12. Specimens with an abnormal number of spermathecae. "3+" indicates three developed spermathecae plus vestigial fourth. An asterisk (*) indicates an otherwise normal-appearing female parasitized by nematodes. A dagger (†) indicates collection by others.

Culicoides	Spermathecae	Date	Trap	County	°N	W
californiensis	3	3 Jul 2001	CO$_2$T	Grand, UT	38.54491	109.51000
californiensis	3	2 Aug 2016	CO$_2$T	Grand, UT	38.57965	109.57394
crepuscularis	3	16 Jul 2019	UVLT	Blaine, ID	43.73340	114.27168
butleri	3+	10 Oct 2019	UVLT	Greenlee, AZ	32.96215	109.30566
cacticola †	3	28 Jun 2019	UVLT	Riverside, CA	33.6422	116.3833
ryckmani †	3	28 May 2008	-	San Diego, CA	-	
lahontan	3	10 Oct 2000	CO$_2$T	Grand, UT	38.54606	109.59159
lahontan †	3	22 May 2018	-	Riverside, CA	-	
saltonensis †	3	22–27 Mar 1982	NJLT	Imperial, CA	-	
species E	3	22 Apr 2003	CO$_2$T	Grand, UT	38.58296	109.56663
reevesi *	0	13 Aug 2002	CO$_2$T	Grand, UT	38.58296	109.56663
reevesi *	0	23 Aug 2016	CO$_2$T	Grand, UT	38.57965	109.57394
mortivallis	3	27 May 2003	UVLT	Grand, UT	38.52860	109.48156

Table 13. Quantitative characters of *Leptoconops*. Data in () are variations. Measurements and ratios are expressed as means. T9alp = male tergite 9 apicolateral processes. f13/f12 = length of flagellomere 13 divided by the length of flagellomere 12. Wing, proboscis, teeth, setae, and spine data are compiled from Clastrier and Wirth (1978) for the Kerteszi group species and Wirth and Atchley (1973) for the others. Species marked (r) were not examined.

	Females							Males		Both sexes			
Leptoconops	Wing mm	Costal ratio	Proboscis ratio	Flagellomeres n	Mandibular teeth	Tarsal claw tooth	Spermathecae n	T9alp gap	f13/f12	Eye hair	Clypeal setae	palpal organ	Tibial comb spines
(Brachyconops)													
californiensis (r)	1.07	0.30	0.77	12	20	+	2	wide	2.4	0	-	pit	4
(Holoconops)													
belkini	1.07	0.43	0.76	11	14–17	0	2	narrow	2.5	0	4	pit	4
Kerteszi group													
americanus	1.25	0.43	0.81	11	16–19	0	3	narrow	~3	0	4 (3-6)	pit	4 (3)
andersoni (r)	1.00	0.43	0.81	11	16–19	0	3	(unknown)		0	4 (5)	pit	4 (3)
arnaudi (r)	1.28	0.43	0.81	11	16–19	0	3	narrow	~3	0	4 (5)	pit	4 (3)
asilomar (r)	1.53	0.43	0.81	11	16–19	0	3	narrow	~3	0	4 (5)	pit	4 (3)
atchleyi (r)	1.37	0.43	0.81	11	16–19	0	3	narrow	~3	0	4 (5)	pit	4 (3)
foulki	1.00	0.43	0.81	11	16–19	0	3	narrow	2.9	0	4 (5)	pit	4 (3)
knowltoni	1.40	0.43	0.81	11	16–19	0	3	narrow	3.0	0	4 (3-5)	pit	4 (3)
reesi (r)	0.95	0.43	0.81	11	16–19	0	3	narrow	~3	0	6 (5-7)	pit	4 (3)
sublettei	0.90	0.43	0.81	11	16–19	0	3	narrow	~3	0	4	pit	4 (3)
whitseli (r)	1.28	0.43	0.81	11	16–19	0	3	narrow	~3	0	4 (5)	pit	4 (3)
(Leptoconops)													
carteri	0.95	0.36	0.68	12	16–18	0	2	wide	1.6	+	10-13	open	4
freeborni (r)	1.85	0.55	0.57	12	19	+	2	wide	2.4	0	2	open	5
mohavensis ♂ (r)	(female unknown)							wide	2.2	0	-	open	4
torrens	0.95	0.36	0.68	12	16–18	0	2	wide	1.6	0	10-13	open	4
(Proleptoconops)													
werneri	0.74	0.21	0.57	12	10–13	+	3	wide	1.4	0	4	open	4

Table 14. Quantitative characters of *Culicoides*. Entries to the right of the median dashed line apply only to females. Data in () are variations. Wing pattern: 0 none, + reduced, ++ extensive but faint or diffuse, +++ extensive and distinct. Eye separations are approximate in ommatidium diameters. Spermathecae "n" is the number of fully developed spermathecae, with a "v" indicating an additional vestigial spermatheca, and "ratio" is the sum of the larger's width and length including any sclerotized neck divided by the sum of the smaller's width and length including any sclerotized necks. Measurements and ratios are expressed as means. All data for species marked (r) and data for wing length and costal, antennal, palpal, and proboscis ratios are compiled from the description references in the species accounts, with emphasis on southwestern United States data, and supplemented or modified from borrowed and collected specimens.

Culicoides	Wing			Sensilla (SCo) pattern		Apical spines			Eye		Antennal ratio	Palpal ratio	Proboscis ratio	Teeth		Scutellar setae	Sclerotized spermathecae			
	Pattern	Female					Tarsomeres													
		mm	costal ratio	Female	Male	Tibial comb	fore	hind	hair	separa-tion				man-dibular	lacinial		n	ratio	neck	ring
(Amossovia)																				
californiensis	+++	1.28	0.52	1-7,9-13	1,(2),(4),12,13	5-6	0	0	0	0.5-1.5	1.12	2.6	1.00	12-14	20-29	21-22	2v	1.03	+	+
cochisensis	+++	1.14	0.52	1-7,9-13	1,11-13	5	0	0	0	0.5-0.7	1.13	2.5	0.86	11-13	21	18	2v	1.14	+	+
oklahomensis	+++	1.06	0.55	1,3,5,7,9-13		5	0	0	0	1.5	1.35	2.5	0.77	11-14		16	2v	1.04	+	+
pecosensis	+++	1.20	0.57	1,(2),3,(4),5,(6),7,9-13		5	0	0	0	0-1.5	1.15	2.4	0.98	14-20	21	22	2v	1.17	+	+
(Avaritia)																				
boydi	++	0.73	0.57	1,(9),10-13	1,10-13	5	0	0	(+)	0	1.00	1.7	0.78	13-15	16-17	5-6	2v	1.10	+	+
chiopterus	++	0.91	0.59	1,9-13	1,11-13	5	0	0	(+)	0	1.15	1.9	0.65	6-12	16	4	2v	1.00	+	+
obsoletus	++	1.20	0.60	1,9-13	1,11-13	5	0	0	0	0	1.14	2.7	0.90	11-17	18	4	2v	1.03	+	+
sanguisuga (r)	++	0.95	0.60	1,9-13		5				0	1.16	3.0	0.91	14-16			2v	1.00	+	+
(Beltranmyia)																				
crepuscularis	+++	1.21	0.56	1-6,(7),(8),(9),10-12,(13)	1,(2),(11),12	4	0 (+)	0	0	1	1.28	2.3	0.95	10-17	21-25	12	1 (v)	-	+	0
(Diphaomyia)																				
bergi	+++	1.28	0.55	1,(2),(3),(4),5-8,(9)		4	0	0	0	0.2-0.8	1.13	2.1	0.78	10-15	17-19	11-13	2v	1.10	+++	+
defoliarti	+++	1.16	0.56	1,(5),(7),(8),9-13	1,11-13	4	0	0	0	0.1-1	1.27	2.3	0.83	12-15	15-19	8-10	2v	1.25	++	+
erikae	+	1.25	0.54	1,(2),(3),(4),(5),6,(7),8-13	1,(10),11-13	4	0	0	0	0.5-0.7	1.24	2.3	0.95	14-15	16-20	6-14	2v	1.04	++	+
haematopotus	+++	1.11	0.60	1,(2),3,(4),5,(6),7-13	1,11-13	4	0	0	0	0.5	1.49	2.4	0.82	11-14	16	10-12	2v	1.20	++	+
inyoensis	++	1.24	0.56	1-8,(9)	1,(6),(7),8,9	4 (5)	0	0	0	0-0.3	0.99	2.0	0.65	10-11	15-16	8-12	2v	1.00	++	+
salihi	+	0.82	0.53	1,(2),3-8	1,(2),(3),6-9	4	0	0	0	0.2	1.12	1.8	0.67	9	20	9	2v	1.02	+++	+
(Drymodesmyia)																				
arizonensis	+++	1.10	0.57	1-3,(4),(5),9-13	1,12,13	4	0	0	0	0.5-1.3	1.35	2.3	0.84	13-16	20	12-16	2v	1.49	+	+
bakeri	+++	1.31	0.53	1-13		4 (5)	0	0	0	0.7	1.08	2.3	0.99	18-24	31	10	2v	1.24	++	+
butleri	+++	1.12	0.51	1-6,(7),(8),9-13	1,12-13	4	0	0	0	0.4	0.99	2.2	0.89	13-17	25-27	12	2v	1.24	0	+
byersi	+++	0.89	0.54	1,3,5,(6),7,9-13	1,12,13	4	0	0	0	0-0.1	1.13	1.7	0.60	9-11	19-20	9	2v	1.07	+	+
cacticola	+++	1.16	0.52	1-5,(6),(7),(8),9-13	1,12,13	4	0	0	0	0.4-1.0	1.12	2.2	0.92	13-15	21-27	8-14	2v	1.15	0	+
copiosus	+++	1.02	0.53	1,9-13	1,12,13	4	0	0	0	0.4	1.03	2.0	0.70	12-14	16-22	14-16	2v	1.17	+	+
hinmani	+++	0.73	0.63	1,9-13	1,12,13	4	0	0	0	0	1.26	2.3	0.77	13-15	16-19	9	2v	1.00	++	+
insolatus	+++	1.19	0.54	1-5,(6),(7),9-13	1,11-13	4	0	0	0	0.1-0.5	1.21	2.0	0.83	13-15	19	10	2v	1.18	0	+
jonesi	+++	1.20	0.52	1-5,(6),(7),(8),9-13	1,12,13	4	0	0	0	0.4	1.03	2.1	0.77	13-18	25-27	12	2v	1.19	0	+
ryckmani	++	0.93	0.55	1,(9),(10),11-13	1,12,13	4	0	0	0	0.4	1.19	2.0	0.70	11-13	17-21	11-12	2v	1.00	0 (+)	+
sitiens	+++	1.42	0.53	1-7,(8),9-13	1,12,13	4 (5)	0	0	0	0.4-0.7	1.15	2.3	0.87	14-18	26-30	12	2v	1.25	0	+
torridus	+++	1.22	0.51	1-5,(6),(7),(8),9-13	1,12,13	4	0	0	0	0.3-0.5	1.21	2.0	0.89	13-15	22-27	8-10	2v	1.20	0	+

Culicoides	Wing			Sensilla (SCo) pattern		Apical spines			Eye		Antennal ratio	Palpal ratio	Proboscis ratio	Teeth		Scutellar setae	Sclerotized spermathecae			
	Pattern	Female		Female	Male	Tibial comb	Tarsomeres		hair	separation				mandibular	lacinial		n	ratio	neck	ring
		mm	costal ratio				fore	hind												
(Haematomyidium)																				
kettlei	+++	1.06	0.55	1,(4),5-8	1,6,(7),8,9,(10)	5 (6)	0	0	0	1	0.91	2.1	0.79	13-14	14-17	8-12	2v	1.10	++	+
stellifer	+++	1.15	0.57	1,(3),(4),(5),6-8	1,(5),6-10	5	0	0	0	≤1	0.97	2.5	0.82	12-16	17-19	8-10	2v	1.13	+++	+
(Monoculicoides)																				
grandensis	++	1.36	0.55	1,6-8	1,6-8	6		+	0	3	0.82	2.0	0.6	0	0		1	-	0	0
occidentalis	+++	1.6	0.55	1,(3),(4),(5),6-8	1,6-8	6-7	+	+	0	2-3		2.3		11-16			1	-	0	0
sonorensis	+++	1.40	0.53	1,(2),(3),(4),5-8	1,(4),(5),6-8	6-7	+	+	0	2-3	0.84	2.3	0.86	11-15	19	10-20	1	-	0	0
(Selfia)																				
brookmani	0	0.95	0.53	1,(2),(3),(4),5-8	1,(3),(4),6,8	4 (5)	+	0	0	0.5-1.2	0.93	1.9	0.77	10-12	12-15	4	0	-	0	0
denningi	0	1.17	0.57	1,(4),5-8	1,6,8	4 (5)	+	+	0	1.2-2.3	1.02	2.7	0.88	11-13	14-18	8	0	-	0	0
hieroglyphicus	0	1.14	0.56	1,(2),(3),4-8	1,(4),6,8	4 (5)	+	+	0	0.5-1.1	1.03	2.1	0.84	11-14	14-17	10-14	0	-	0	0
jacksoni	0	1.16	0.54	1,(2),3-8	1,(2),(3),(4),6,8	4	+	+	0	0.8-1.1	0.93	2.2	0.81	11-13	13-16		0	-	0	0
jamesi	0	1.21	0.56	1,(2),3-8	1,(3),(4),6,8	4 (5)	+	+	0	0.9-1.5	1.00	2.5	0.88	11-13	15-17	8-12	0	-	0	0
moabensis	0	1.00	0.53	1,(2),3-8	1,(2),(3),4,6,8	4	+	0	0	0.1-0.9	0.96	1.9	0.8	10-13	12-15	8	0	-	0	0
tenuistylus	0	1.26	0.58	1,(2),3-8	1,5-8	4 (5)	+	+	0	1.2-1.8	1.00	2.2	0.79	11-13	15-17	8-10	0	-	0	0
(Sensiculicoides)																				
kibunensis	+	1.43	0.59	1-13	1,(2),(11),12,13	4 (5)	0	0	0	0.3-1	1.39	2.3	0.85	11-15	17-25	12-19	2v	1.00	0 (+)	+
travisi	+	1.35	0.62	1-13	1,11-13	4 (5)	0	0	0	1	1.52	2.5	0.86	14-15	23-24	10-16	2v	1.20	0	+
(Silvaticulicoides)																				
sublettei	++	1.19	0.55	1,(4),(5),(6),(7),(8),(9),10-13	1,12,13	4	0	0	0	0.2	1.07	2.4	0.95	14-16	17-21	8-9	2v	1.00	+	0 (+)
usingeri	+	1.32	0.57	1,(5),(6),(7),(8),9-13	1,12,13	4 (5)	0	+	0	0.7	1.05	2.2	0.79	15	19	15	2v	1.06	+	0 (+)
vetustus	+	1.24	0.54	1, (9),(10),11-13	1,12,13	4 (5)	0	0	0	1	0.97	2.1	0.95	14-15	18-19	10-14	2v	1.05	+	0
(Silvicola)																				
cockerellii	+++	1.87	0.62	1,9-13	1,11-13	6 (7)	+	+	0	0	1.03	2.7	0.95	13-16	20	10	2v	1.00	++	+
freeborni	+++	1.58	0.59	1,(7),9-13	1,11-13	6 (7)	+	0	0	0	0.97	2.2	0.75	13-17	17-20	12-16	2v	1.03	+	+
lahontan	+++	1.71	0.61	1,(8),9-13	1,(9),11-13	6 (7)(5)	0	0	0	0	0.98	2.1	0.80	12-17	15-19	6-12	2v	1.00	+	+
neofagineus	+++	1.55	0.61	1,(8),9-13	1,11-13	6 (7)	0	0	0	0	0.87	2.8	0.82	13-16	20	14	2v	1.10	+	+
neomontanus	++	1.83	0.61	1,(2),(3),(4),(5),(6),(7),(8),9-13	1,11-13	6 (7)	+	+	0	0	1.02	2.7	0.80	12-17	20-23	10	2v	1.00	++	+
saltonensis	+++	1.80	0.61	1,(5),(7),(8),9-13	1,11-13	6 (7)	0	0	0	0-0.1	0.94	2.2	0.77	14	17	10-12	2v	1.06	++	+
sierrensis	+++	1.93	0.60	1,(5),(7),9-13	1,11-13	6 (7)	+	+	0	0	1.03	3.0	1.00	13-16	18-20	12	2v	1.10	++	+
tristriatulus (r)	+++	2.20	0.65	1,9-13		6 (7)			0	>1	1.11	4.2	0.85	11-17			2v	1.03	++	+
species D	+++	2.06	0.60	1,(5),(6),(7),(8),9-13		6	+	+	0	0	0.89	2.8	0.87	15-16	15-16	12	2v	1.14	++	+
species E	+++	1.99	0.60	1,9-11,?,?		6	+	+	0	0	-	2.2	0.78	14	16	14	3	-	++	+
(Wirthomyia)																				
bottimeri	0	0.99	0.53	1,(2),3,(4),5-8	1,(5),6-8,(9),(10)	5 (6)	+	0 (+)	0	0-0.6	0.98	2.1	0.65	9-16	25-37	9-12	2v	1.21	+	0
Daedalus group																				
daedalus (r)	+++	1.01	0.62	1,9-13		4			0	0	1.34	2.0	0.68	12-13			2v	1.18	+	
pampoikilus	+++	1.52	0.54	1,(2),3,(4),5,(6),7,9-13	1,12,13	4	0	0	0	0-0.1	1.55	1.9	0.72	14-15	23	18	2v	1.12	+	0
Leoni group																				
reevesi	+++	0.75	0.56	1,6-8	1	4	0	0	+	1-1.5	0.70	2.0	0.90	16-19	13-16	4-6	1v	-	+++	+

Culicoides	Wing			Sensilla (SCo) pattern		Apical spines			Eye		Antennal ratio	Palpal ratio	Proboscis ratio	Teeth		Scutellar setae	Sclerotized spermathecae			
	Pattern	Female		Female	Male	Tibial comb	Tarsomeres		hair	separation				mandibular	lacinial		n	ratio	neck	ring
		mm	costal ratio				fore	hind												
Limai group																				
luglani	+++	1.22	0.53	1,(2),(3),4-8,(9)	1,(7),8-10	4	0	0	0	0.1	0.95	2.1	0.95	13-16	21	8-18	2v	1.10	+++	+
Mohave group																				
hoguei (r)	++	1.22	0.57	1,(5),6-8	1,6-10	4			0	2	0.89	2.5	0.94 (0.74)	13 (18)			2v	1.00	+++	+
mohave	++	1.09	0.54	1,(4),(5),6-8	1,6-8,(9),(10)	4	0	0	0	0.5	1.11	2.1	0.67	14	18-19	6-8	2v	1.14	+++	+
Palmerae group																				
calexicanus	+++	1.34	0.54	1,3,5,(6),7,9,11-13	1,(2),11,12	4	+	+ (0)	0	1-2	1.05	2.2	0.75	12-16	15-19	13-17	2v	1.10	+	0
hawsi	+	1.31	0.59	1,(2),3,(4),5,(6),7,(8),9-13	1,(2),(4),11,?	4	+	+	0	1-1.5	1.65	2.4	0.77	14-15	22-25	8-20	2v	1.43	0 (+)	+
leechi (r)	+	1.61	0.59	1-13	1-13	4			0	2	1.18	2.2	0.90	15			2v	1.00	+	0
novamexicanus (r)	+++	1.23	0.56	1,(2),3,(4),5,7,9,(10),11-13		4			0	1.8	1.02	2.2	0.92	14-16			2v	1.00	+	0
oregonensis (r)	+	1.58	0.57	1-13		4			0	1-2	1.23	2.4	0.86	16			2v	1.00	0	0
palmerae	+++	1.44	0.56	1-13	1,2,(3),(4),(5),11-13	4 (5)	+	+	0	1-1.5	1.26	2.3	0.72	13-16	21-26	14-16	2v	1.03	0	0 (+)
utahensis	++	1.47	0.57	1-5,(6),7,(8),9,(10),11-13	1-12	4	+ (0)	+ (0)	0	1-1.5	1.20	2.0	0.80	14	23-25	12-14	2v	1.01	+	0 (+)
species C	++	1.10	0.54	1,3,5,7,9,(10),11-13		4	+	0	0	1.5	1.14	2.0	0.68	8	13	12	2v	1.03	+	0
Piliferus group																				
cavaticus	+++	1.60	0.56	1-13	1,12,13	4-5	0	0	0	1-2	1.00	2.2	0.99	15-18	23	26-30	2v	1.07	0	+
chewaclae	+	0.95	0.61	1,3,5,7,(9),11-13		4	0	0	0	0.5	1.36	2.1	0.58	13-15	20	10	2v	1.32	0	+
doeringae	+++	1.28	0.57	1,3,5,7,(9),(10),11-13	1,12,13	4	0	0	0	0.2-1.0	1.59	2.6	0.88	12-15	21-26	8-10	2v	1.39	0 (+)	+
lophortygis (r)	++	1.16	0.58	1,3,(5),(7),11-13		4			0	>1	1.50	2.9	0.96	13-15	22-26		2v	1.31	+	+
unicolor	0 +	1.37	0.56	1, 11-13		5	0		0	0	1.08	2.4	0.75	11	17	9	2v	1.01	+	+
species A	+	1.13	0.59	1,3,5,7,9,(10),11-13	1,12,13	4	0	0	0	0.5-0.8	1.53	2.3	0.71	11-15	18-23	9-12	2v	1.32	+	+
species B	++	1.35	0.60	1,3,5,(6),7-13		4	0	0	0	0.1-0.3	1.57	2.2	0.74	12-15	19-23	9-14	2v	1.39	0 (+)	+
Saundersi group																				
atchleyi	0	1.95	0.66	1,9-13		5 (4)	0	+	+	0.7-0.9	1.14	2.2	0.65	0 (7)	0	8	2v	1.00	+	+
saundersi (r)	0	2.30	0.66	1,9-13		6			+	1-2	1.06	2.9	0.93	14-20			2v	1.00	+	+
Stonei group																				
mortivallis	0	1.02	0.58	1,(5),6-12	1,8,11,12	4	+	+	0	1.5	1.12	2.2	0.79	12	15-16	10-12	2v	1.00	++	0
owyheensis	0	1.10	0.60	1,5-12		4	+	+	0	1.5	1.00	2.2	0.83	11-13	16-18	10-11	2v	1.00	++	0
stonei	0	1.15	0.57	1,(2),3-12		4	+	+	0	1.5	1.13	2.5	0.86	12	17	9-11	2v	1.00	++	0
werneri	0	1.08	0.57	1,(5),(7),8-12	1,8,11,12	4	+ (0)	+ (0)	0	1-1.5	1.02	2.1	0.79	11-13	15-17	11-13	2v	1.15	++	0
unplaced																				
monoensis (r)	0	1.15	0.53	1,12-13					0	wide	0.97	3.0	0.69				2v		0	+
nanellus (r)	++	1.10	0.63	1-5,7,9-13		5			0	~0.5	1.02	2.0	0.68	11			2v	1.06	0 (+)	+
posoensis	+	0.99	0.57	1,9-13	1,11-13	4	0	0	0	2	1.10	2.6	0.78	11-13	16	10	2v	1.00	+	+
species F	+	1.42	0.60	1,3,5,7,(8),9,11-13		4	+	+	0	0.5	1.80	2.2	0.62	13	21	12	2v	1.4	+	+

Table 15. Pale leg-banding on *Culicoides*. ++ = distinct, + = faint or indistinct, ± = faint to absent, ? = undetermined. Shading indicates darker pigmentation. Data for species marked (r) are compiled from the literature.

Culicoides	Fore femur		Fore tibia		Mid femur		Mid tibia		Hind femur		Hind tibia	
	basal	apical	basal	apical	basal	apical	basal	apical	basal	apical	basal	apical
Amossovia												
californiensis	++	++	++	++	++	++	++	++	++	++	++	++
cochisensis	++	++	++		+	+	++				++	++
oklahomensis	+	++	++		+	++	++		+	+	++	++
pecosensis	++	++	++		++	++	++		+	++	++	++
(Avaritia)												
boydi												
chiopterus												
obsoletus			±				±				±	
sanguisuga (r)			±				±				±	
(Beltranmyia)												
crepuscularis	++	++	++		±		++				++	
(Diphaomyia)												
bergi	++	++	++			++	++				++	+
defoliarti	++	++	++		+	+	++		+		++	±
erikae	+	+	++	+			++				++	
haematopotus	++	++	++	+	+	++	++	±	++		++	++
inyoensis	+		++		+		++				++	+
salihi	+	+	+		+		+		+		+	
(Drymodesmyia)												
arizonensis	+		+				+				+	
bakeri	+	++	++		+	+	++		+		++	
butleri	+	++	++		+	±	++		+	±	++	
byersi	+	++	++		+		++				++	
cacticola	+	++	++	±	+	+	++	±	+		++	±
copiosus	+	++	++				++				++	
hinmani	+	+	+		+	+	+		+	+	+	+
insolatus	+	++	++		±		++				++	
jonesi	+	++	++		+	±	++		+	±	++	
ryckmani	+	+	+				+				+	
sitiens	+	++	++		+	+	++		+	±	++	
torridus	+	++	++		+	++	++		+		++	
(Haematomyidium)												
kettlei	+	++	++	+	+	++	++		+		++	++
stellifer	++	++	++	+	+	++	++	±	+		++	++
(Monoculicoides)												
grandensis	+											
occidentalis	++	++	++		+	++	++		+		++	
sonorensis	++	++	++		+	++	++		+		++	
(Selfia)												
brookmani			±									
denningi	+	+	+									
hieroglyphicus	+	+	+				±				+	
jacksoni	+	+	+									
jamesi	±	+	±									
moabensis												
tenuistylus			+									
(Sensiculicoides)												
kibunensis	+	+	+		+		+		+		+	
travisi	+	+	++		+		++		+		+	
(Silvaticulicoides)												
sublettei	+	+	+		+		+				+	

Culicoides	Fore femur		Fore tibia		Mid femur		Mid tibia		Hind femur		Hind tibia	
	basal	apical	basal	apical	basal	apical	basal	apical	basal	apical	basal	apical
usingeri	+	+	+		±		+				+	
vetustus	+	+	±		±							
(Silvicola)												
cockerellii	+										±	
freeborni	+											
lahontan	±											
neofagineus	+										++	
neomontanus	±										±	
saltonensis	±				±							
sierrensis	+				+		±				++	
tristriatulus (r)	?											
species D	+				+						±	
species E	+											
(Wirthomyia)												
bottimeri			+									
Daedalus group												
daedalus (r)	?	++	++		?	++	++		?	±	++	±
pampoikilus	+	++	++		+	+	++		+		++	
Leoni group												
reevesi	+	+	++		+	+	++		++		++	+
Limai group												
luglani	+	++	++		+	++	++		+	++	++	++
Mohave group												
hoguei (r)	?	?	+				+				+	
mohave	+	±	+				+				+	
Palmerae group												
calexicanus	+		+				+				+	
hawsi	+	+	+				+				+	
leechi (r)	?											
novamexicanus (r)	+		+				+				+	
oregonensis (r)	?											
palmerae	+	+	+			±	+				+	
utahensis	+	±	+				+				+	
species C	+	+	+				+				+	
Piliferus group												
cavaticus	+	±	++		+		++		+		++	
chewaclae	±	+	+		±	±	+				+	
doeringae	++	++	++		+	±	++		++		++	
lophortygis (r)	?	++	++		?	?	++				++	
unicolor	±				±				±			
species A	++	++	++		++	++	++		++		++	
species B	±	++	++		+	+	++		±		++	+
Saundersi group												
atchleyi		+	+				+				+	
saundersi (r)		?	?				?				?	
Stonei group												
mortivallis									±			
owyheensis									±			
stonei												
werneri	±		±	±	±				±			
unplaced												
monoensis (r)												
nanellus (r)			+				+				+	
posoensis			+				+		±		+	
species F	+	+	++		+	+	+				+	

Table 16. Comparison of SCo pattern, wing pattern, and eye separation on *Culicoides doeringae*. Parentheses indicate SCo on only one antenna. Eye separations are in ommatidium diameters. An x indicates the number of specimens with the same eye separation.

SCo pattern	n	Eye separation		
		with less distinct wing	with more distinct wing	
1, 3, 5, 7, 11–13	4	0.5 x2	0.1	1.0
1, 3, 5, 7, (9), 11–13	2	0.1	0.3	
1, 3, 5, 7, 9, 11–13	3		0.2	0.3
			0.5	
1, (3), (4), 5, 7, 9, 11–13	1		0.1	
1, 3, 5, 7, 9, (10), 11–13	1		1.0	
1, 3, 5, 7, 9–13	16	0.1	0.2 x2	0.3 x3
		0.2	0.5 x3	0.7 x3
		0.3	0.9	1.0

Table 17. Sensilla coeloconica patterns on Stonei group females. The dashed lines represent species divisions. Specimens with a 1–12 pattern on one antenna or with an equivalent reduction of 0–2 SCo from the basic 1–12 pattern were identified as *C. stonei.* Those with a 1, 5–12 pattern on one antenna, or were identified by ratios (Table 18), or had equivalent SCo reductions were identified as *C. mortivallis* or *C. owyheensis.* Those with a 1, 7–12 or more reduced pattern were identified as *C. werneri.* Others were not determined.

SCo pattern combinations	Reduction from 1–12 pattern	n	State
1–12 + 1–12	0	2	UT
1–12 + 1, 4–12	2	1	UT
1, 3–12 + 1, 3–12	2	3	UT
1, 3–12 + 1, 3, 5–12	3	1	UT
1, 3–12 + 1, 4–12	3	3	UT
1, 2, 4–12 + 1, 5–12	4	1	UT
1, 3, 5–12 + 1, 3, 5–12	4	4	UT
1, 3, 5–12 + 1, 4–12	4	1	UT
1, 3–12 + 1, 5–12	4	2	UT
1, 4–12 + 1, 4–12	4	9	UT
1, 3, 5–12 + 1, 4, 6–12	5	1	UT
1, 3, 5–12 + 1, 5–12	5	2	UT
1, 4–12 + 1, 5–12	5	8	UT
1, 5–12 + 1, 5–12	6	39	UT
1, 5–12 + 1, 5, 7–12	7	1	UT
1, 5–12 + 1, 6–12	7	3	AZ, UT
1, 5, 7–12 + 1, 5, 7–12	8	1	UT
1, 6–12 + 1, 6–12	8	1	UT
1, 5, 8–12 + 1, 8–12	11	1	AZ
1, 8–12 + 1, 8–12	12	2	AZ

Table 18. Identification of Stonei group females based on measurements and ratios. Specimens have SCo patterns for *C. mortivallis* and *C. owyheensis*. Column headings: (f7+f8)/f9 is lengths of flagellomeres 7+8 divided by the length of flagellomere 9; prob/f9 is length of proboscis divided by length of flagellomere 9; palp/f9 is length of palpal segment 3 divided by length of flagellomere 9. Wing length was not used for species determination. Ratios are equally weighted for calculation of mean variation, which is the criterion for species determination. Daggers (†) indicate data that are anomalous for the species determinations. Asterisks (*) indicate specimens with SCo patterns exactly between the ideal for *C. stonei* (1–12) and *C. mortivallis*/*owyheensis* (1, 5–12).

Wing length mm	Ratios			Mean variation of ratios	Determination	Collection date	Week
	(f7+f8)/f9	palp/f9	prob/f9				
Random Grand County, Utah, specimens with SCo pattern 1,5–12:							
1.07†	1.37	1.62	3.51	−0.115	*C. mortivallis*	2 Sep 2003	35
1.09†	1.32	1.71	3.67	−0.097	*C. mortivallis*	29 Aug 2000	35
1.00	1.44	1.58	3.88	−0.075	*C. mortivallis*	16 Sep 2003	37
1.05	1.36	1.86	3.61	−0.067	*C.mortivallis*	2 Sep 2003	35
1.02	1.33	1.86	3.75	−0.062	*C. mortivallis*	12 Sep 2006	37
1.02	**1.40**	**1.80**	**3.70**	**−0.061**	***mortivallis* criteria** (Jones & Wirth 1978)		
1.02	1.46	1.71	3.89	−0.047	*C. mortivallis*	5 Sep 2006	36
1.01	1.44	1.85	3.71	−0.042	*C. mortivallis*	31 Aug 2010	35
1.07	1.51	1.88	3.94	−0.002	intermediate	6 Sept 2000	36
1.06	**1.50**	**1.90**	**3.95**	**0.000**	**median of criteria**		
1.13	1.59	1.94	3.86†	0.019	*C. owyheensis*	2 Sep 2003	35
1.07	1.67	1.91	4.03	0.046	*C. owyheensis owyheensis*	20 Sep 2001	38
1.10	**1.60**	**2.00**	**4.20**	**0.061**	***owyheensis* criteria** (Jones & Wirth 1978)		
* Utah specimen with nematode and protozoan parasites (SCo patterns 1,3–12 and 1,4–12):							
1.29†	1.46	1.85	3.82	−0.030	*C. mortivallis* *	7 May 2002	19
Utah specimen with 3 spermathecae (SCo patterns 1,3–12 and 1,5–12):							
1.34†	1.35	1.70	3.84	−0.079	*C. mortivallis*	27 May 2003	21
Utah specimen with mite larva (SCo pattern 1,6–12):							
-	1.46	1.85	3.97†	−0.017	*C. mortivallis*	23 Jun 2004	25
Utah specimen with nematode and protozoan parasites (SCo pattern 1,5–12):							
1.20†	1.45	1.82	3.91	−0.030	*C. mortivallis*	20 Jun 2002	25
Utah specimen with abdominal infection (SCo pattern 1,5–12):							
1.11	1.53	1.81	4.00	−0.006	intermediate	2 Jul 2002	27
* Utah specimen reared from mud from alkaline pool (SCo patterns 1,3–12 and 1,4–12), associated with male:							
1.22†	1.47	1.63	3.75	−0.072	*C. mortivallis* *	17 Sep 2020	38
Arizona specimen (SCo patterns 1,5–12 and 1,6–12):							
0.94	1.46	1.76	3.88	−0.038	*C. mortivallis*	10 Oct 2019	41

Table 19. Species for which data on immatures and their habitats and life cycles have been reported. X = substantial information. M = minimal details. U = uncertain identification. Consult the species accounts for details and references.

Species	Immature's habitat	Descriptions			Life cycle
		egg	larva	pupa	
Leptoconops					
(Brachyconops)					
californiensis					
(Holoconops)					
belkini					
Kerteszi group					
americanus	X	X	X	X	X
andersoni					
arnaudi	X	X	X	X	X
asilomar	X			X	
atchleyi					
foulki	X				U
knowltoni	X				U
reesi					U
sublettei					
whitseli	X			X	
(Leptoconops)					
carteri	X	X	X		X
freeborni					
mohavensis					
torrens	X				X
(Proleptoconops)					
werneri					
Culicoides					
(Amossovia)					
californiensis	X		X	X	
cochisensis	X		X		
oklahomensis	X		X	X	
pecosensis					
(Avaritia)					
boydi		X	X	X	X
chiopterus	X		X	X	
obsoletus	X	X	X	X	
sanguisuga	X		X	X	X
(Beltranmyia)					
crepuscularis	X		X	X	
(Diphaomyia)					
bergi	X			X	
defoliarti	X			X	
erikae	M			X	
haematopotus	X		X	X	
inyoensis					
salihi					
(Drymodesmyia)					
arizonensis	X				
bakeri					
butleri					
byersi	X				
cacticola	X	X	X	X	X
copiosus	X				
hinmani	X		X	X	
insolatus	X				
jonesi	X		X		
ryckmani	X				
sitiens	X				
torridus	X				
(Haematomyidium)					
kettlei	X	X	X	X	X
stellifer	X		X	X	X
(Monoculicoides)					
grandensis	X			X	
occidentalis	X		X	X	
sonorensis	X	X	X	X	X
(Selfia)					
brookmani	X	X	X	X	X
denningi	X		X	X	
hieroglyphicus	X		X	X	
jacksoni	X		X	X	X
jamesi	X		X	X	
moabensis					
tenuistylus	X		X	X	
(Sensiculicoides)					
kibunensis	U		X	X	
travisi	X		X	X	
(Silvaticulicoides)					
sublettei	X				
usingeri					
vetustus		X	X	X	X
(Silvicola)					
cockerellii					
freeborni	X	X	X	X	X
lahontan	X	X	X	X	X
neofagineus	X		X		
neomontanus	X	X			
saltonensis					
sierrensis					
tristriatulus	X	X	X	X	X
(Wirthomyia)					
bottimeri					
Daedalus group					
daedalus					
pampoikilus					
Leoni group					
reevesi					
Limai group					
luglani					

Species	Immature's habitat	Descriptions			Life cycle
		egg	larva	pupa	
Mohave group					
hoguei					
mohave	X		M		
Palmerae group					
calexicanus					
hawsi					
leechi					
novamexicanus					
oregonensis					
palmerae					
utahensis		X			
Piliferus group					
cavaticus	X		X	X	
chewaclae					
doeringae					
lophortygis					
unicolor					
Saundersi group					
atchleyi					
saundersi					
Stonei group					
mortivallis	X			U	
owyheensis					
stonei	X			X	
werneri					
unplaced					
monoensis					
nanellua	X				
posoensis					

Table 20. Vertebrate hosts. Only the midge species that have host records were included. Host species and references are in the individual midge species accounts. X = midges collected from a host, or the host was identified by blood meal analysis. N = midges collected from a possible host's nest. O = only swarming around a possible host. U = an uncertain midge identification.

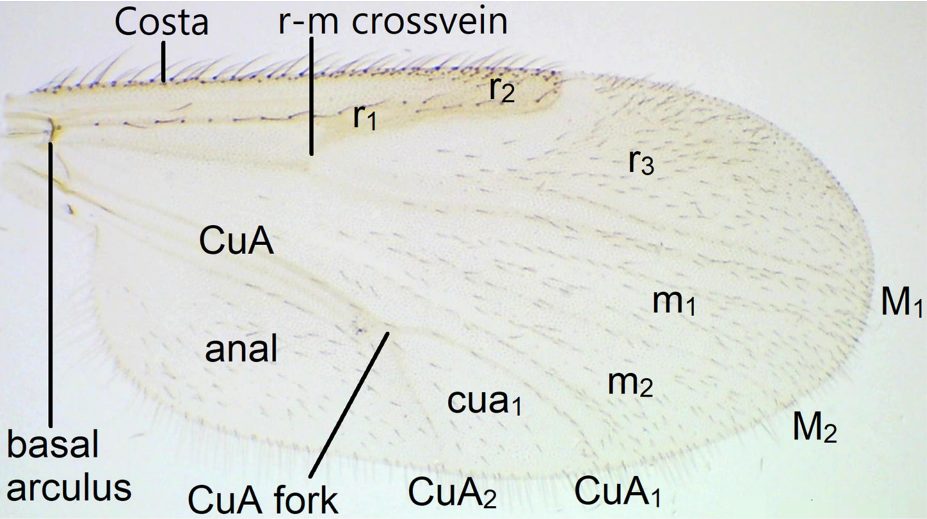
	Aves											Mammalia													Reptilia
								Passeriformes				Ungulata			Carnivora			Glires				Chiroptera	Primates	Marsupialia	
Species	Accipitridae	Anatidae	Columbidae	Odontophoridae	Phasianidae	Picidae	Strigidae	Corvoidea	Muscicapoidea	Passeroidea	Sylvioidea	Bovidae	Cervidae	Equidae	Canidae	Felidae	Procyonidae	Cavidae	Leporidae	Muridae	Sciuridae	Vespertilionidae	Hominidae	Didelphidae	Phrynosomatidae
Leptoconops																									
(Brachyconops)																									
californiensis																							O		X
(Holoconops)																									
belkini					X							X							X						
Kerteszi group														X									X		
americanus	N											X	X					X	X				X		
andersoni												X	X												
arnaudi															X	X							X		
asilomar																							X		
atchleyi												X													
foulki					X							X							X	X			X		
knowltoni												X		X					X				X		
reesi												X											X		
sublettei								N				X	X										X		
(Leptoconops)																									
carteri																							X		
torrens												X		X									X		
(Proleptoconops)																									
werneri				X																			X		
Culicoides																									
(Avaritia)																									
boydi												X											X		
chiopterus					X							X	X	X									X		
obsoletus					X							X	X	X					X	X	X		X		
sanguisuga		X	X	X				X		X		X		X				X	X	X		X	X	X	
(Beltranmyia)																									
crepuscularis		X	X	X	X	X	X	X	X	X		X					X	X	X	X	X		X		
(Diphaomyia)																									
bergi				X																					
haematopotus		X	X	X	X			X		X		X	X					X	X	X			X	X	
(Drymodesmyia)																									
cacticola					X							X													
hinmani					X													X	X	X			X		
ryckmani											N														
sitiens					X														X						

	Aves										Mammalia												
							Passeriformes				Ungulata				Carnivora		Glires				Primates		Marsupialia
Species	Accipitridae	Anatidae	Casuariidae	Columbidae	Odontophoridae	Phasianidae	Corvoidea	Muscicapoidea	Passeroidea	Sylvioidea	Bovidae	Cervidae	Equidae	Suidae	Canidae	Procyonidae	Caviidae	Leporidae	Muridae	Sciuridae	Cercopithecidae	Hominidae	Didelphidae
(Haematomyidium)																							
kettlei											X												
stellifer						X	X				X	X				X	X	X		X		X	X
(Monoculicoides)																							
occidentalis											X	X	X	X	X			X					
sonorensis			X			X					X	X	X	X	X		X	X	X		X	X	
(Selfia)																							
brookmani											X	X						X					
denningi											U		X									X	
hieroglyphicus											U		X					X					
jamesi											X		X										
tenuistylus					X							X						X					
(Sensiculicoides)																							
kibunensis	N			X		X		X	X	X	X			X								X	
travisi		X		X	X	X			X		X		X				X	X	X			X	X
(Silvaticulicoides)																							
sublettei													X										
(Silvicola)																							
cockerellii											X											X	
freeborni												X						X					
lahontan											X												
neofagineus					X							X										X	
neomontanus											X		X					X				X	
tristriatulus																						X	
(Wirthomyia)																							
bottimeri					X																		
Leoni group																							
reevesi												X										X	
Mohave group																							
hoguei																						X	
mohave						X					X												
Palmerae group																							
utahensis											X	X						X		X			
Piliferus group																							
cavaticus					X																		
lophortygis					X																		
Saundersi group																							
saundersi							N															X	
Stonei group																							
mortivallis											U											X	
owyheensis											X												
stonei											U	X											
werneri																		X					

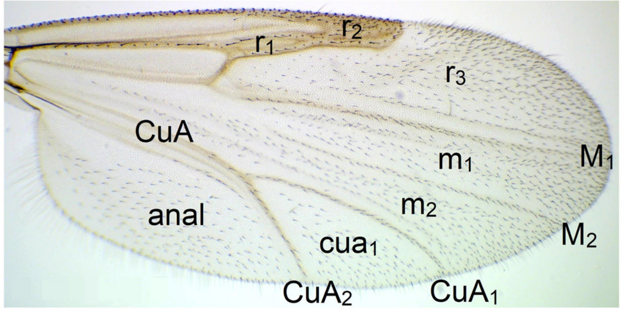
1 *L.* (*Holoconops*) sp. ♀

2 *C. sonorensis* ♀

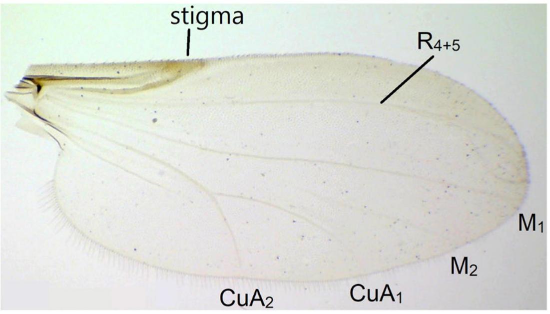
Figures 1–2. Female lateral habitus (in alcohol). **1)** *Leptoconops* (*Holoconops*) Kerteszi group. **2)** *Culicoides* (*Monoculicoides*) *sonorensis*.



3 *C. stonei* ♀



4 *C. atchleyi* ♀



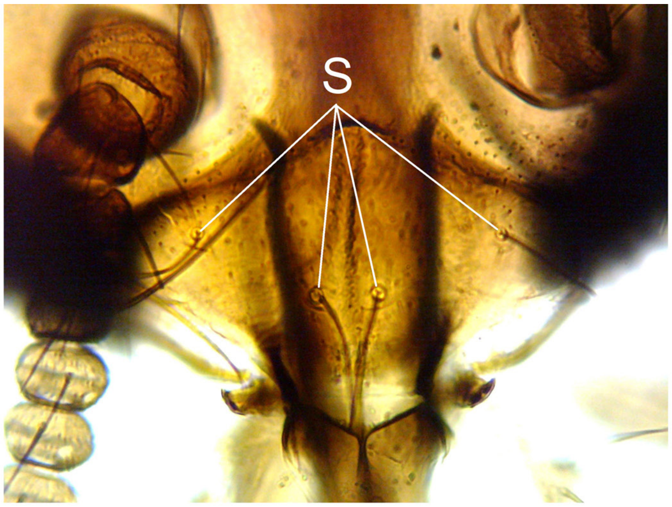
5 *L. torrens* ♀

6 *L. torrens* ♀

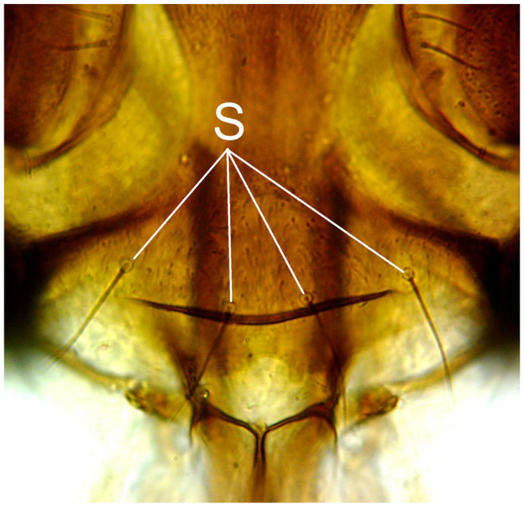
7 *C. stonei* ♀

8 *L. californiensis* ♀

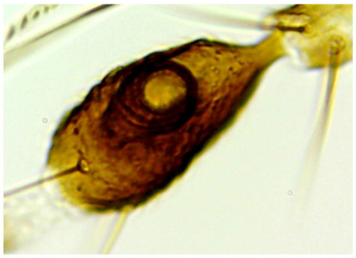
Figures 3–8. Female wings with cells (lower case) and veins (upper case) labeled. **3)** *Culicoides stonei*. **4)** *C. atchleyi* (Bonneville County, ID). **5)** *Leptoconops torrens*. Female abdomen, ventral view. **6)** *L. torrens*. **7)** *C. stonei*. **8)** *L. californiensis*, dorsal habitus (in alcohol, Yuma County, AZ [Carl Olson, with permission]).



9 *L. americanus* ♀



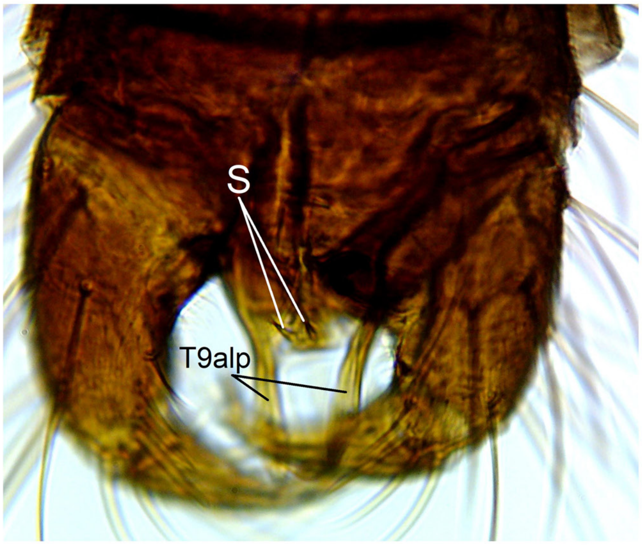
10 *L. knowltoni* ♀



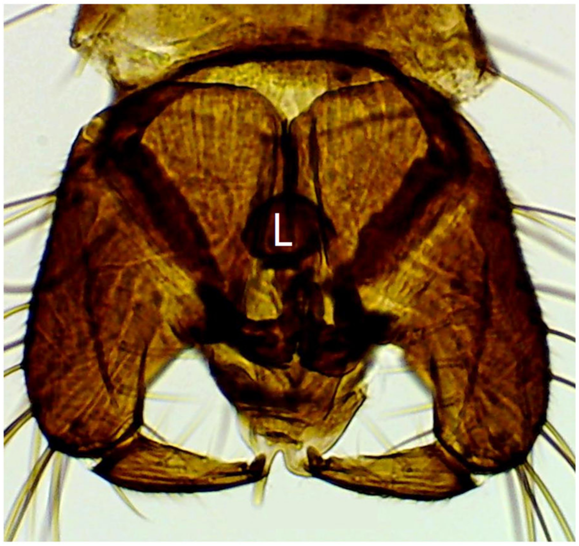
11 *L. knowltoni* ♀

12 *L. carteri* ♀

13 *L. werneri* ♀



14 *L. werneri*

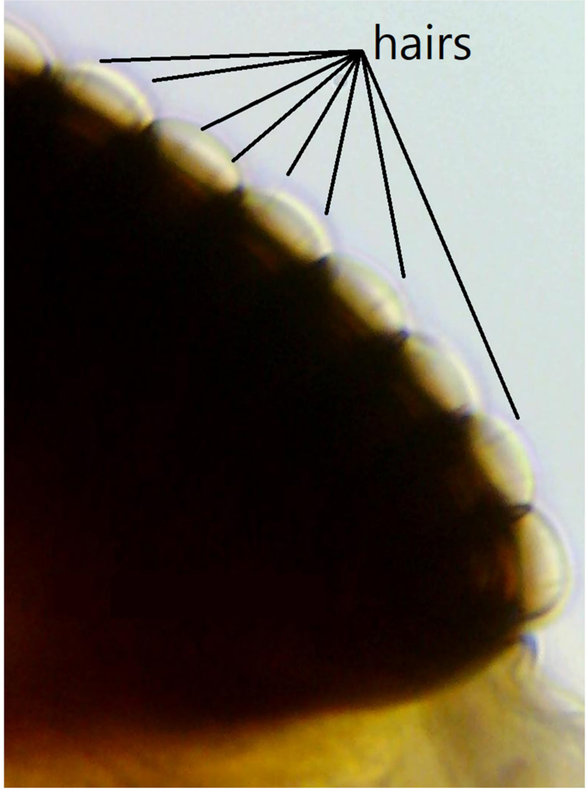


15 *L. belkini*

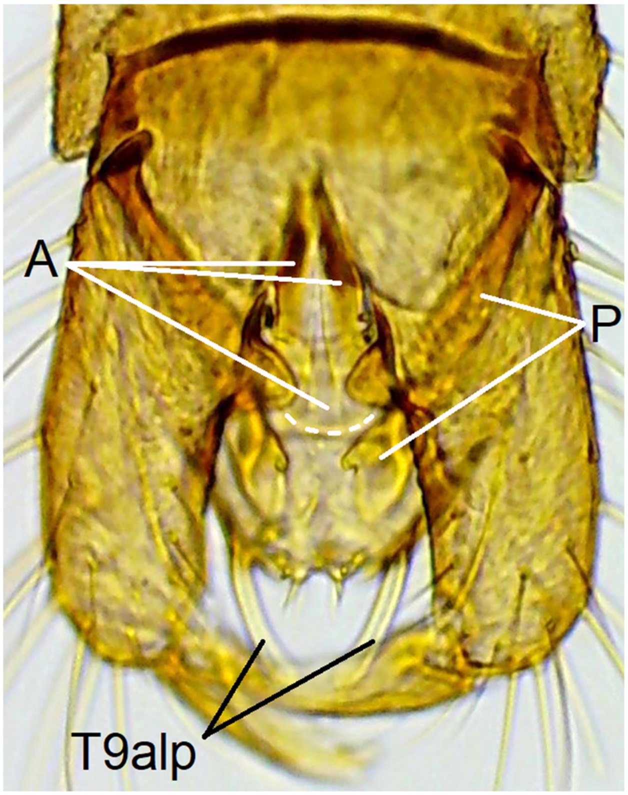
Figures 9–15. 9) *Leptoconops americanus* female clypeus, setae (s). **10)** *L. knowltoni* female clypeus. **11)** *L. knowltoni* female palpal segment 3. **12)** *L. carteri* female palpal segment 3 (Yolo County, CA). **13)** *L. werneri* female tarsomeres 4–5 and claw (paratype, Imperial County, CA [UCRC]). **14)** *L. werneri* male genitalia, ventral view, tergite 9 apicolateral processes (T9alp), meso-posterior lobe setae (s) (Riverside County, CA [UCRC]). **15)** *L. belkini* male genitalia, ventral view, tergite 9 sclerotized lobe (L) (Riverside County, CA [UCRC]).

16 *L. carteri*

17 *L. carteri*

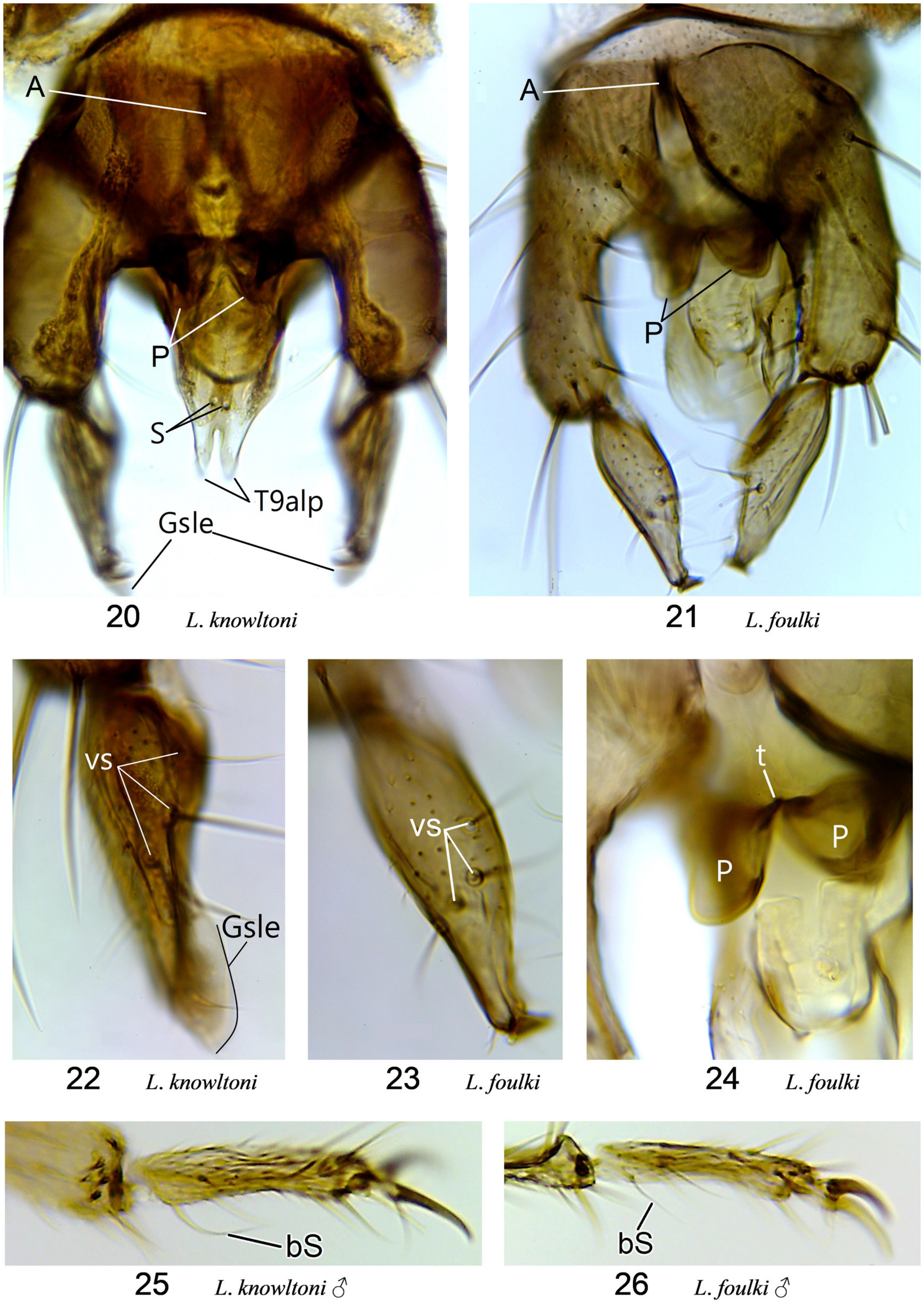


18 *L. carteri* ♀



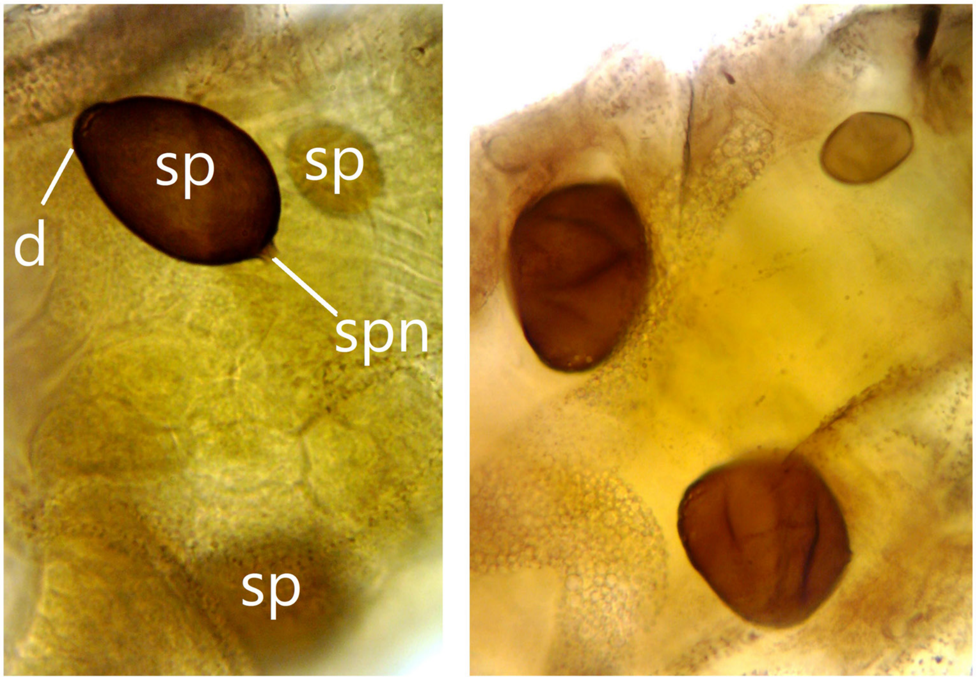
19 *L. carteri*

Figures 16–19. *Leptoconops carteri* (Yolo County, CA). **16)** Female terminalia with normal spermathecae. **17)** Variant with spermathecae similar to those more typical of *L. torrens*. **18)** Lateral view of lower portion of eye showing interommatidial pubescence. **19)** Male genitalia, ventral view, proximal sclerites and distal shieldlike fusion of the aedeagus (A), proximal and distal sclerites of a paramere (P), tergite 9 apicolateral processes (T9alp).



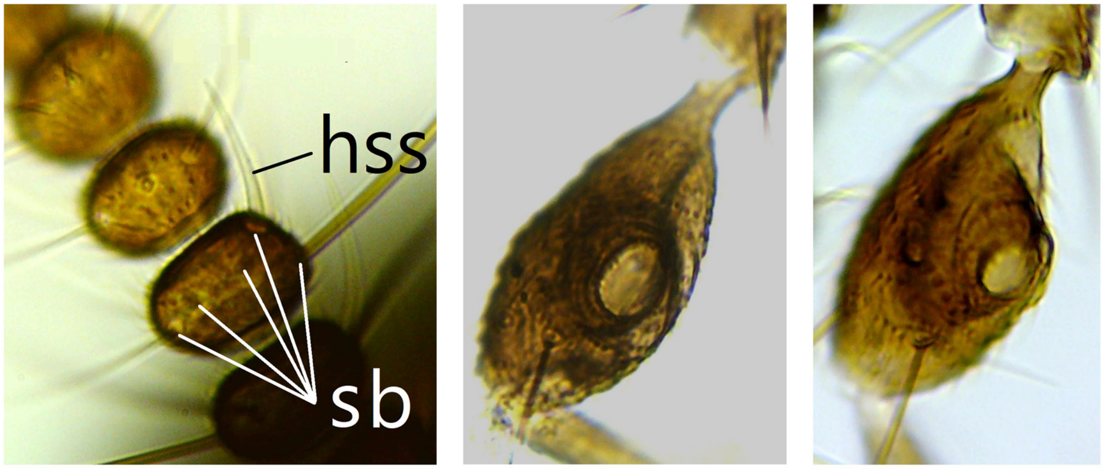
Figures 20–26. 20) *Leptoconops knowltoni* male genitalia, ventral view, aedeagus (A), parameres (P), tergite 9 ventro-posterior setae (s), apicolateral processes (T9alp), gonostylus apical lamelliform expansion (Gsle). **21)** *L. foulki* male genitalia, ventral view. **22)** *L. knowltoni* gonostylus, ventral setae (vs). **23** *L. foulki* gonostylus. **24)** *L. foulki* parameres (P), proximal tooth (t). Male tarsomere 5, basal seta (bS). **25)** *L. knowltoni*. **26)** *L. foulki*.

27 *L. knowltoni* ♀



28 *L. foulki*

29 *L. americanus*



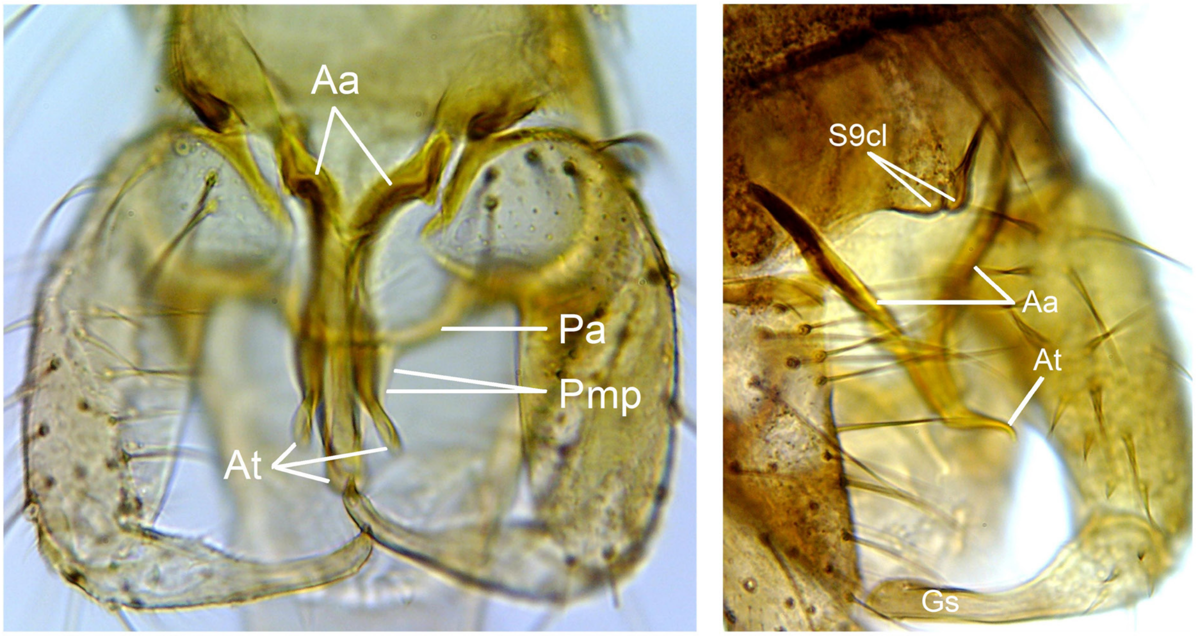
30 *L. sublettei* ♀

31 *L. sublettei* ♀

32 *L. foulki* ♀

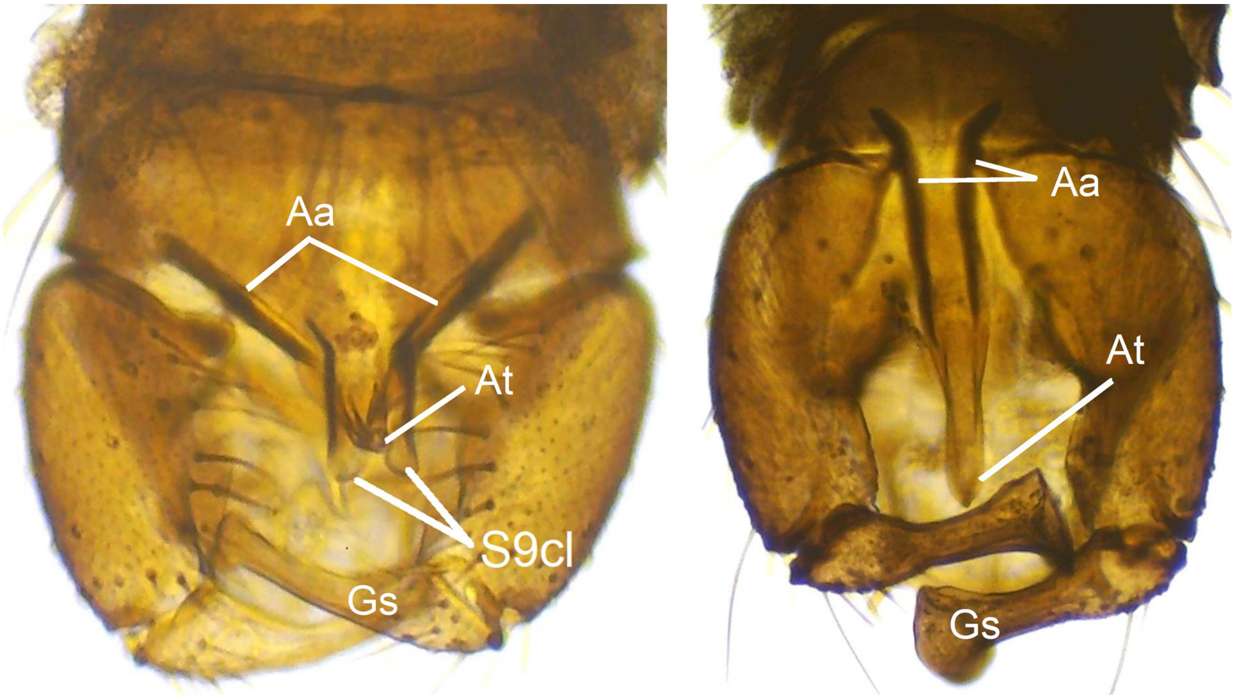
Figures 27–32. Female *Leptoconops*. **27)** *L. knowltoni* flagellomeres 9–11, median black seta (s). Spermathecae (sp), diverticulum (d), neck (spn). **28)** *L. foulki*. **29)** *L. americanus*. **30)** *L. sublettei* flagellomeres 3–6, flagellomere 4 seta bases (sb), hyaline sensory seta (hss). Palpal segment 3. **31)** *L. sublettei*. **32)** *L. foulki*.

33 *C.* (*Selfia*) sp. ♀ 34 *C. brookmani*

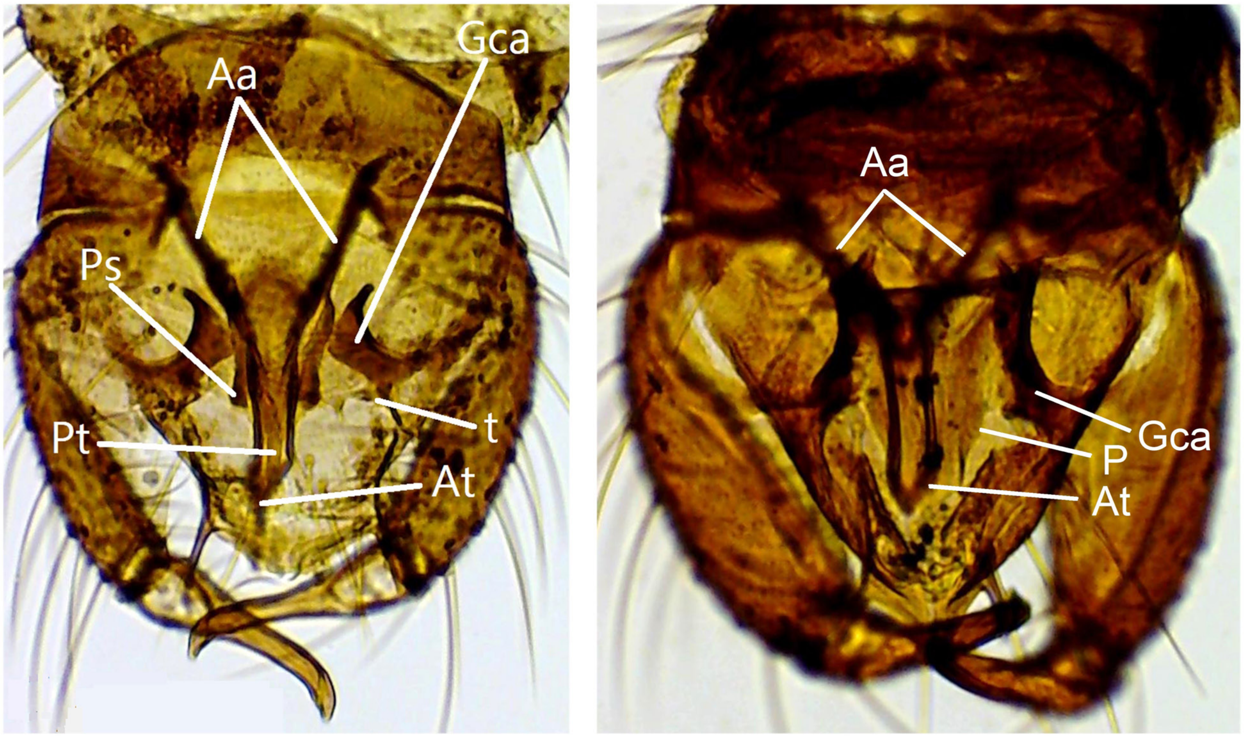


35 *C. moabensis* 36 *C. denningi*

Figures 33–36. 33) *Culicoides moabensis* female (top) and unidentified brown *C.* subgenus *Selfia* female (bottom), lateral habitus (in alcohol). Male genitalia, ventral view focused on aedeagus. **34)** *C. brookmani*, basal arm of paramere (Pa), distal tip of median process of paramere delineated (Pt), basal arm of aedeagus (Aa), tip of median process of aedeagus (At), gonocoxite (Gc), gonostylus (Gs). **35)** *C. moabensis,* median process of paramere (Pmp) (paratype). **36)** *C. denningi*, sternite 9 caudal lobes (S9cl).

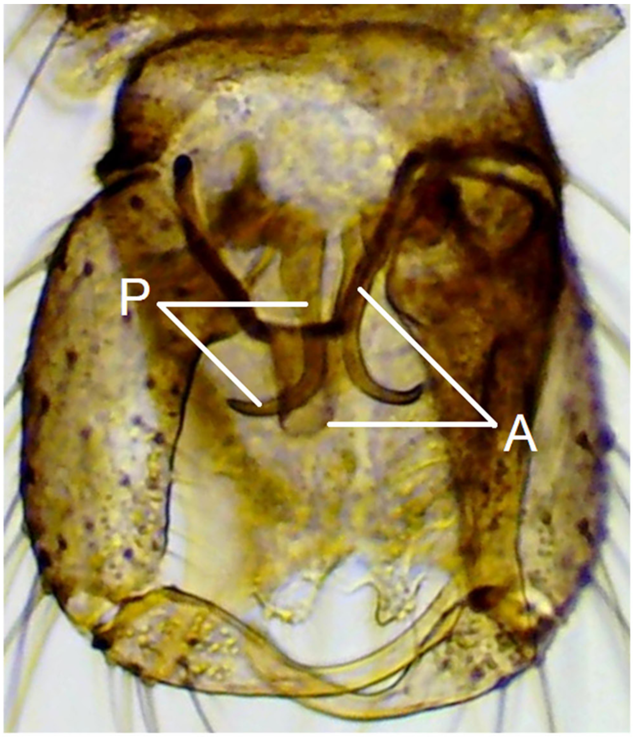


37 *C. hieroglyphicus* 38 *C. jamesi*

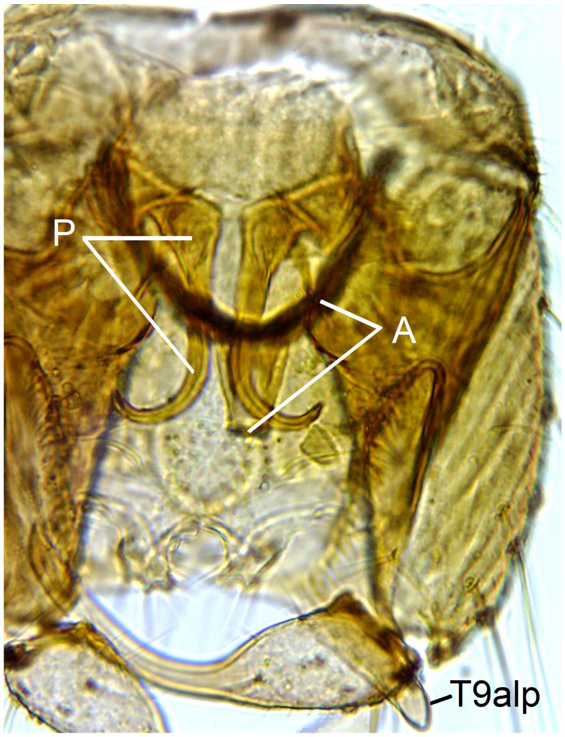


39 *C. jacksoni* 40 *C. tenuistylus*

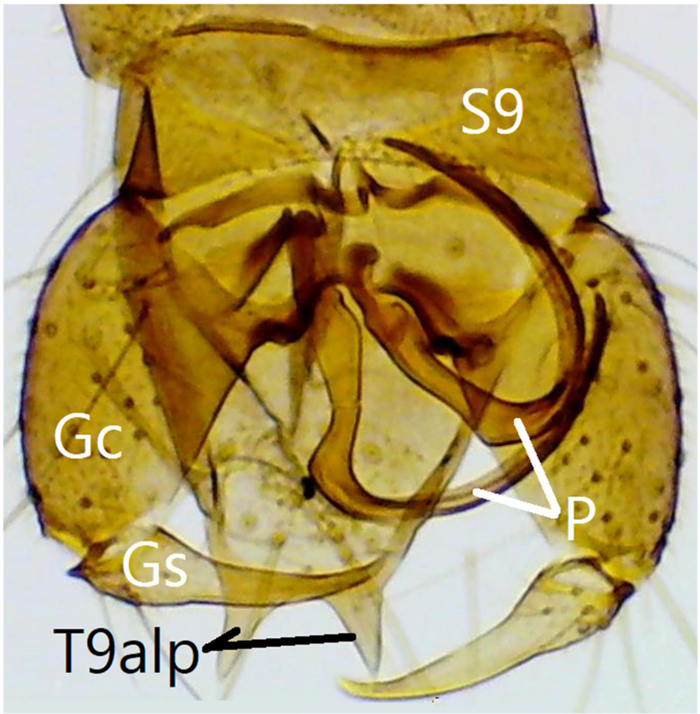
Figures 37–40. Male genitalia of *Culicoides*, ventral view focused on aedeagus. **37)** *C. hieroglyphicus*, basal arms of aedeagus (Aa), tip of median process of aedeagus (At), gonostylus (Gs), sternite 9 caudal lobes (S9cl). **38)** *C. jamesi*. **39)** *C. jacksoni*, paramere shoulder (Ps), apodeme of gonocoxite (Gca) tooth (t), tip of median process of paramere (Pt). **40)** *C. tenuistylus*, parameres (P) (Ventura County, CA).



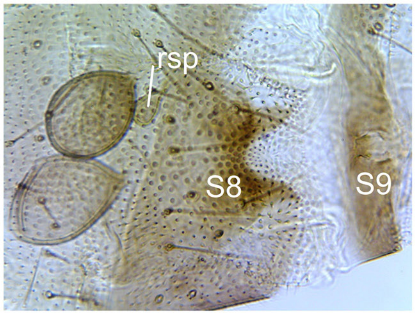
41 *C. mortivallis*



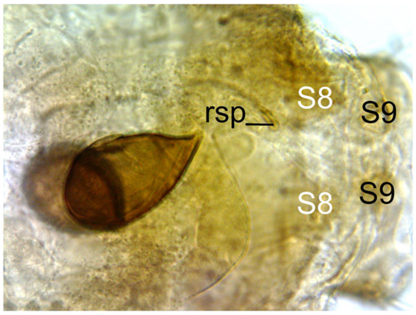
42 *C. werneri*



43 *C. bottimeri*

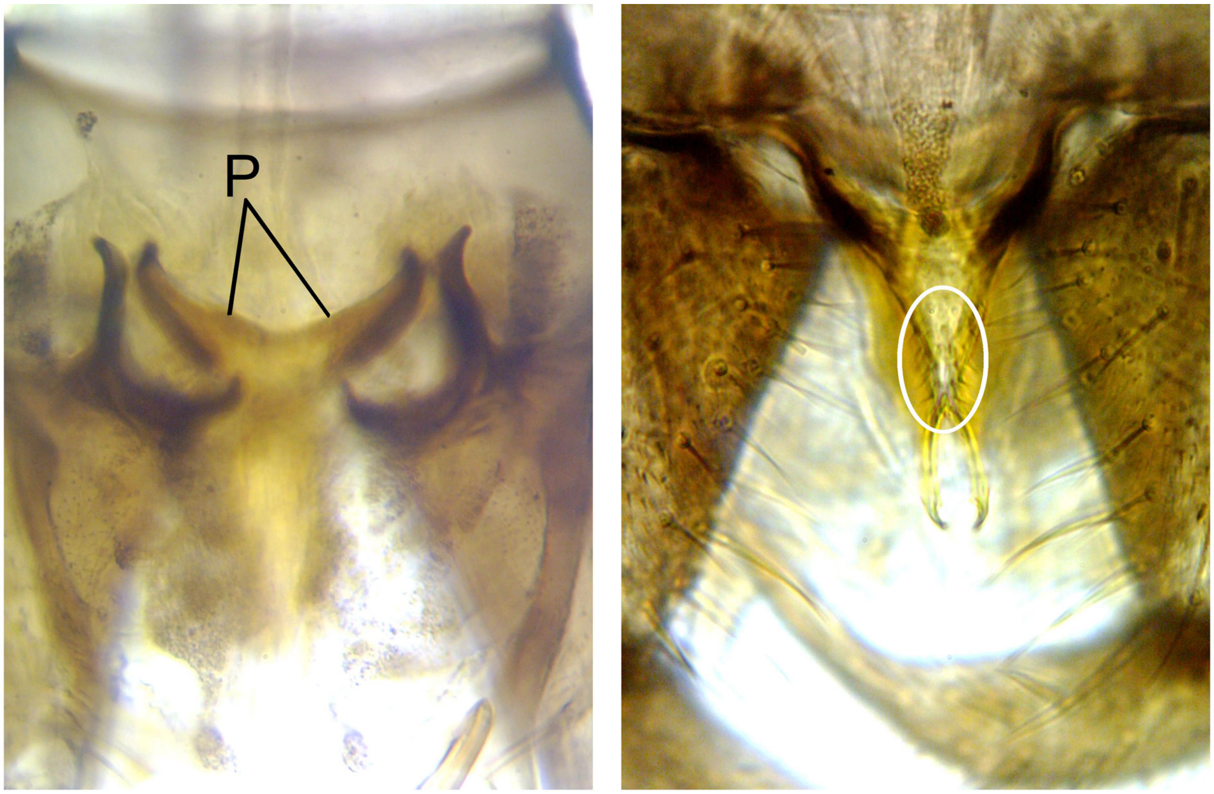


44 *C. bottimeri*



45 *C. stonei*

Figures 41–45. Male genitalia of *Culicoides*, ventral view, gonocoxite (Gc), gonostylus (Gs), paramere (P), aedeagus (A), apicolateral processes of tergite 9 (T9alp), sternite 9 (S9). **41)** *C. mortivallis*. **42)** *C. werneri* (paratype, Pima County, AZ [FSCA]). **43)** *C. bottimeri*. Spermathecae, rudimentary third spermatheca (rsp), sternite 8 (S8), sternite 9 (S9). **44)** *C. bottimeri*. **45)** *C. stonei*.

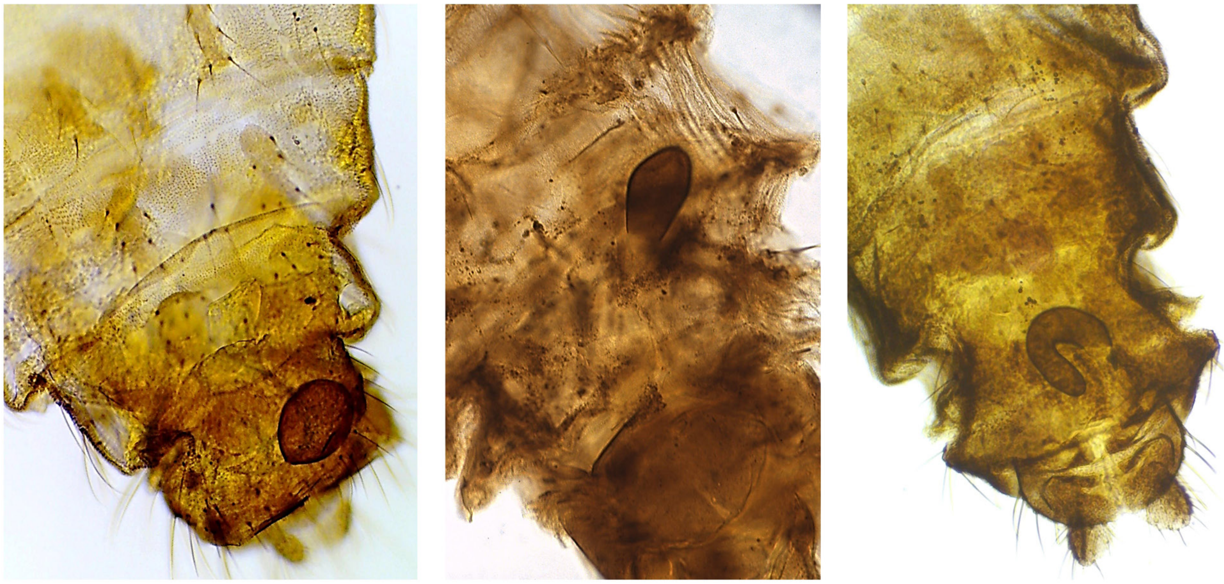


46 *C. sonorensis* 47 *C. sonorensis*

48 *C. occidentalis* 49 *C. occidentalis*

Figures 46–49. Male genitalia of *Culicoides* subgenus *Monoculicoides*, ventral view. **46)** *C. sonorensis*, focused on fused base of parameres (P). **47)** *C. sonorensis*, focused on aedeagus (not to same scale), spicules circled. **48)** *C. occidentalis*, focused on fused base of parameres (P). **49)** *C. occidentalis*, focused on aedeagus (not to same scale).

50 *C. sonorensis* ♂ 51 *C. occidentalis* ♂

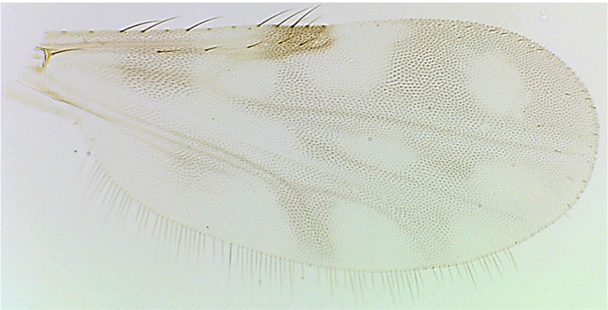


52 *C. crepuscularis* 53 *C. grandensis* 54 *C. sonorensis*

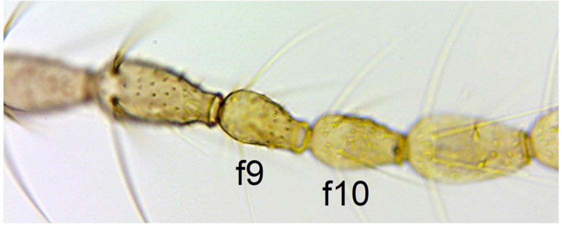
55 *C. sonorensis* ♀

Figures 50–55. 50) *Culicoides sonorensis* male wing. **51)** *C. occidentalis* male wing. Spermathecae. **52)** *C. crepuscularis*. **53)** *C. grandensis* (paratype). **54)** *C. sonorensis*. **55)** *C. sonorensis*, lateral view (anterior to left) of female mesonotum showing prescutal pit (presct pit) and dark patches around seta bases.

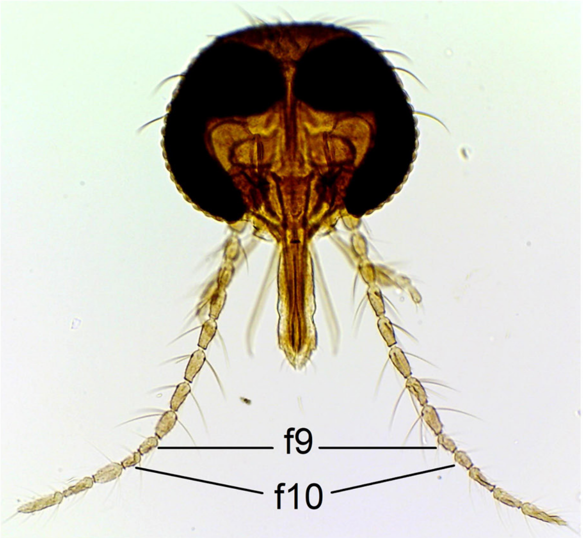
56 *C. reevesi* ♀



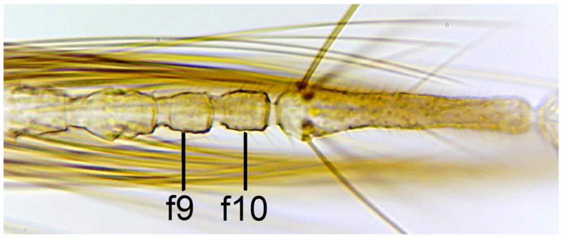
57 *C. reevesi* ♂



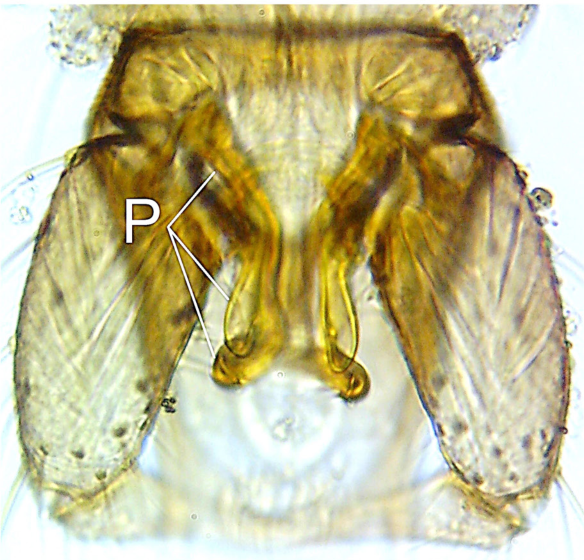
58 *C. reevesi* ♀



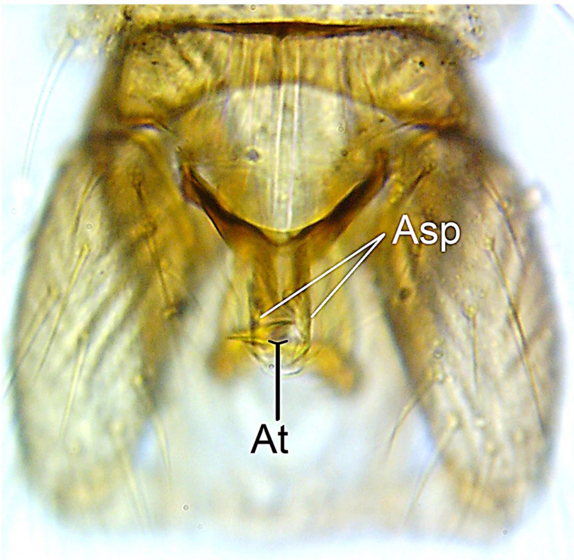
60 *C. reevesi* ♀



59 *C. reevesi* ♂

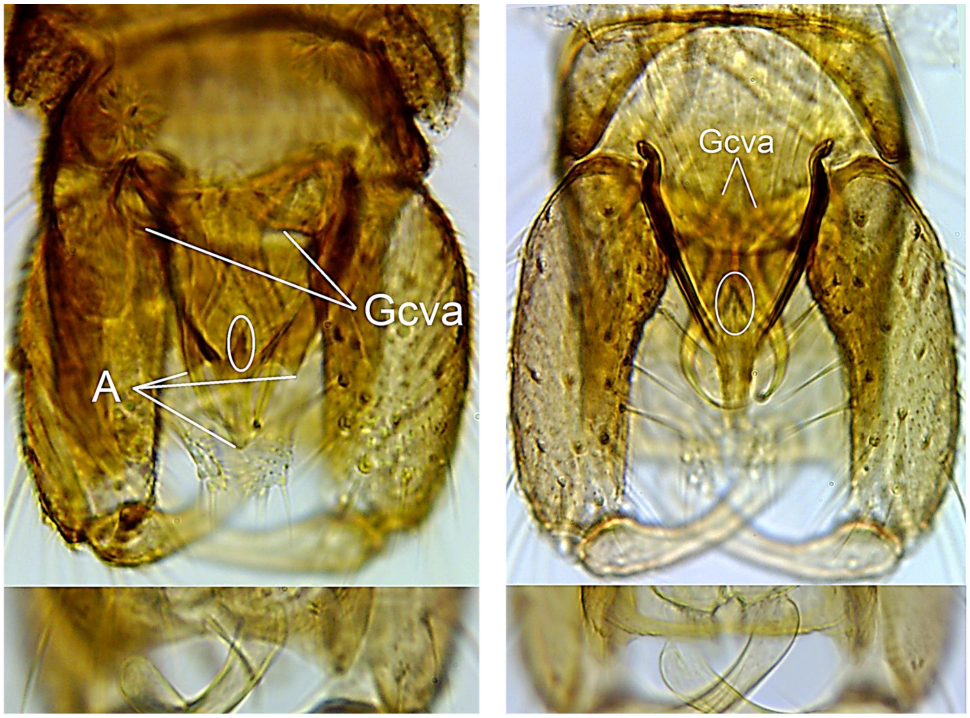


61 *C. reevesi*



62 *C. reevesi*

Figures 56–62. *Culicoides reevesi*. **56)** Female wing. **57)** Male wing. **58)** Female antennal flagellomeres 9 (f9) and 10 (f10). **59)** Male antennal flagellomeres 9 (f9) and 10 (f10). **60)** Female head. **61)** Male genitalia, ventral view, focused on left paramere (P). **62)** Focused on aedeagus, tip (At), subapical processes (Asp) (Lake County, CA).



63 *C. boydi*

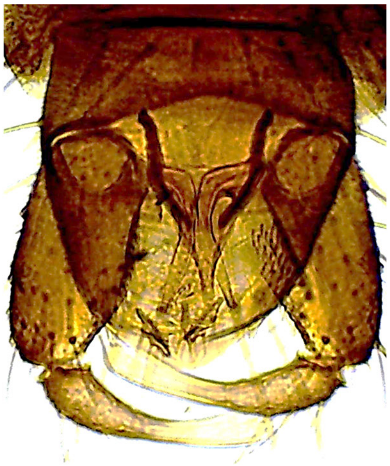
64 *C. chiopterus*

65 *C. obsoletus*

Figures 63–65. Male genitalia of *Culicoides* subgenus *Avaritia*, ventral view. Upper images focused on aedeagus (A). Lower insets focused on caudal margin of tergite 9. Ventral apodeme of gonocoxite labeled (Gcva). Anterior-directed median process of aedeagus circled. **63)** *C. boydi* (Riverside County, CA [BM]). **64)** *C. chiopterus* (MD [FSCA]). **65)** *C. obsoletus* (MD [FSCA]).

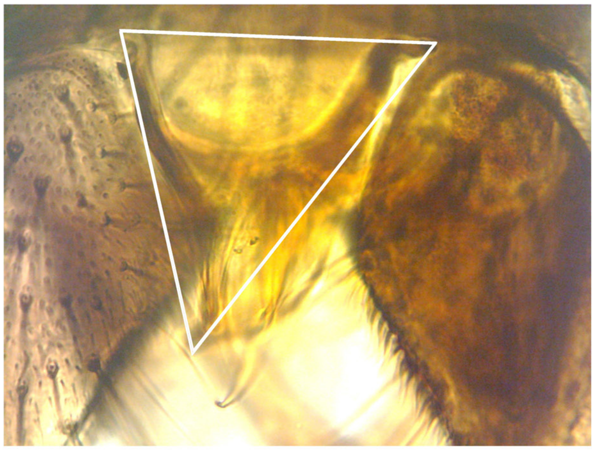
66 *C. cockerellii*

67 *C. freeborni*



68 *C. lahontan*

69 *C. neofagineus*

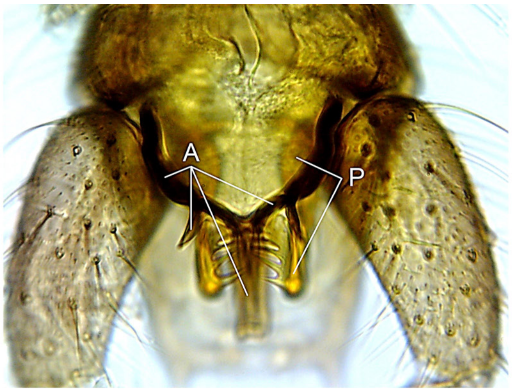


70 *C. neomontanus*

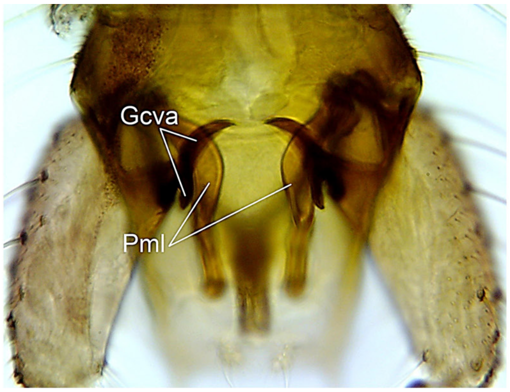
71 *C. saltonensis*

72 *C. sierrensis*

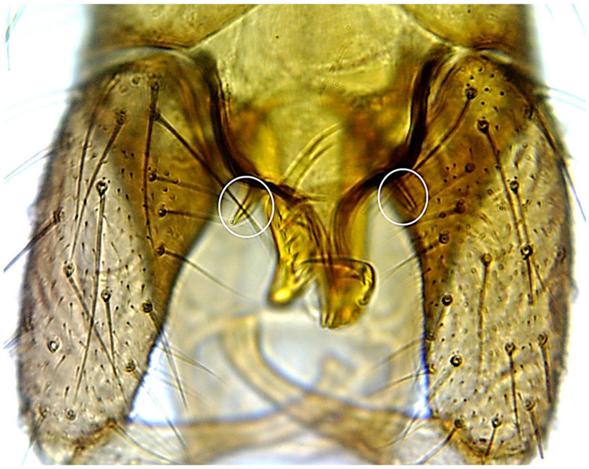
Figures 66–72. Male genitalia of *Culicoides* subgenus *Silvicola*, ventral view. **66)** *C. cockerellii* (Bonneville County, ID). **67)** *C. freeborni* (San Diego County, CA [BM]). **68)** *C. lahontan*. **69)** *C. neofagineus* (paratype, Mendocino County, CA [FSCA]). **70)** *C. neomontanus*, basal and apical tips of aedeagus triangulated. **71)** *C. saltonensis* (Imperial County, CA [FSCA]). **72)** *C. sierrensis* (paratype, Modoc County, CA [FSCA]).



73 *C. defoliarti-haematopotus*

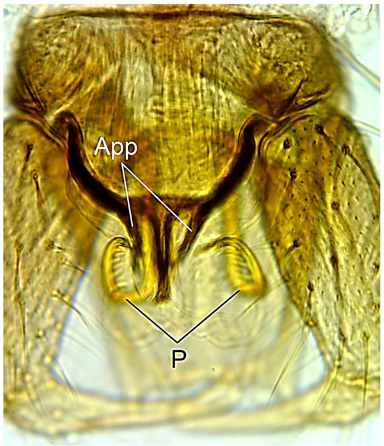


74 *C. defoliarti-haematopotus*

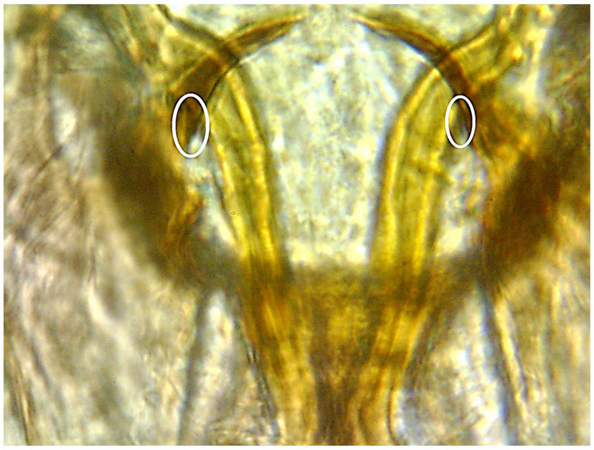


75 *C. inyoensis*

76 *C. erikae*

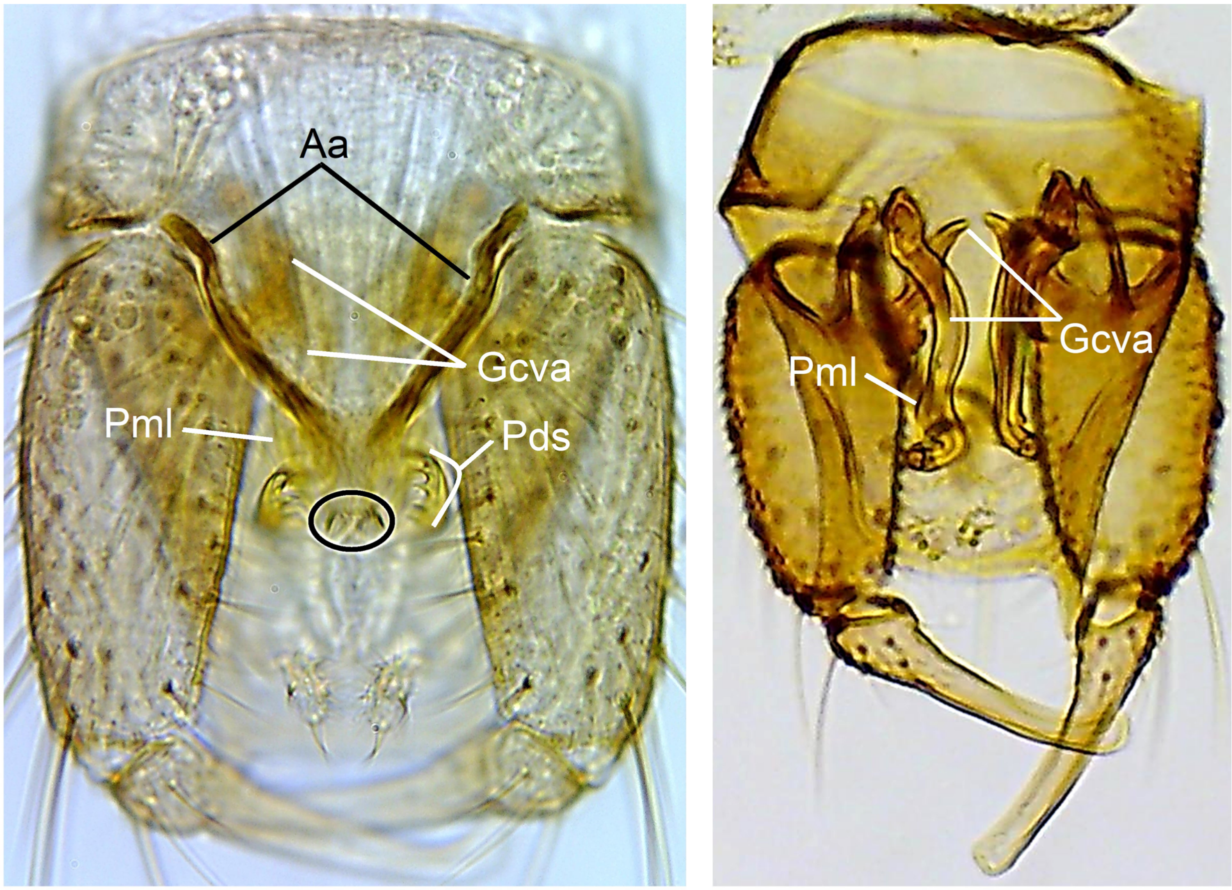


77 *C. salihi*



78 *C. salihi*

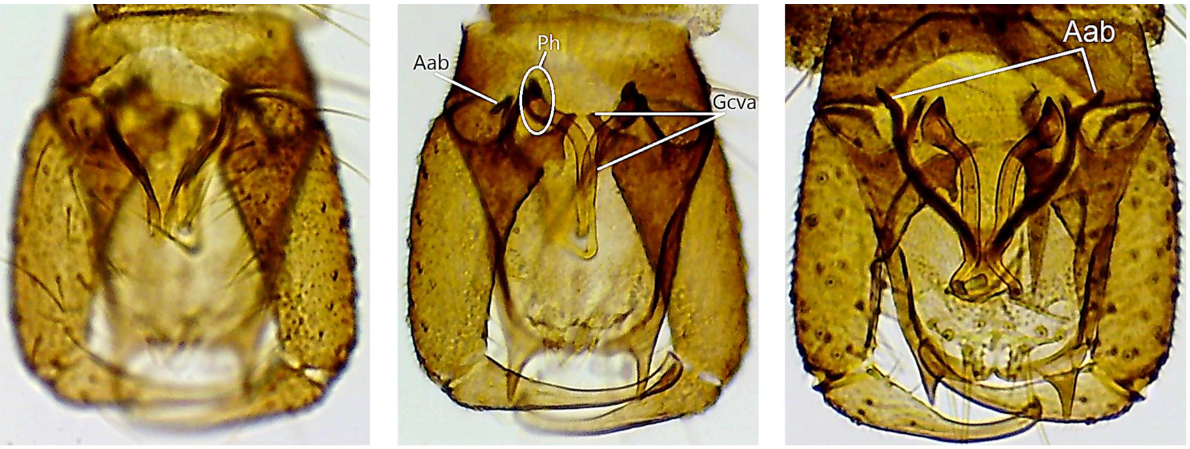
Figures 73–78. Male genitalia of *Culicoides* subgenus *Diphaomyia*, ventral view. **73)** *C. defoliarti-haematopotus*, focused on aedeagus (A), paramere (P). **74)** *C. defoliarti-haematopotus*, focused on ventral apodemes of gonocoxites (Gcva) and median lobes on parameres (Pml). **75)** *C. inyoensis*, posterior projections on basal arms of aedeagus circled. **76)** *C. erikae*, median lobes on parameres circled. **77)** *C. salihi*, focused on aedeagus and parameres, posterior projections on basal arms of aedeagus (App). **78)** *C. salihi*, focused on posterior portion of ventral apodemes of gonocoxites, circled.



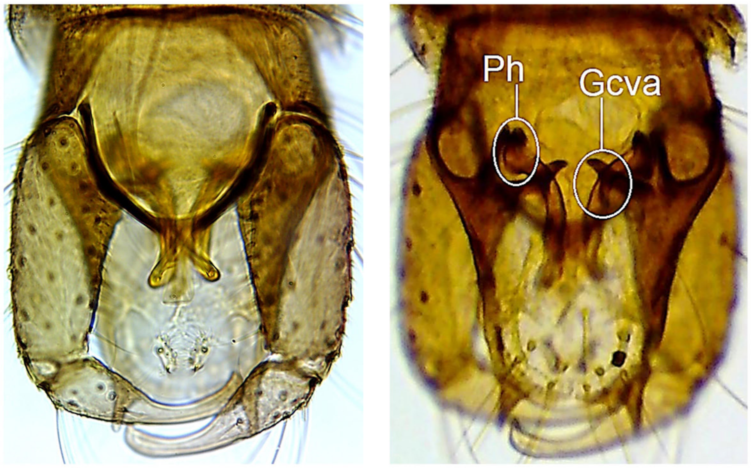
79 *C. mohave*

80 *C. kettlei*

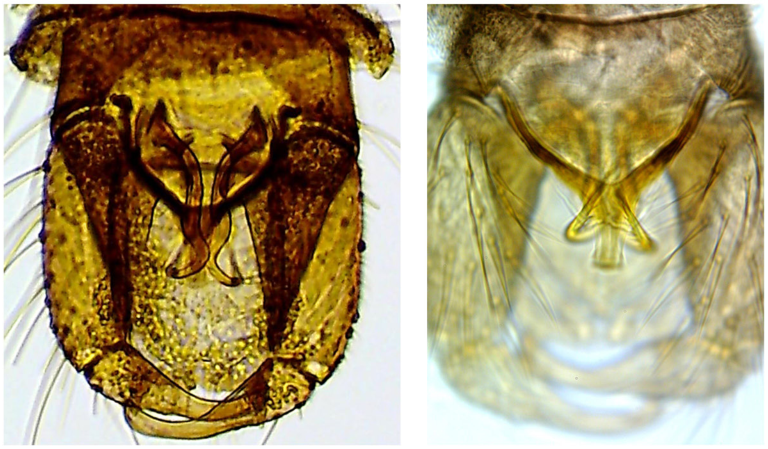
Figures 79–80. Male genitalia of *Culicoides*, ventral view, basal arms of aedeagus (Aa), submedian lobe on paramere (Pml), ventral apodeme of gonocoxite (Gcva), distal spines of paramere (Pds). **79)** *C. mohave*, apex of aedeagus circled (San Bernardino County, CA [FSCA]). **80)** *C. kettlei* (Riverside County, CA [BM]).



81 *C. cavaticus* 82 *C. cavaticus* 83 *C. cavaticus*

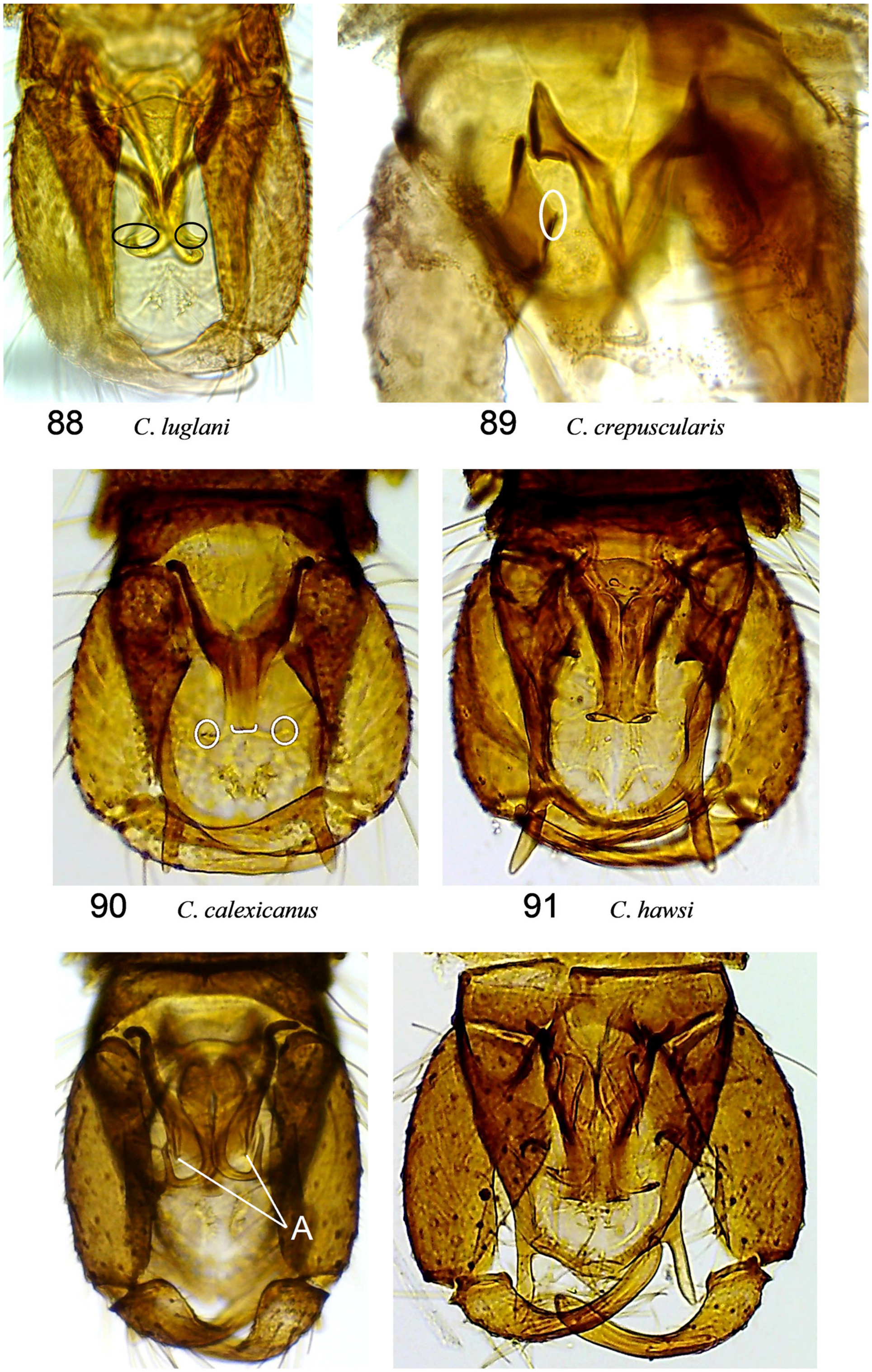


84 *C. doeringae* 85 *C. doeringae*



86 Piliferus gr. sp. A 87 Piliferus gr. sp. A

Figures 81–87. Male genitalia of *Culicoides* Piliferus group, ventral view. **81)** *C. cavaticus*, focused on aedeagus. **82)** *C. cavaticus*, focused on aedeagus arm base (Aab), basal head of paramere (Ph), ventral apodeme of gonocoxite (Gcva) (paratype, Sacramento County, CA [FSCA]). **83)** *C. cavaticus* (Grand County, UT). **84)** *C. doeringae*, focused on aedeagus. **85)** *C. doeringae*, focused on basal head of paramere (Ph), ventral apodeme of gonocoxite (Gcva). **86, 87)** *C.* Piliferus group species A variations.



88 *C. luglani*

89 *C. crepuscularis*

90 *C. calexicanus*

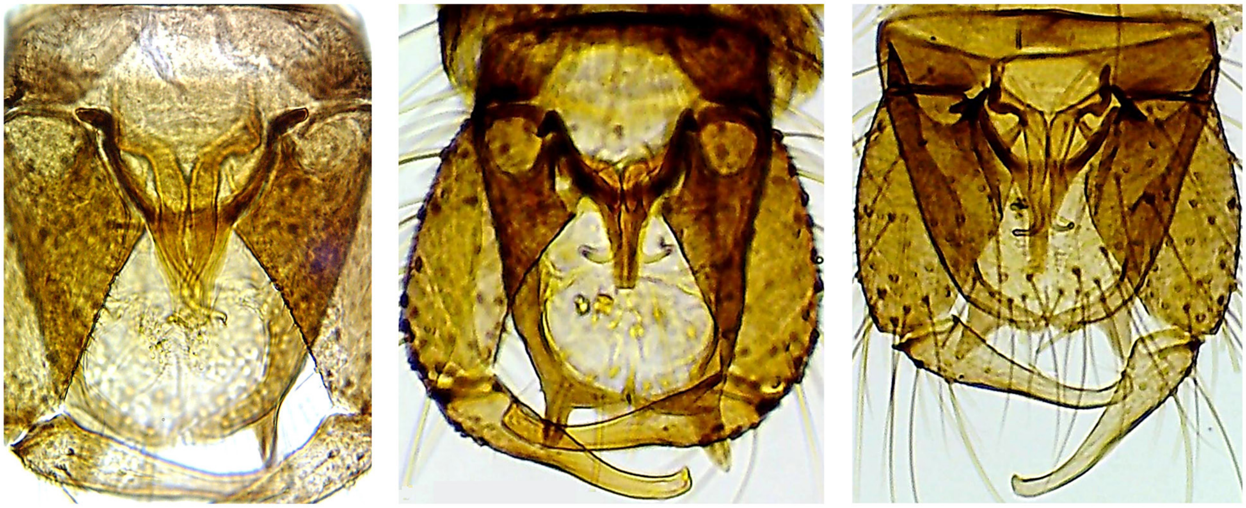
91 *C. hawsi*

92 *C. palmerae*

93 *C. utahensis*

Figures 88–93. Male genitalia of *Culicoides*, ventral view. **88)** *C. luglani*, submedian processes of parameres circled. **89)** *C. crepuscularis*, ventral apodeme of gonocoxite circled. **90)** *C. calexicanus*, apices of parameres circled, apex of aedeagus delineated. **91)** *C. hawsi* (paratype, Modoc County, CA [FSCA]). **92)** *C. palmerae*, sharp lateral shoulders on median process of aedeagus indicated (A). **93)** *C. utahensis*.

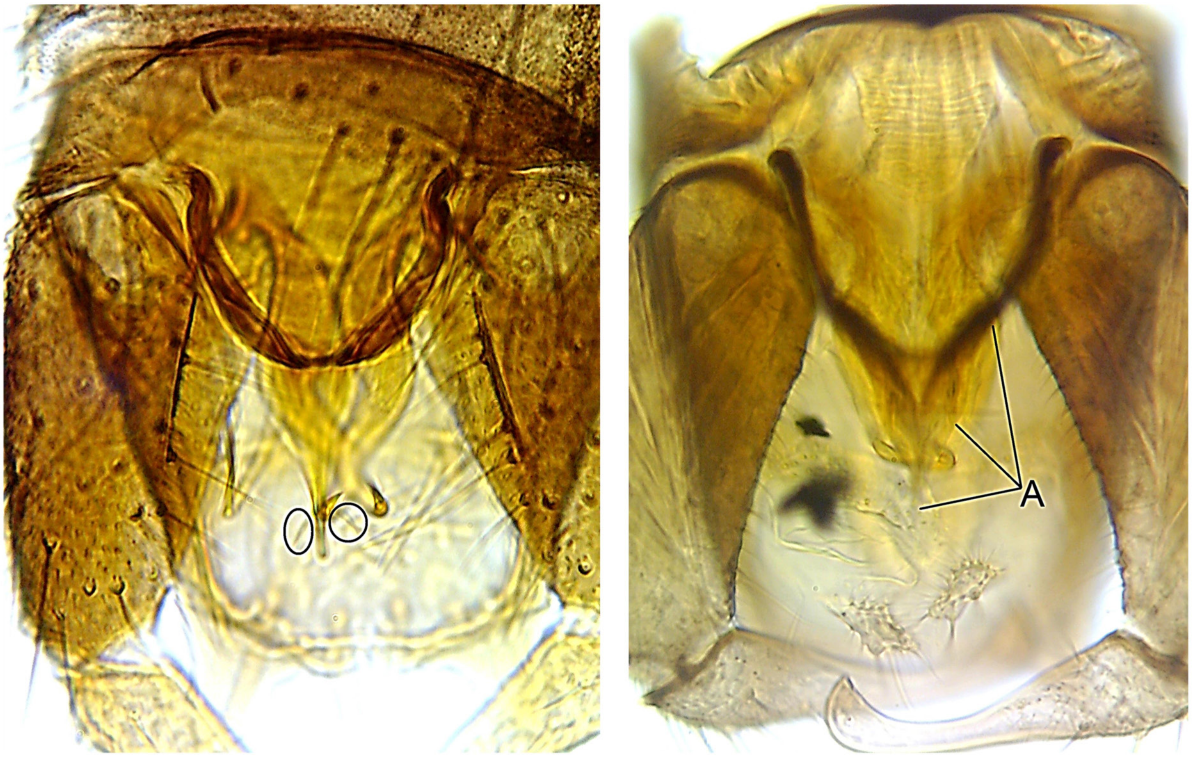
94 *C. sublettei* **95** *C. usingeri* **96** *C. vetustus*



97 *C. posoensis* **98** *C. kibunensis* **99** *C. travisi*

Figures 94–99. Male genitalia of *Culicoides*, ventral view. Ventral apodeme of gonocoxite and apex of paramere circled on Fig. 94–96. **94)** *C. sublettei* (Gillespie County, TX [FSCA]). **95)** *C. usingeri*. **96)** *C. vetustus* (San Bernardino County, CA [BM]). **97)** *C. posoensis* (paratype, Kern County, CA [FSCA]). **98)** *C. kibunensis*. **99)** *C. travisi* (VA [FSCA]).

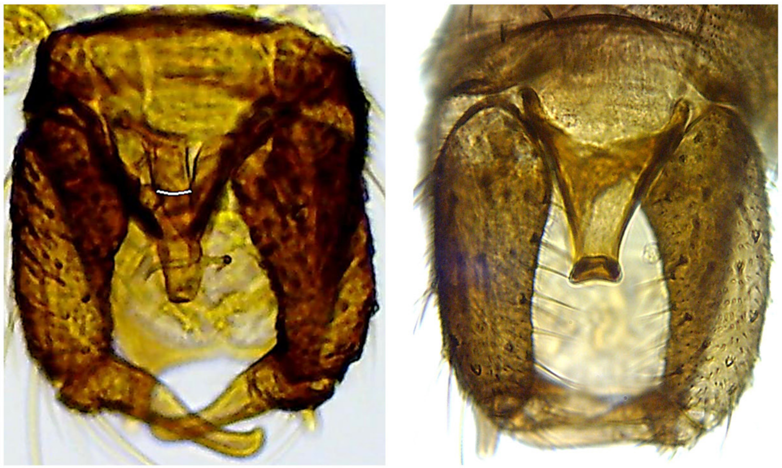
100 *C. californiensis* 101 *C. cochisensis*

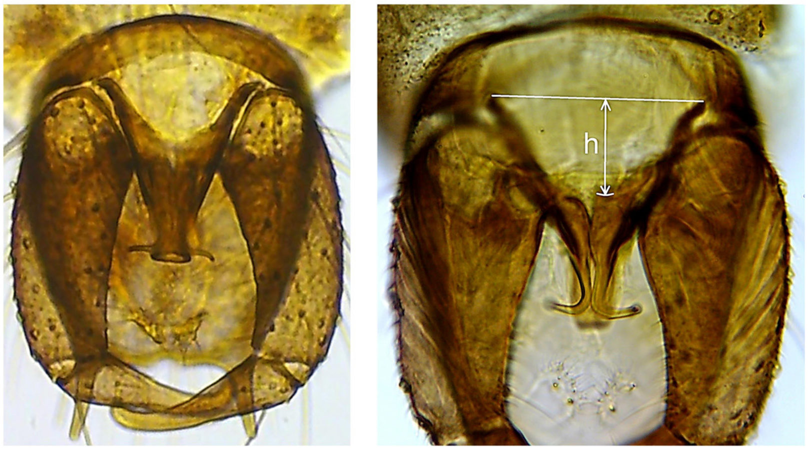


102 *C. oklahomensis* 103 *C. pampoikilus*

Figures 100–103. Male genitalia of *Culicoides*, ventral view. **100)** *C. californiensis*, left edge of paramere (P), right edge of aedeagus (A), lateral aedeagal spines (As). **101)** *C. cochisensis* (Cochise County, AZ [UCRC]). **102)** *C. oklahomensis*, aedeagus filaments circled (LA [FSCA]). **103)** *C. pampoikilus* (Cochise County, AZ [UCRC]).


104 *C. butleri* 105 *C. butleri*


106 *C. cacticola* 107 *C. jonesi*

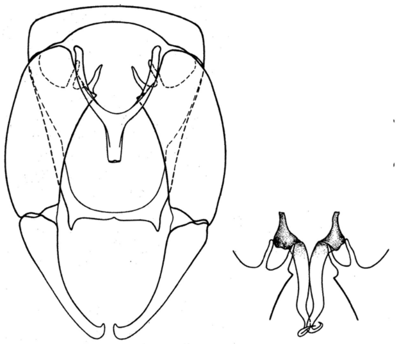


108 *C. sitiens* 109 *C. torridus*

Figures 104–109. Male genitalia of *Culicoides* subgenus *Drymodesmyia*, ventral view. **104)** *C. butleri* (Greenlee County, AZ). **105)** *C. butleri* (Gila County, AZ [FSCA]). **106)** *C. cacticola*, bottom of basal arch of aedeagus delineated (San Diego County, CA [BM]). **107)** *C. jonesi* (Greenlee County, AZ). **108)** *C. sitiens*. **109)** *C. torridus*, height (h) of basal arch of aedeagus indicated (San Diego County, CA [BM]).

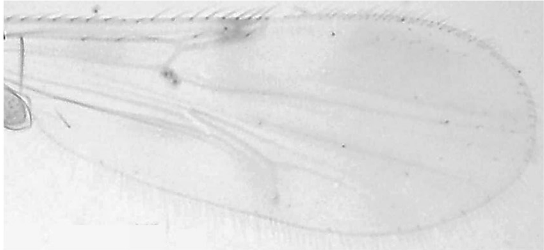
110 *C. insolatus* 111 *C. arizonensis* 112 *C. copiosus*

113 *C. ryckmani* 114 *C. byersi* 115 *C. hinmani*

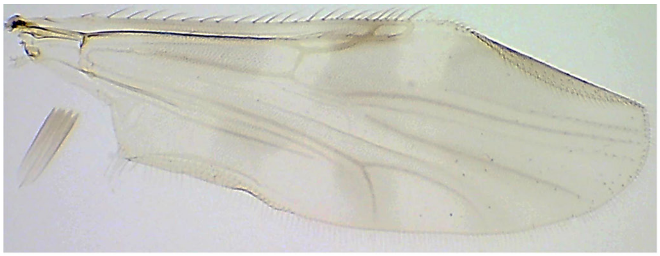


116 *C. daedalus*

Figures 110–116. Male genitalia of *Culicoides*, ventral view. **110)** *C. insolatus*, aedeagus tip (A), sternite 9 ventro-posterior membrane spicules (s) delineated (Sonora, Mexico [FSCA]). **111)** *C. arizonensis*, sternite 9 ventro-posterior membrane spicules circled (Yuma County, AZ [UCRC]). **112)** *C. copiosus*, sternite 9 ventro-posterior membrane spicules circled (San Diego County, CA [BM]). **113)** *C. ryckmani*, dorsal apodeme of gonocoxite (Gcda) and ventral apodeme (Gcva) circled (San Diego County, CA [BM]). **114)** *C. byersi*, dorsal apodeme of gonocoxite (Gcda) and ventral apodeme (Gcva) circled. **115)** *C. hinmani*, aedeagus basal tips of basal arms, bottom of basal arch, and tip of median process indicated (A), ventral apodeme of gonocoxite (Gcva) and dorsal apodeme (Gcda) circled. **116)** *C. daedalus*: genitalia with parameres removed (left); parameres and gonocoxal apodemes (right, to same scale) (Panama, from Wirth and Blanton 1959: 320, Fig. 25).

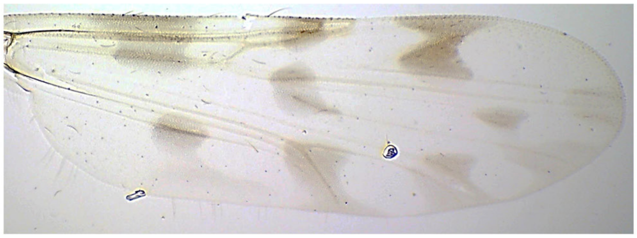


117 *C. boydi* ♂

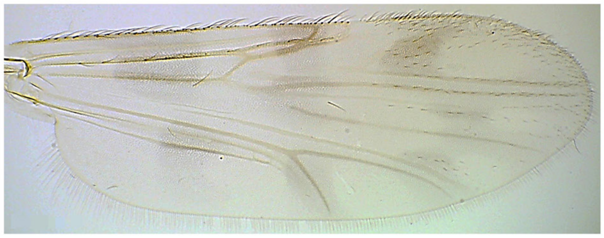


118 *C. obsoletus* ♂

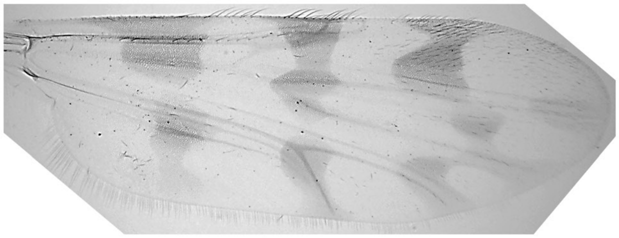
119 *C. cockerellii* ♂



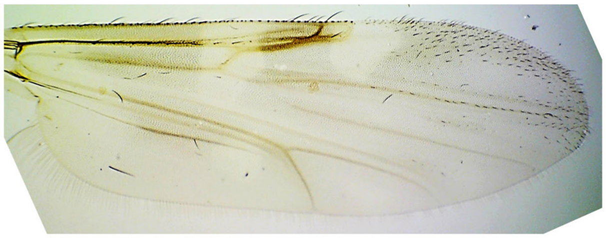
120 *C. freeborni* ♂



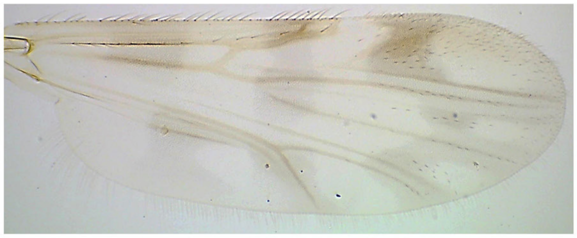
121 *C. lahontan* ♂



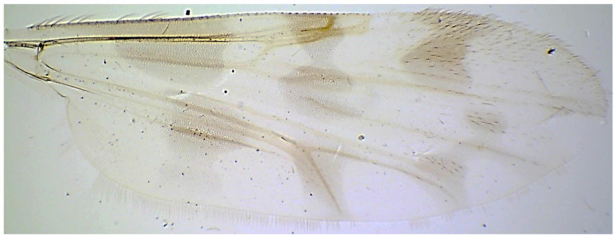
122 *C. neofagineus* ♂



123 *C. neomontanus* ♂

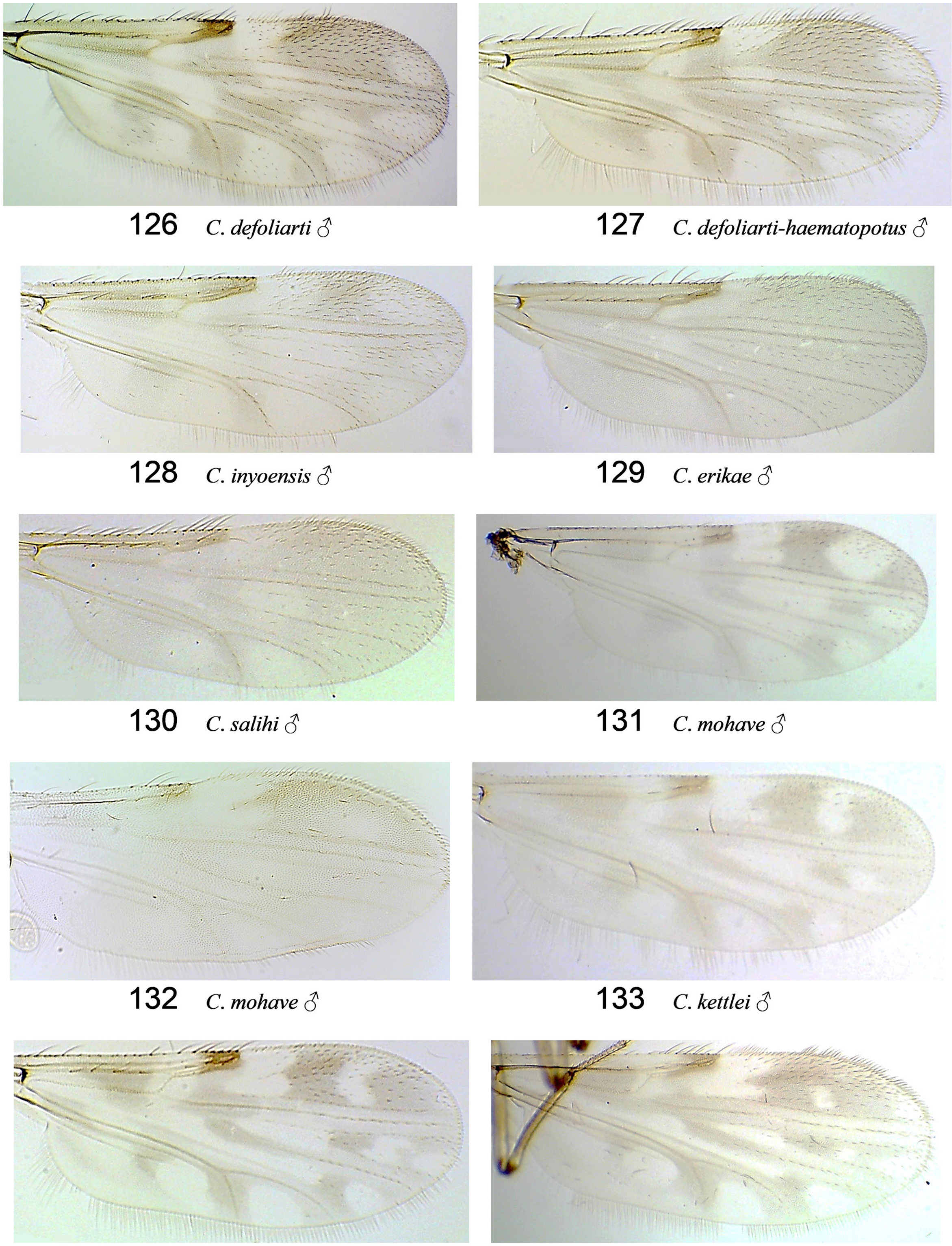


124 *C. saltonensis* ♂



125 *C.* sierrensis ♂

Figures 117–125. Male wings of *Culicoides* subgenera *Avaritia* and *Silvicola*. **117)** *C. boydi* (in grayscale) (Riverside County, CA [BM]). **118)** *C. obsoletus* (MD [FSCA]). **119)** *C. cockerellii* (Bonneville County, ID). **120)** *C. freeborni* (San Diego County, CA [BM]). **121)** *C. lahontan*. **122)** *C. neofagineus* (in grayscale) (paratype, Mendocino County, CA [FSCA]). **123)** *C. neomontanus*. **124)** *C. saltonensis* (Imperial County, CA [FSCA]). **125)** *C. sierrensis* (paratype, Modoc County, CA [FSCA]).



126 *C. defoliarti* ♂

127 *C. defoliarti-haematopotus* ♂

128 *C. inyoensis* ♂

129 *C. erikae* ♂

130 *C. salihi* ♂

131 *C. mohave* ♂

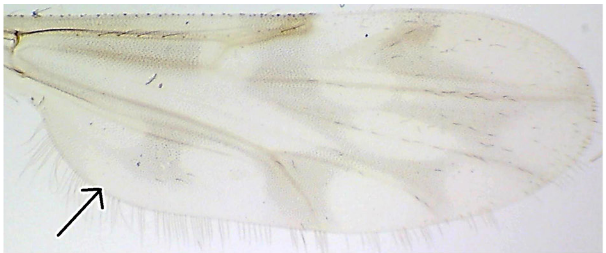
132 *C. mohave* ♂

133 *C. kettlei* ♂

134 *C. stellifer* ♂

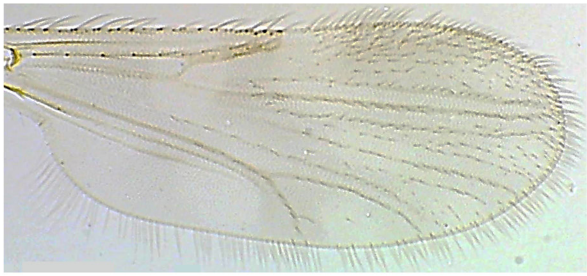
135 *C. stellifer* ♂

Figures 126–135. Male wings of *Culicoides*. **126)** *C. defoliarti*. **127)** *C. defoliarti-haematopotus*. **128)** *C. inyoensis*. **129)** *C. erikae*. **130)** *C. salihi*. **131)** *C. mohave*, distinct form (Riverside County, CA). **132)** *C. mohave*, faint form (San Bernardino County, CA [FSCA]). **133)** *C. kettlei* (Riverside County, CA [BM]). **134)** *C. stellifer*, typical. **135)** *C. stellifer*, variant.

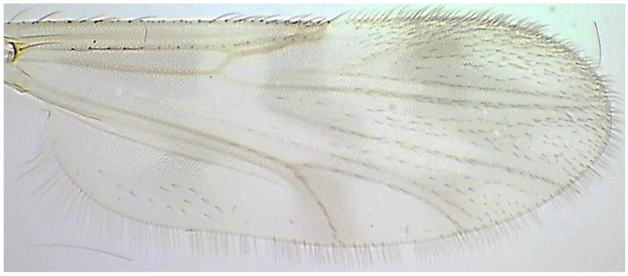


136 *C. cavaticus* ♂

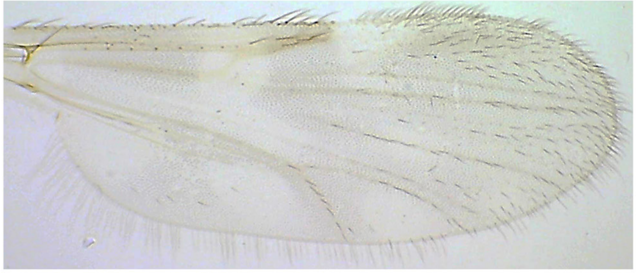
137 *C. cavaticus* ♂



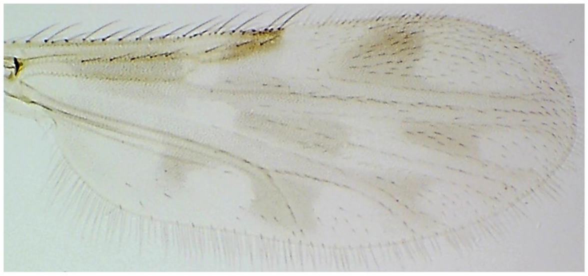
138 *C. doeringae* ♂



139 *C. doeringae* ♂

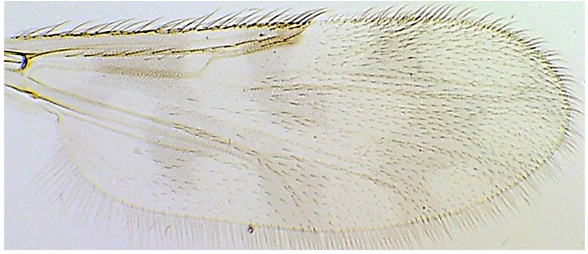


140 Piliferus gr. sp. A ♂

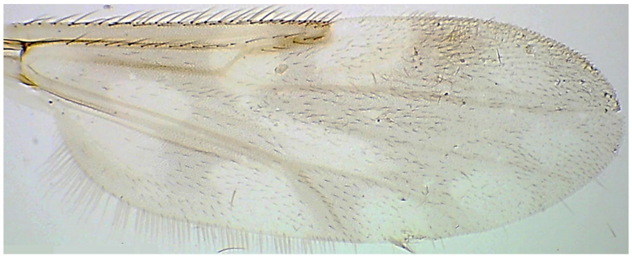


141 *C. luglani* ♂

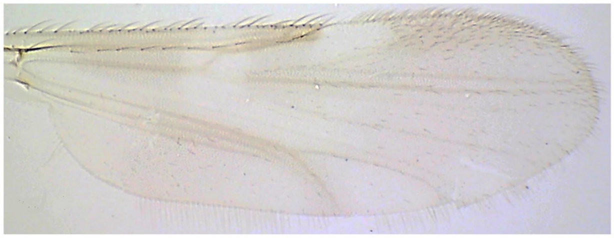
Figures 136–141. Male wings of *Culicoides*. **136)** *C. cavaticus*, arrow points to marginal posteromedian pale band of anal cell (Grand County, UT). **137)** *C. cavaticus*, arrow points to marginal posteromedian pale patch of anal cell (paratype, Sacramento County, CA [FSCA]). **138)** *C. doeringae*, less prominent form. **139)** *C. doeringae*, more prominent form. **140)** *C.* Piliferus group species A. **141)** *C. luglani*.



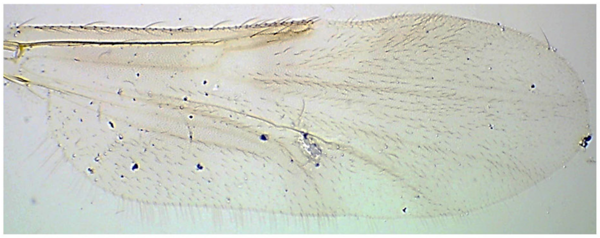
142 *C. crepuscularis* ♂



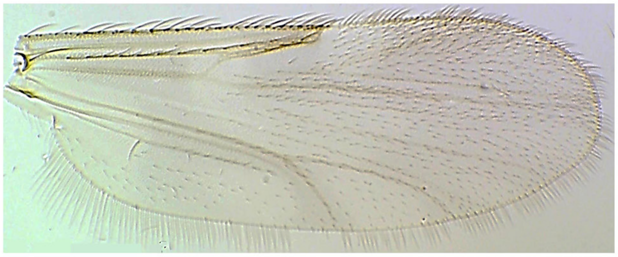
143 *C. crepuscularis* ♂



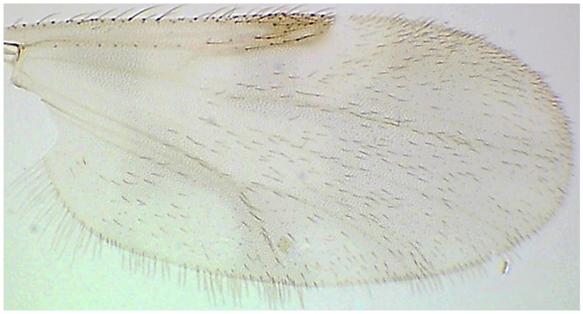
144 *C. calexicanus* ♂



145 *C. hawsi* ♂

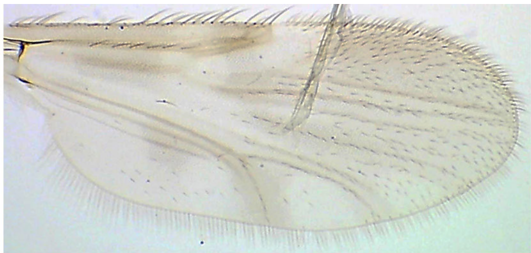


146 *C. palmerae* ♂

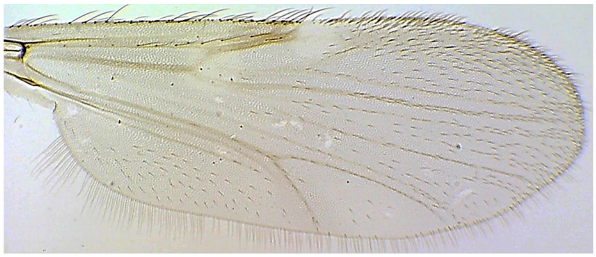


147 *C. utahensis* ♂

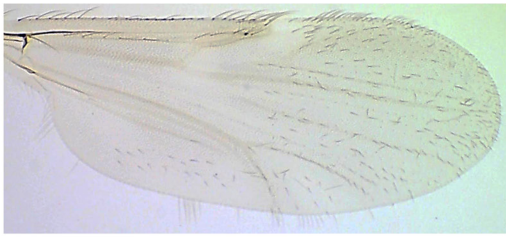
Figures 142–147. Male wings of *Culicoides*. **142)** *C. crepuscularis*, typical. **143)** *C. crepuscularis*, variant without medial pale spot in m_1. **144)** *C. calexicanus*. **145)** *C. hawsi* (paratype, Modoc County, CA [FSCA]). **146)** *C. palmerae*. **147)** *C. utahensis*.



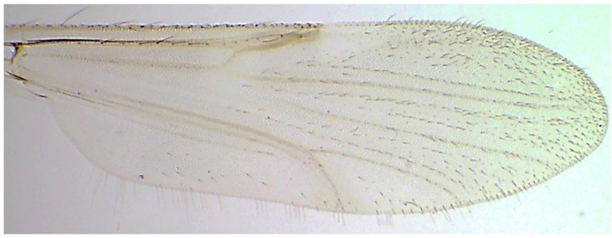
148 *C. sublettei* ♂



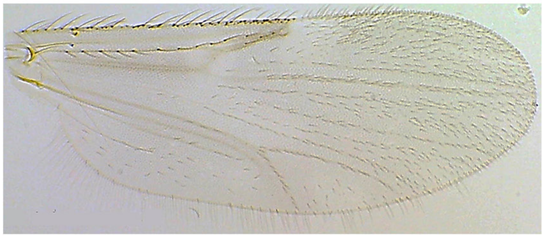
149 *C. usingeri* ♂



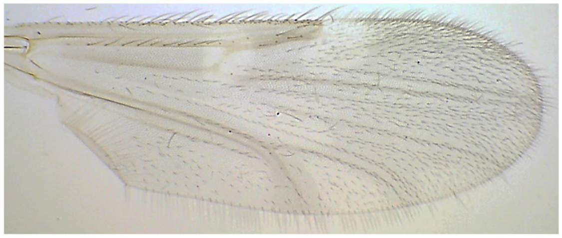
150 *C. vetustus* ♂



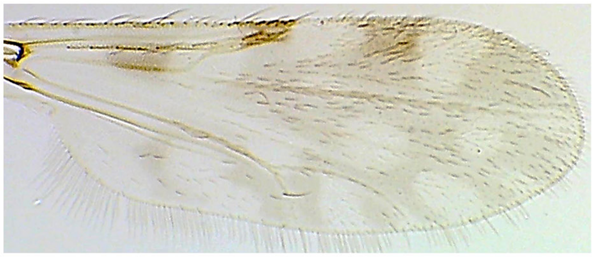
151 *C. posoensis* ♂



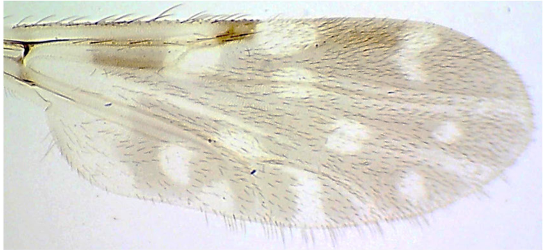
152 *C. kibunensis* ♂



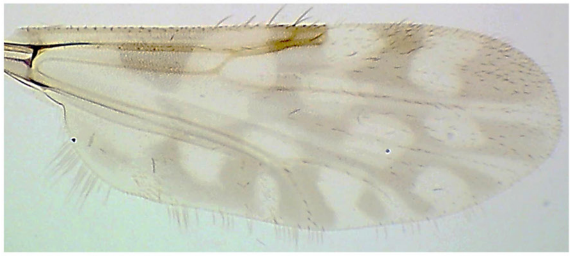
153 *C. travisi* ♂



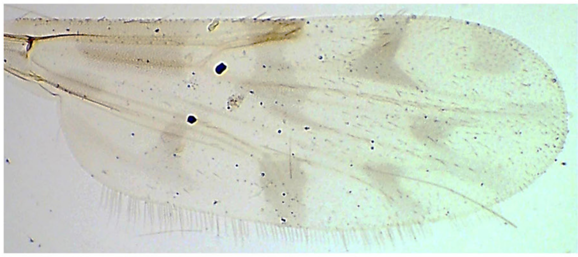
154 *C. californiensis* ♂



155 *C. cochisensis* ♂

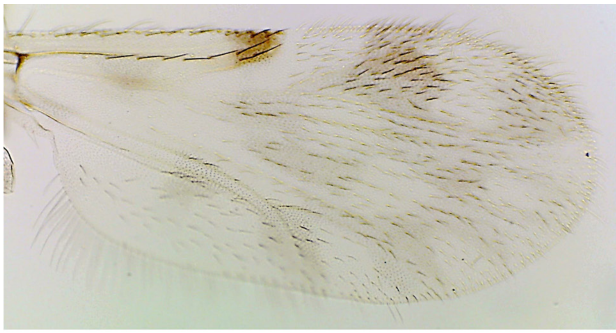


156 *C. oklahomensis* ♂

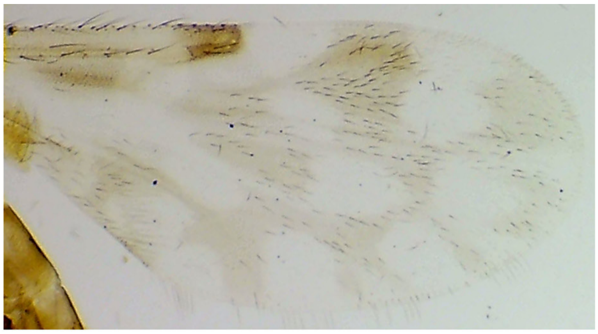


157 *C. pampoikilus* ♂

Figures 148–157. Male wings of *Culicoides*. **148)** *C. sublettei* (Gillespie County, TX [FSCA]). **149)** *C. usingeri*. **150)** *C. vetustus* (paratype, San Bernardino County, CA [BM]). **151)** *C. posoensis* (paratype, Kern County, CA [FSCA]). **152)** *C. kibunensis*. **153)** *C. travisi* (VA [FSCA]). **154)** *C. californiensis*. **155)** *C. cochisensis* (Cochise County, AZ [UCRC]). **156)** *C. oklahomensis* (LA [FSCA]). **157)** *C. pampoikilus* (Cochise County, AZ [UCRC]).



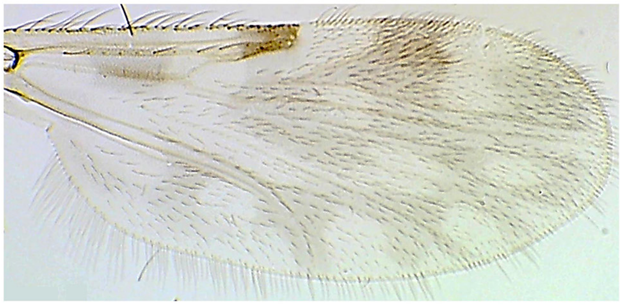
158 *C. butleri* ♂



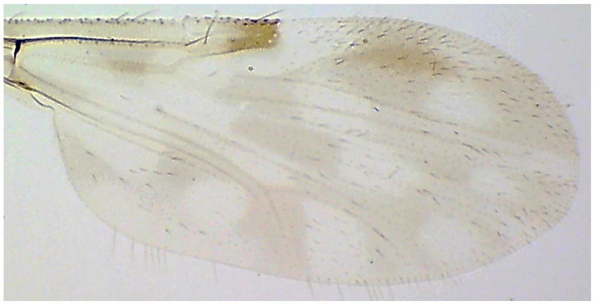
159 *C. butleri* ♂

160 *C. cacticola* ♂

161 *C. jonesi* ♂

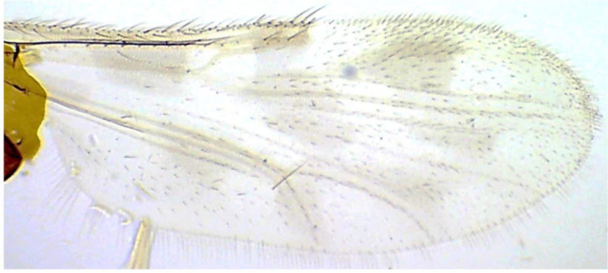


162 *C. sitiens* ♂

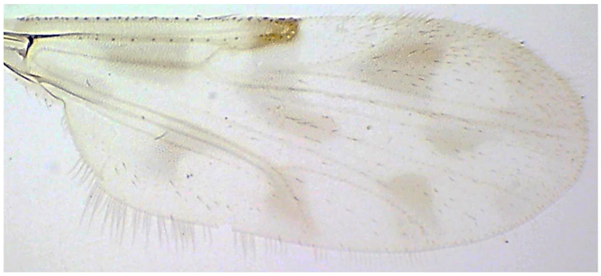


163 *C. torridus* ♂

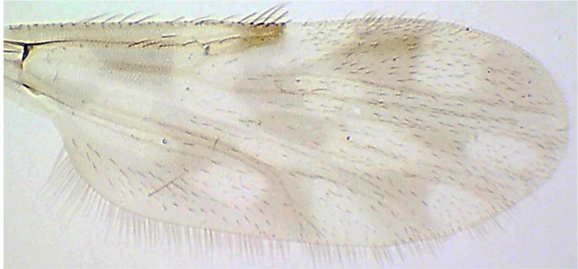
Figures 158–163. Male wings of *Culicoides* subgenus *Drymodesmyia*. **158)** *C. butleri* (Greenlee County, AZ). **159)** *C. butleri* (Gila County, AZ [FSCA]). **160)** *C. cacticola* (San Diego County, CA [BM]). **161)** *C. jonesi* (Greenlee County, AZ). **162)** *C. sitiens*. **163)** *C. torridus* (San Diego County, CA [BM]).



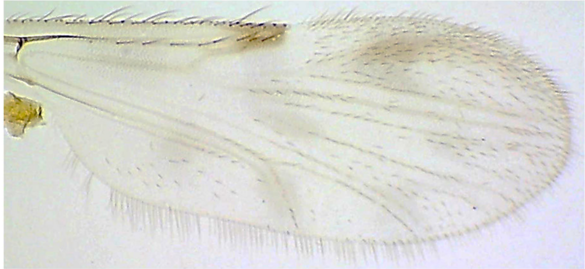
164 *C. arizonensis* ♂



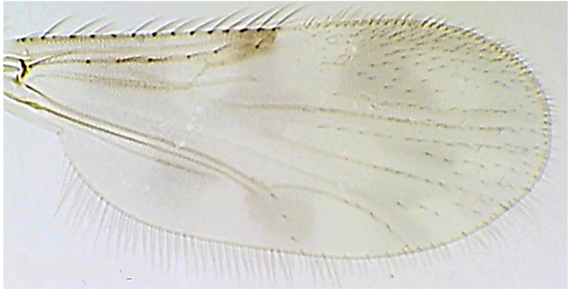
165 *C. copiosus* ♂



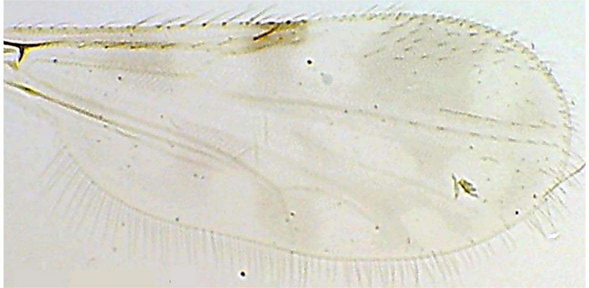
166 *C. insolatus* ♂



167 *C. ryckmani* ♂

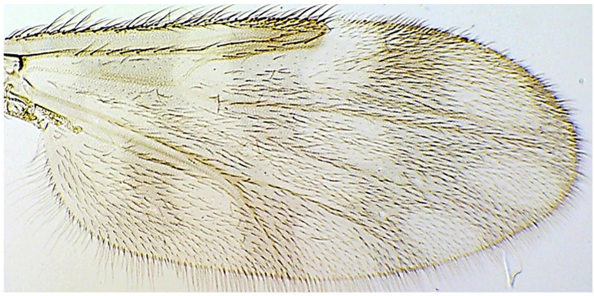


168 *C. byersi* ♂

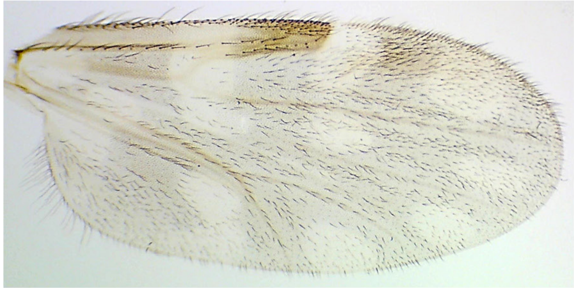


169 *C. hinmani* ♂

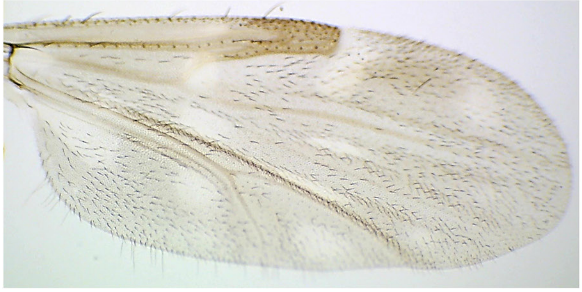
Figures 164–169. Male wings of *Culicoides* subgenus *Drymodesmyia*. **164)** *C. arizonensis* (Yuma County, AZ [UCRC]). **165)** *C. copiosus* (San Diego County, CA [BM]). **166)** *C. insolatus* (Sonora, Mexico [FSCA]). **167)** *C. ryckmani* (San Diego County, CA [BM]). **168)** *C. byersi*. **169)** *C. hinmani*.



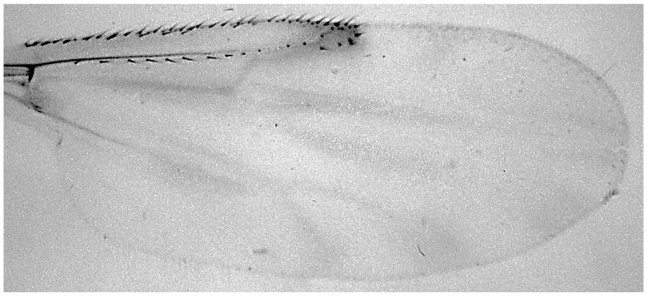
170 *C. crepuscularis* ♀



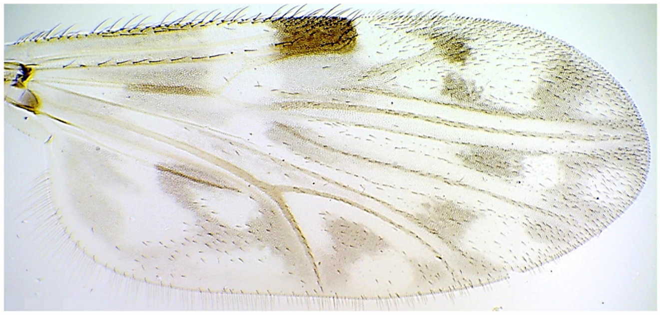
171 *C. crepuscularis* ♀



172 *C. crepuscularis* ♀

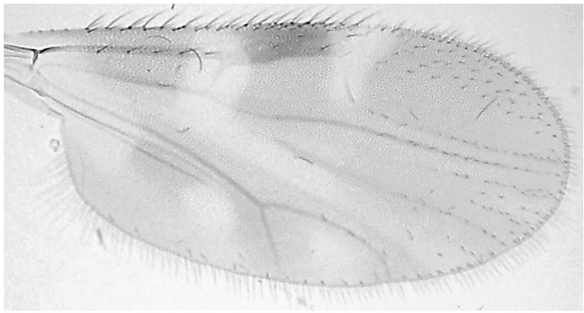


173 *C. grandensis* ♀



174 *C. sonorensis* ♀

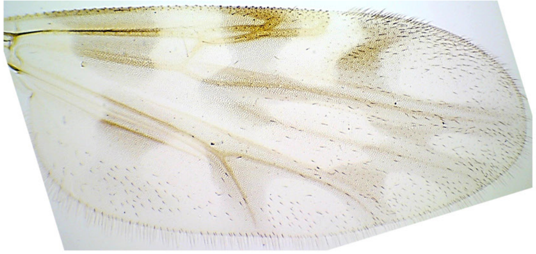
175 *C. boydi* ♀



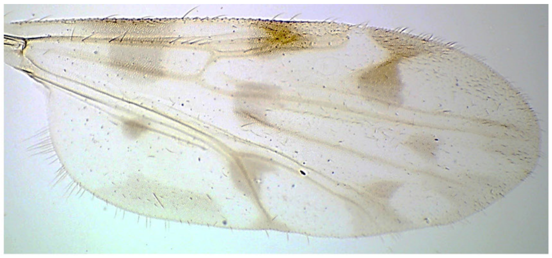
176 *C. chiopterus* ♀

177 *C. obsoletus* ♀

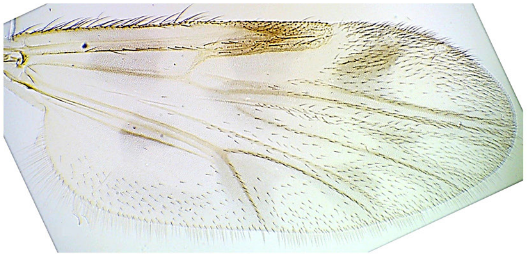
Figures 170–177. Female wings of *Culicoides*. **170)** *C. crepuscularis*, typical. **171)** *C. crepuscularis*, variant without medial pale spot in m_2 (Bonneville County, ID). **172)** *C. crepuscularis*, variant with three spermathecae and greatly diminished spots (Blaine County, ID). **173)** *C. grandensis* (in grayscale) (paratype). **174)** *C. sonorensis*. **175)** *C. boydi* (San Bernardino County, CA [BM]). **176)** *C. chiopterus* (in grayscale) (MD [FSCA]). **177)** *C. obsoletus* (Sonoma County, CA [UCRC]).



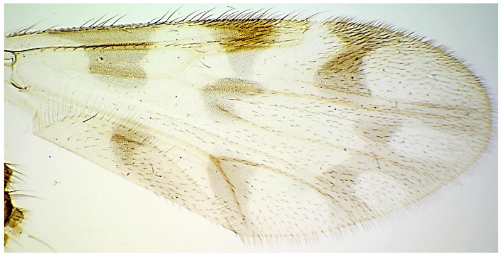
178 *C. cockerellii* ♀



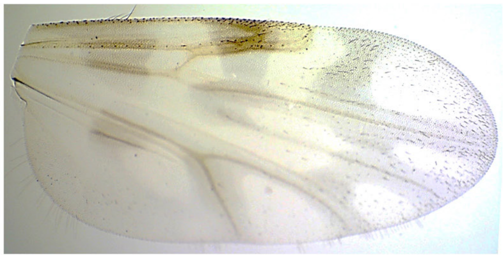
179 *C. freeborni* ♀



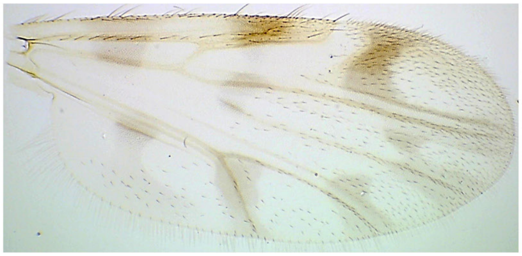
180 *C. lahontan* ♀



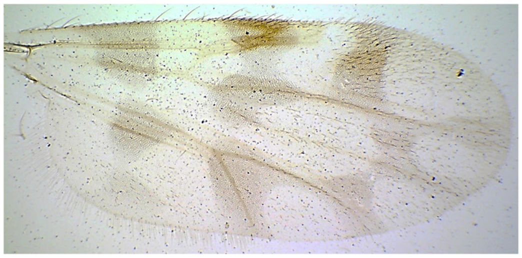
181 *C. neofagineus* ♀



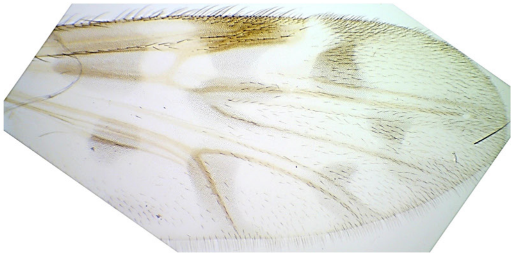
182 *C. neomontanus* ♀



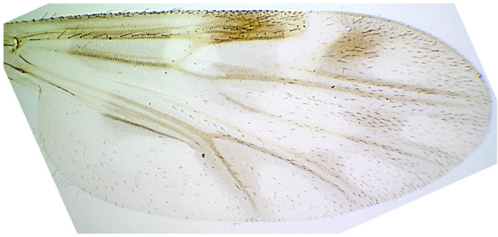
183 *C. saltonensis* ♀



184 *C. sierrensis* ♀



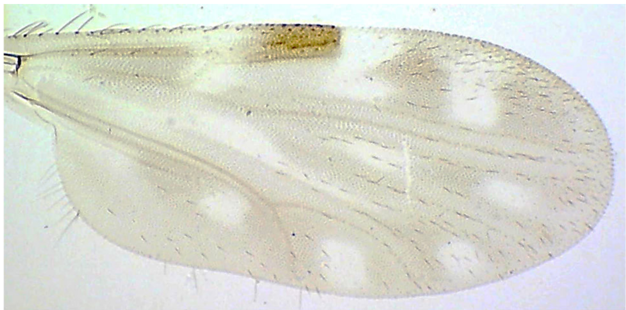
185 *Silvicola* sp. D ♀

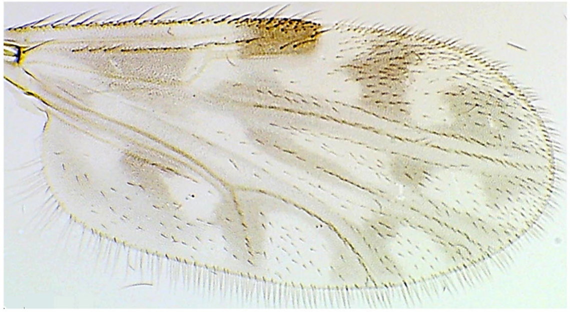


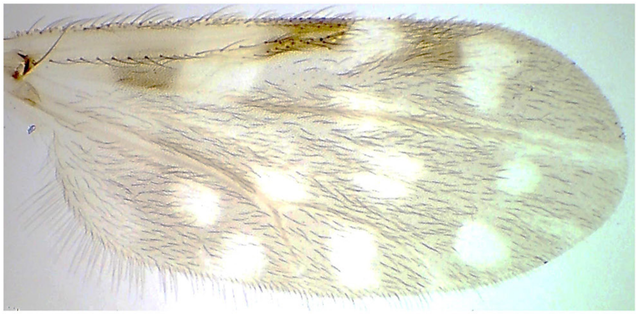
186 *Silvicola* sp. E ♀

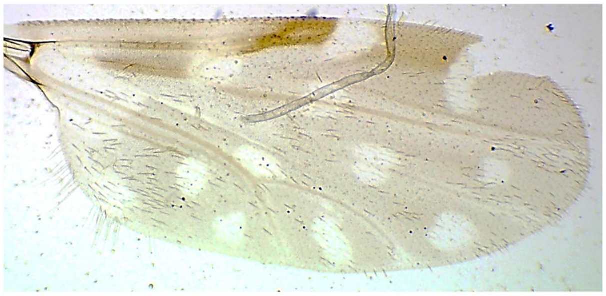
Figures 178–186. Female wings of *Culicoides* subgenus *Silvicola*. **178)** *C. cockerellii* (WY). **179)** *C. freeborni* (San Diego County, CA [BM]). **180)** *C. lahontan*. **181)** *C. neofagineus* (paratype, Mendocino County, CA [FSCA]). **182)** *C. neomontanus*. **183)** *C. saltonensis* (Imperial County, CA [FSCA]). **184)** *C. sierrensis* (paratype, Modoc County, CA [FSCA]). **185)** *C.* (*Silvicola*) species D. **186)** *C.* (*Silvicola*) species E.


187 *C. kettlei* ♀

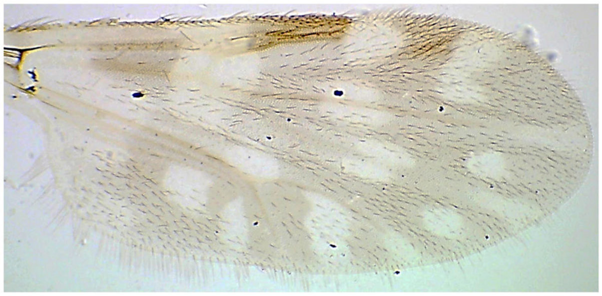

188 *C. kettlei* ♀

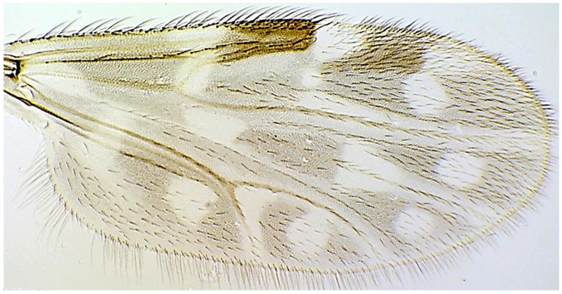

189 *C. stellifer* ♀


190 *C. californiensis* ♀

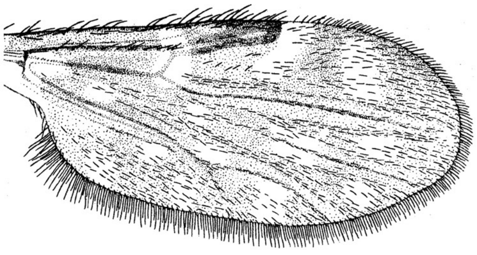

191 *C. cochisensis* ♀


192 *C. oklahomensis* ♀

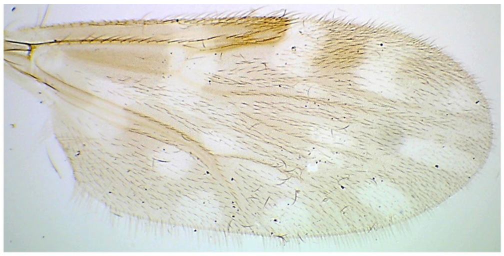

193 *C. pecosensis* ♀


194 *C. bergi* ♀

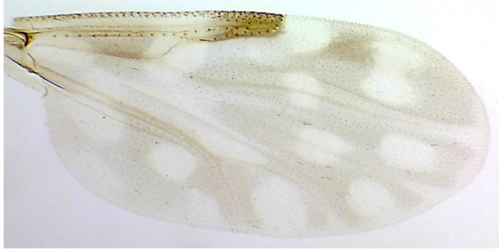
Figures 187–194. Female wings of *Culicoides*. **187)** *C. kettlei*, variant (Riverside County, CA [BM]). **188)** *C. kettlei*, typical (Riverside County, CA [BM]). **189)** *C. stellifer*. **190)** *C. californiensis*. **191)** *C. cochisensis* (Cochise County, AZ [UCRC]). **192)** *C. oklahomensis* (LA [FSCA]). **193)** *C. pecosensis* (Terrell County, TX [FSCA]). **194)** *C. bergi*.



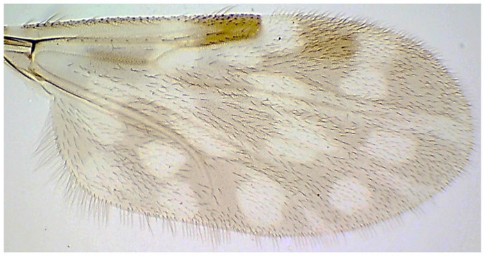
195 *C. daedalus* ♀



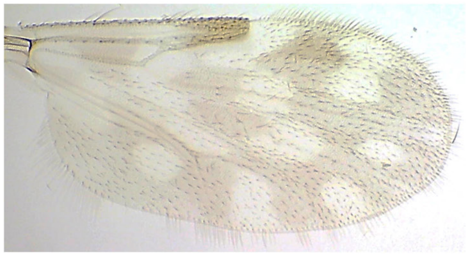
196 *C. pampoikilus* ♀



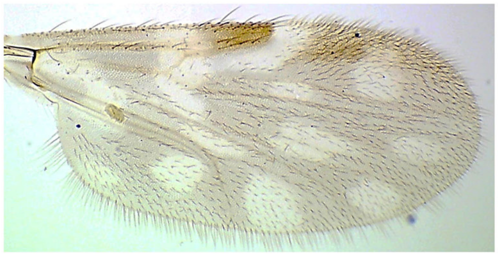
197 *C. bakeri* ♀



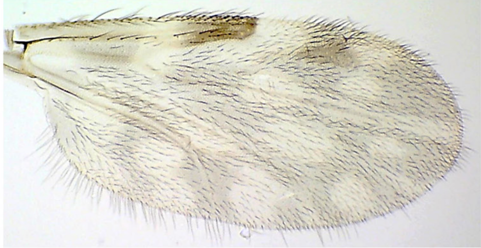
198 *C. butleri* ♀



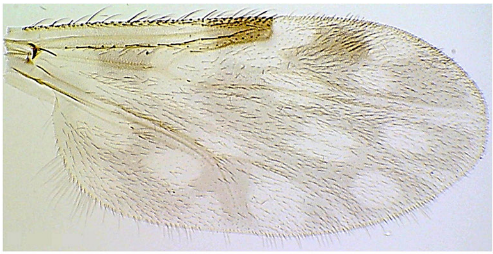
199 *C. cacticola* ♀



200 *C. insolatus* ♀



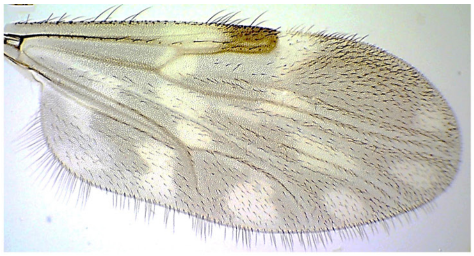
201 *C. jonesi* ♀

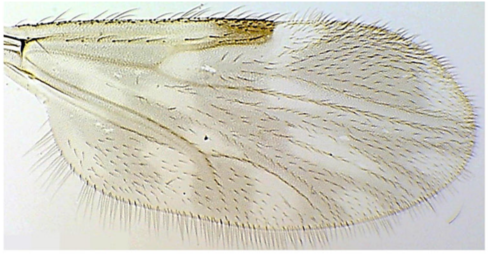


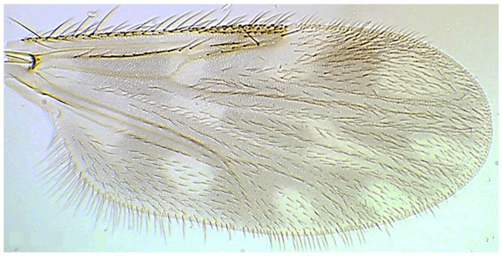
202 *C. sitiens* ♀

203 *C. torridus* ♀

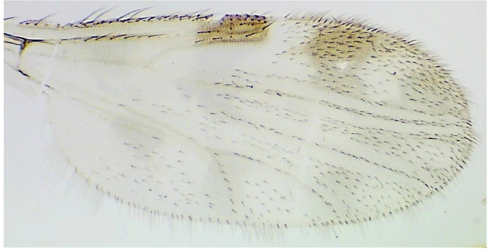
Figures 195–203. Female wings of *Culicoides*. **195)** *C. daedalus* (Panama, from Wirth and Blanton 1959: 320, Fig. 25). **196)** *C. pampoikilus* (Lincoln County, NM [FSCA]). **197)** *C. bakeri* (Riverside County, CA). **198)** *C. butleri* (Cochise County, AZ [FSCA]). **199)** *C. cacticola* (Orange County, CA [UCRC]). **200)** *C. insolatus* (Sonora, Mexico [FSCA]). **201)** *C. jonesi* (Greenlee County, AZ). **202)** *C. sitiens*. **203)** *C. torridus* (San Diego County, CA [BM]).

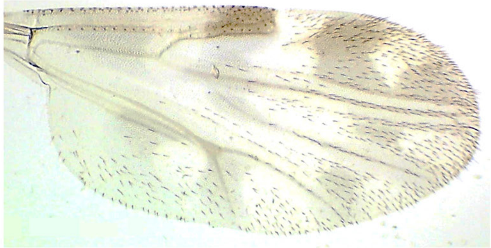

204 *C. defoliarti* ♀

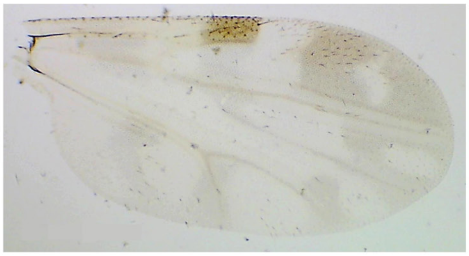

205 *C. haematopotus* ♀


206 *C. luglani* ♀


207 *C. mohave* ♀

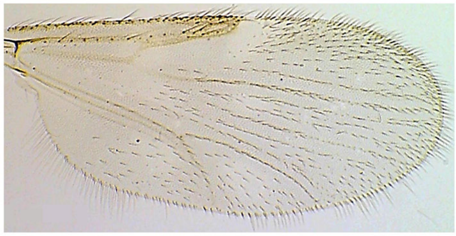

208 *C. mohave* ♀


209 *C. mohave* ♀

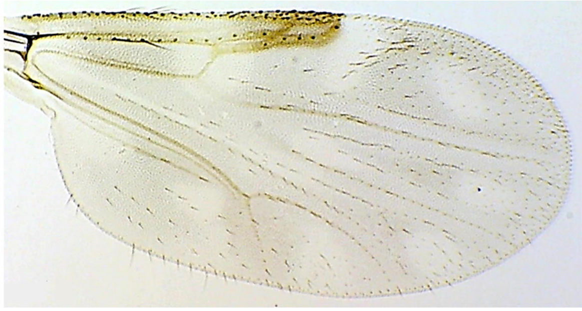

210 *C. mohave* ♀


211 *C. inyoensis* ♀


212 *C. inyoensis* ♀

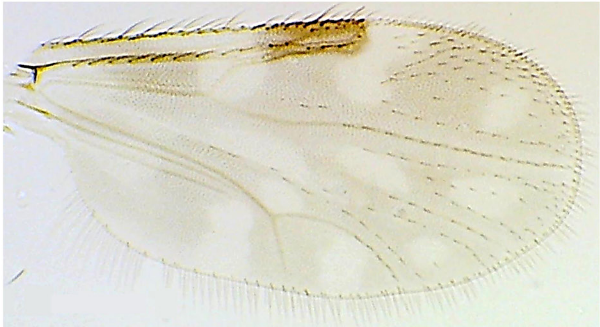

213 *C. salihi* ♀

Figures 204–213. Female wings of *Culicoides*. **204)** *C. defoliarti*. **205)** *C. haematopotus*. **206)** *C. luglani*. **207)** *C. mohave*, common form (Riverside County, CA [BM]). **208–210)** *C. mohave*, variants (Riverside County, CA). **211)** *C. inyoensis* (Grand County, UT). **212)** *C. inyoensis* (Saratoga Spring, San Bernardino County, CA [FSCA]). **213)** *C. salihi*.



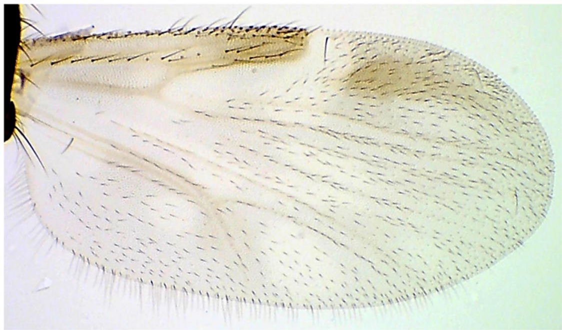
214 *C. byersi* ♀

215 *C. arizonensis* ♀

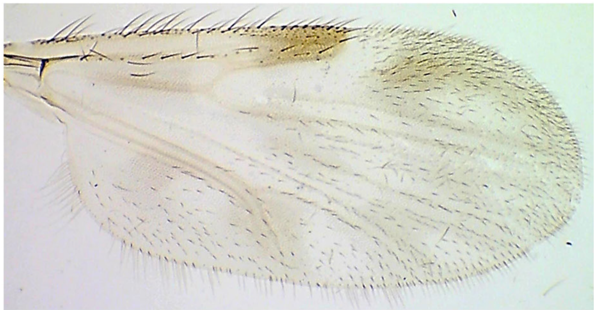


216 *C. hinmani* ♀

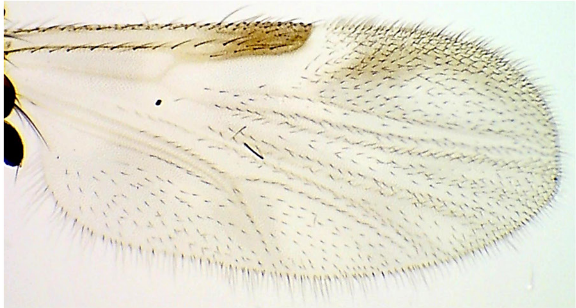
217 *C. copiosus* ♀



218 *C. copiosus* ♀

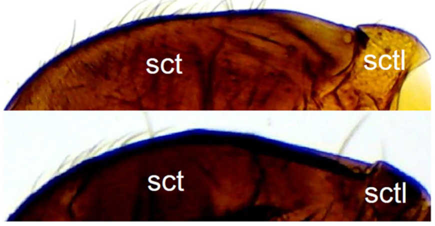


219 *C. ryckmani* ♀

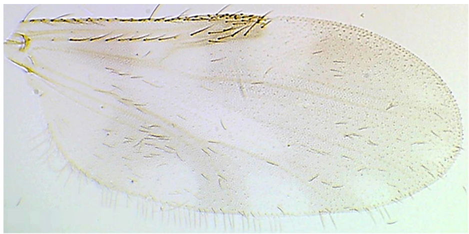


220 *C. ryckmani* ♀

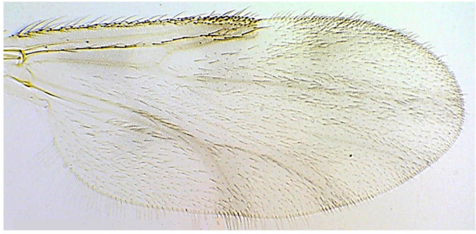
Figures 214–220. Female wings of *Culicoides* subgenus *Drymodesmyia*. **214)** *C. byersi*. **215)** *C. arizonensis* (Yuma County, AZ [UCRC]). **216)** *C. hinmani*. **217)** *C. copiosus* (San Diego County, CA [BM]). **218)** *C. copiosus* (Washington County, UT). **219)** *C. ryckmani* (San Diego County, CA [BM]). **220)** *C. ryckmani* (San Bernardino County, CA).



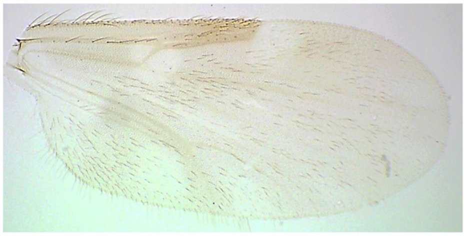
221 *C. calexicanus* ♀, *C. utahensis* ♀



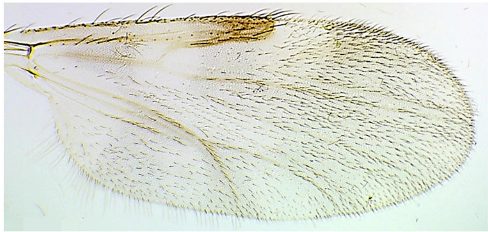
222 Palmerae gr. sp. C ♀



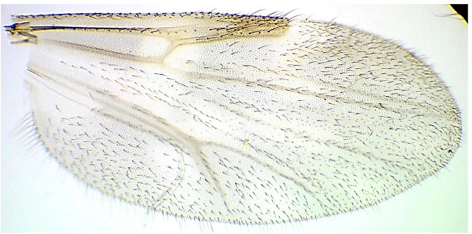
223 *C. calexicanus* ♀



224 *C. hawsi* ♀



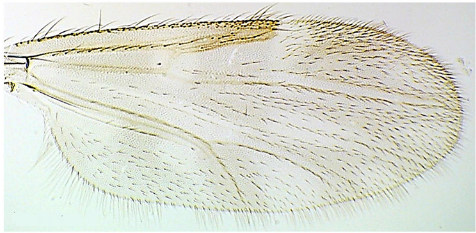
225 *C. palmerae* ♀



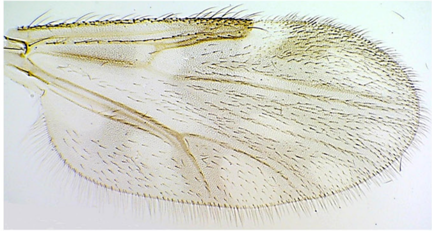
226 Sp. F ♀

227 *C. unicolor* ♀

228 *C. cavaticus* ♀

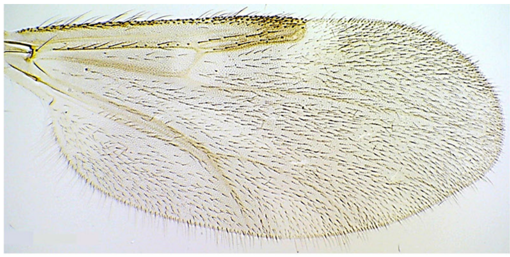


229 *C. doeringae* ♀

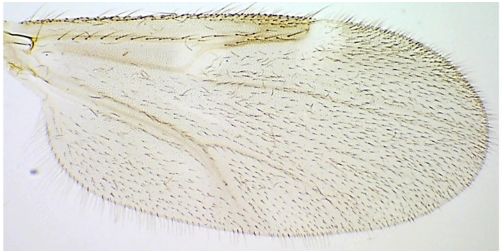


230 *C. doeringae* ♀

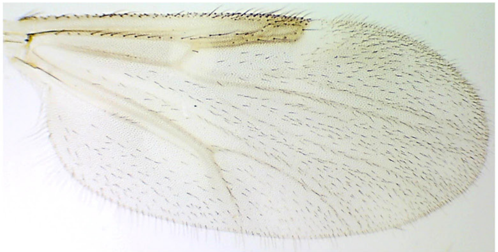
Figures 221–230. 221) Lateral view of female *Culicoides* mesonotum (anterior to left), scutum (sct), scutellum (sctl): *C. calexicanus*, top; *C. utahensis*, bottom. Female wings of *Culicoides*. **222)** *C.* Palmerae group species C. **223)** *C. calexicanus*. **224)** *C. hawsi*. **225)** *C. palmerae*. **226)** Unplaced species F (Bonneville County, ID). **227)** *C. unicolor* proximal portion; distal portion lost but would not have pale spots (Bonneville County, ID). **228)** *C. cavaticus*, arrow points to (faint) marginal posteromedian pale patch of anal cell (in grayscale) (Mendocino County, CA [FSCA]). **229)** *C. doeringae*, less prominent form. **230)** *C. doeringae*, more prominent form.



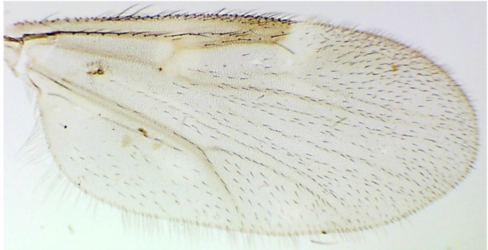
231 *C. kibunensis* ♀



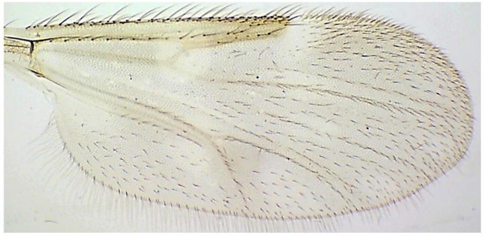
232 *C. travisi* ♀



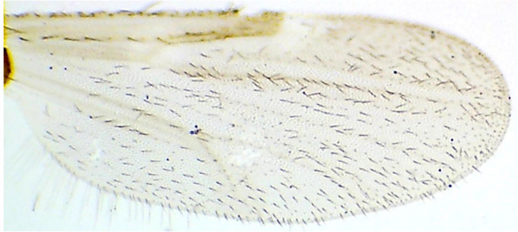
233 Piliferus gr. sp. B ♀



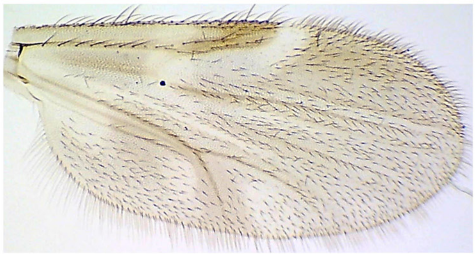
234 *C. chewaclae* ♀



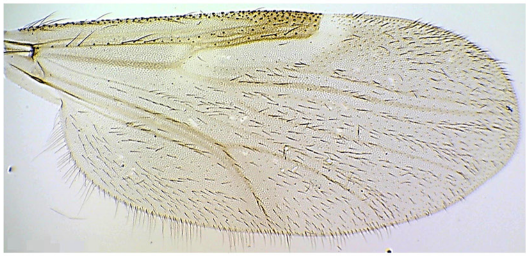
235 Piliferus gr. sp. A ♀



236 *C. posoensis* ♀

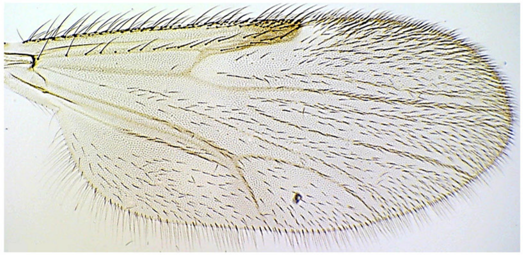


237 *C. sublettei* ♀



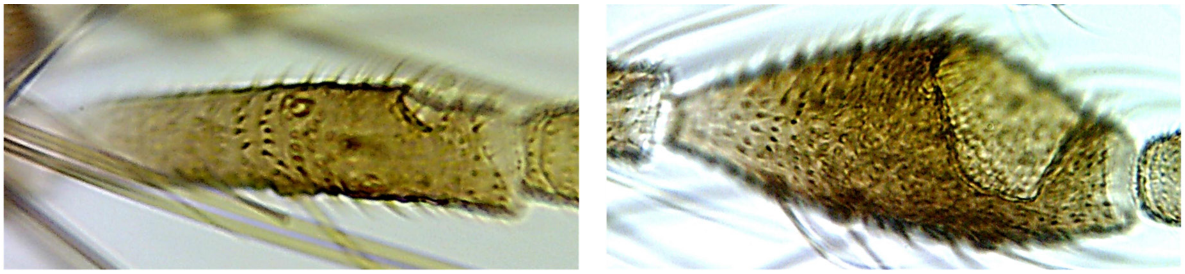
238 *C. usingeri* ♀

239 *C. vetustus* ♀



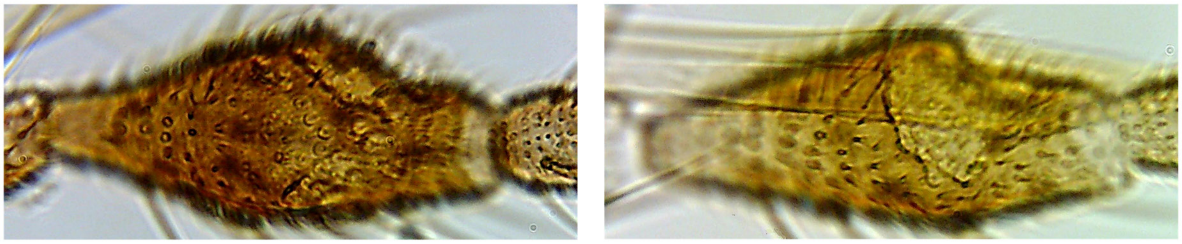
240 *C. erikae* ♀

Figures 231–240. Female wings of *Culicoides*. **231)** *C. kibunensis*. **232)** *C. travisi* (VA [FSCA]). **233)** *C.* Piliferus group species B (Montrose County, CO). **234)** *C. chewaclae* (San Juan County, UT). **235)** *C.* Piliferus group species A. **236)** *C. posoensis* (paratype, Kern County, CA [FSCA]). **237)** *C. sublettei* (Gillespie County, TX [FSCA]). **238)** *C. usingeri*. **239)** *C. vetustus* (paratype, San Bernardino County, CA [BM]). **240)** *C. erikae*.



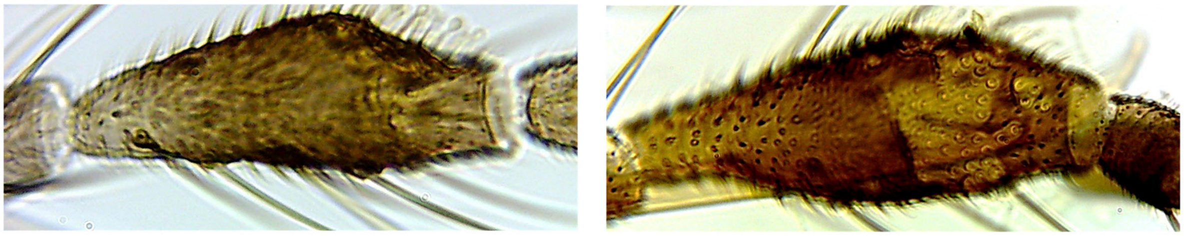
241 *C. lahontan* ♂

242 *C. lahontan* ♀



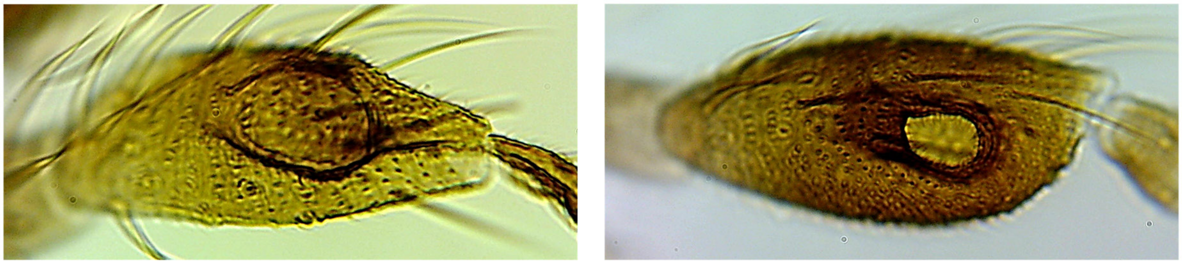
243 *C. freeborni* ♀

244 *C. neofagineus* ♀



245 *C. neomontanus* ♀

246 *Silvicola* sp. D ♀



247 *C. californiensis* ♀

248 *C. sitiens* ♀

249 *C. hinmani* ♀

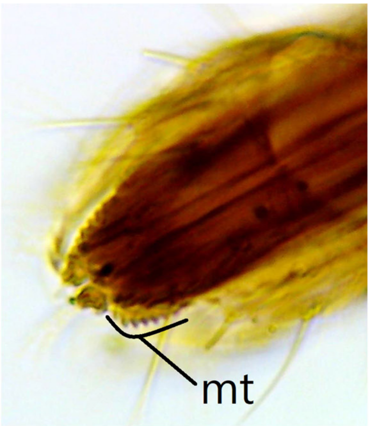
Figures 241–249. Palpal segment 3 of *Culicoides* (not to scale). **241)** *C. lahontan* male. Females: **242)** *C. lahontan*. **243)** *C. freeborni* (San Diego County, CA [BM]). **244)** *C. neofagineus* (paratype, Mendocino County, CA [FSCA]). **245)** *C. neomontanus*. **246)** *C.* (*Silvicola*) species D. **247)** *C. californiensis*. **248)** *C. sitiens*. **249)** *C. hinmani* (pore of pit outlined).

250 *C. byersi* ♀ *C. hinmani* ♀

251 *C. utahensis* ♂

252 *C. salihi* ♂

253 Palmerae gr. sp. C ♀

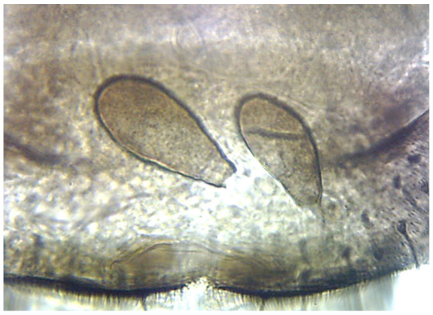


254 Palmerae gr. sp. C ♀

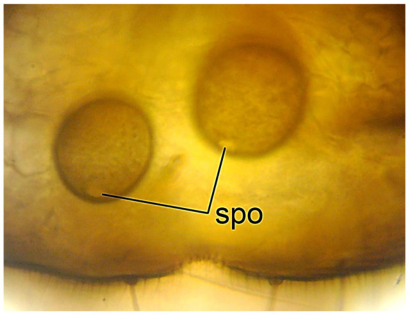
Figures 250–254. 250) Lateral view of thoraxes of female *Culicoides* (anterior ends to left), showing slide-mounted color contrast and leg-banding: *C. byersi*, left; *C. hinmani*, right. **251)** *C. utahensis* male head. **252)** *C. salihi* male head. **253)** *C.* Palmerae group species C, female head. **254)** *C.* Palmerae group species C, mandibular teeth (mt).

255 *C. sitiens*

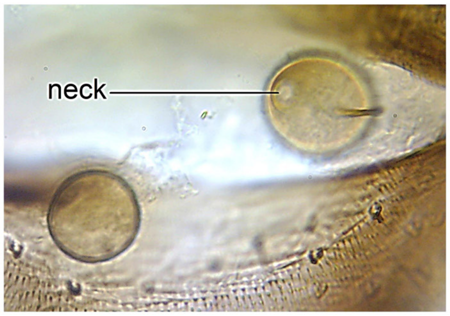
256 *C. jonesi*



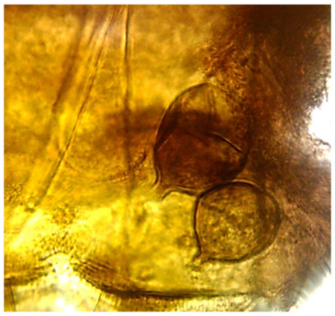
257 *C. butleri*



258 *C. cacticola*

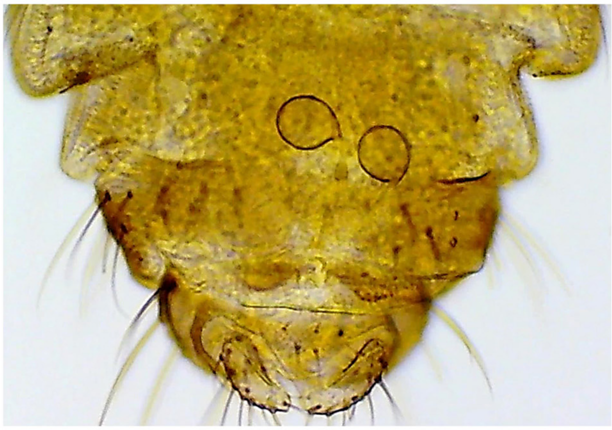


259 *C. bakeri*



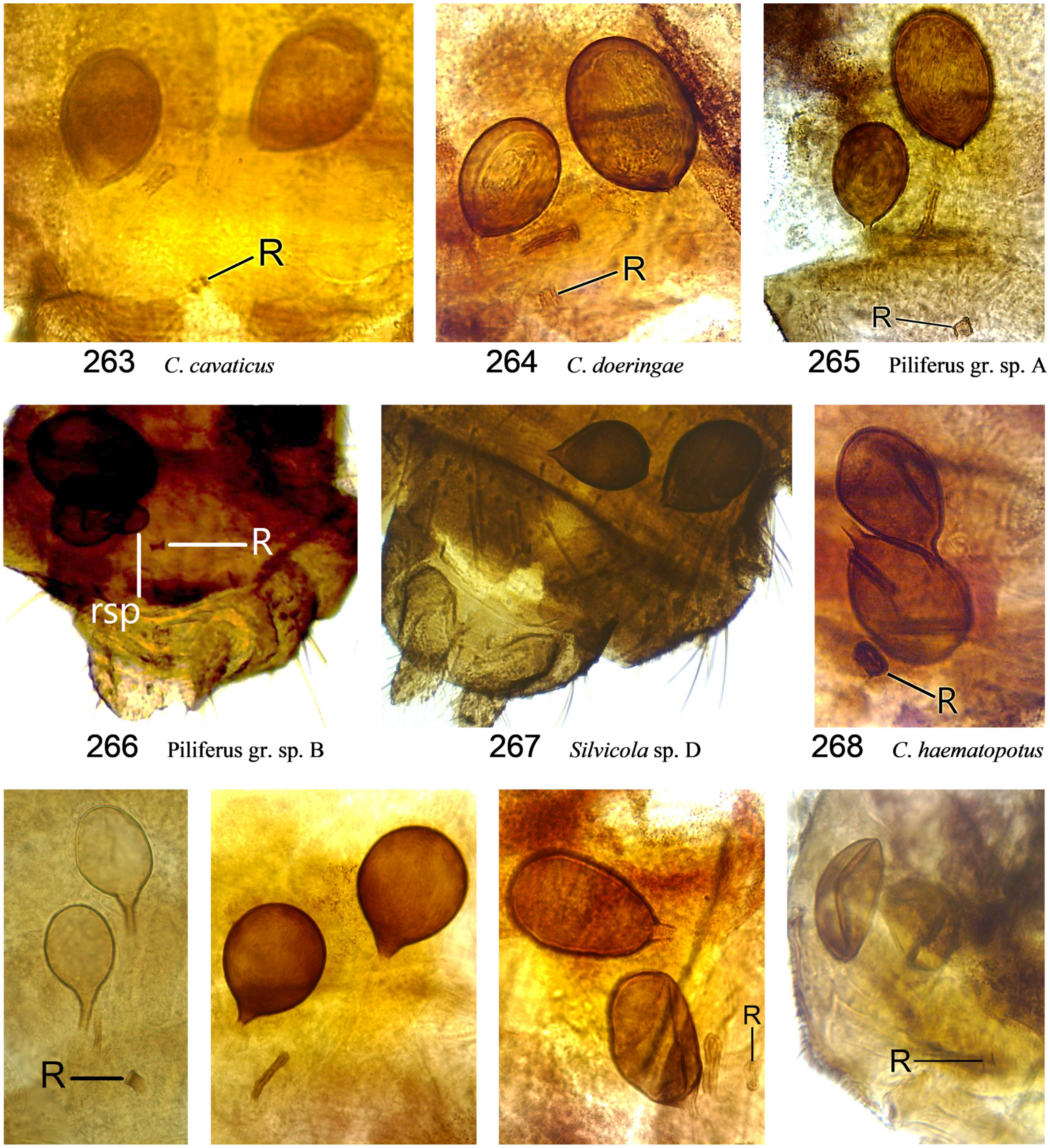
260 *C. copiosus*

261 *C. copiosus*



262 *C. ryckmani*

Figures 255–262. Spermathecae of *Culicoides* subgenus *Drymodesmyia*. **255)** *C. sitiens*. **256)** *C. jonesi* (Greenlee County, AZ). **257)** *C. butleri* (Greenlee County, AZ). **258)** *C. cacticola*, spermathecal opening (spo) (Greenlee County, AZ). **259)** *C. bakeri* (Riverside County, CA). **260)** *C. copiosus* (Washington County, UT). **261)** *C. copiosus* (San Diego County, CA [BM]). **262)** *C. ryckmani* (San Diego County, CA [BM]).

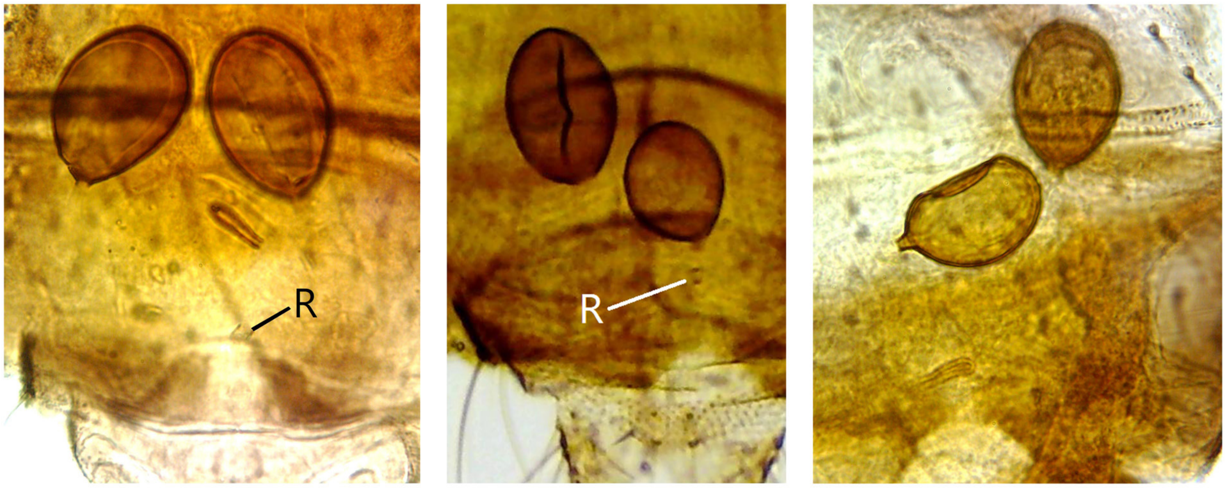


263 *C. cavaticus* 264 *C. doeringae* 265 Piliferus gr. sp. A

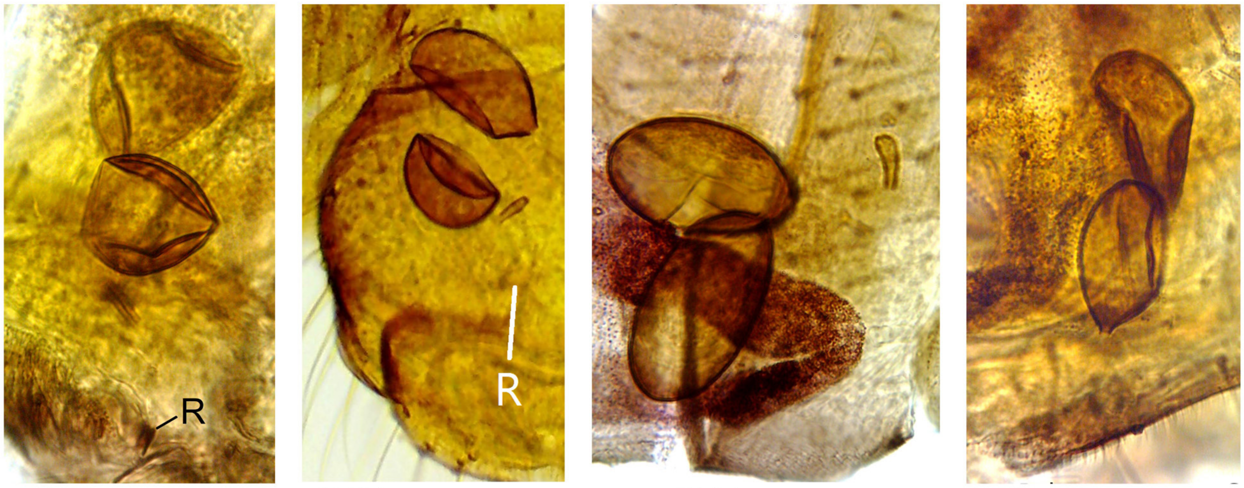
266 Piliferus gr. sp. B 267 *Silvicola* sp. D 268 *C. haematopotus*

269 *C. salihi* 270 *C. usingeri* 271 *C. erikae* 272 *C. posoensis*

Figures 263–272. Spermathecae of *Culicoides*, ring (R) on spermathecal duct indicated. **263)** *C. cavaticus* (Mendocino County, CA [FSCA]). **264)** *C. doeringae*. **265)** *C.* Piliferus group species A. **266)** *C.* Piliferus group species B, showing the pyriform rudimentary spermatheca (rsp), fairly common in this species. **267)** *C.* (*Silvicola*) species D. **268)** *C. haematopotus*. **269)** *C. salihi*. **270)** *C. usingeri*. **271)** *C. erikae*. **272)** *C. posoensis* (paratype, Kern County, CA [FSCA]).

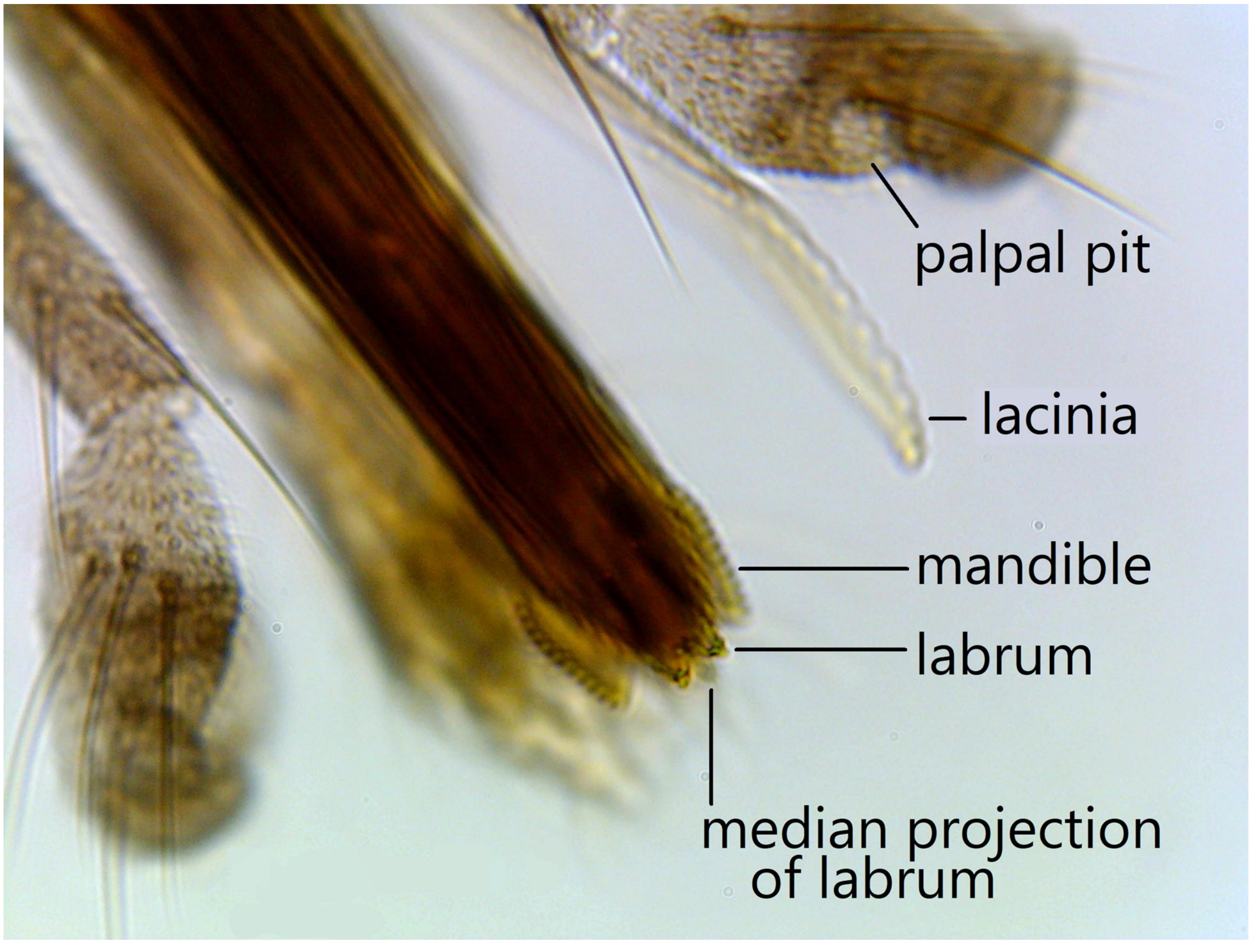


273 *C. kibunensis* 274 *C. travisi* 275 *C. calexicanus*

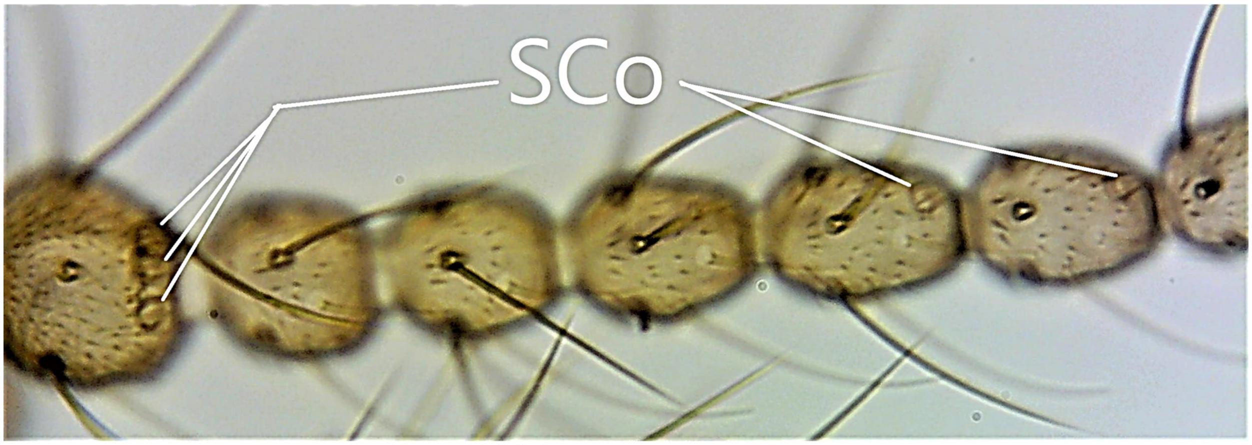


276a *C. hawsi* 276b *C. hawsi* 277 *C. palmerae* 278 Palmerae gr. sp. C

Figures 273–278. Spermathecae of *Culicoides*, ring (R) on spermathecal duct indicated. **273)** *C. kibunensis*. **274)** *C. travisi* (VA [FSCA]). **275)** *C. calexicanus*. **276 a, b)** *C. hawsi*. **277)** *C. palmerae*. **278)** *C.* Palmerae group species C.

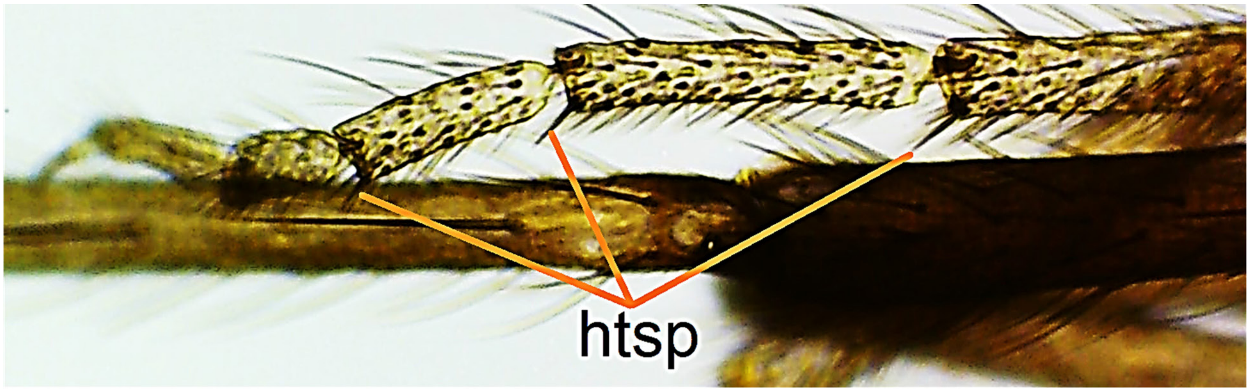


279 *C. unicolor* ♀



280 *C. mortivallis* ♀

Figures 279–280. 279) *Culicoides unicolor* mouthparts (Bonneville County, ID). **280)** *C. mortivallis* proximal flagellomeres showing SCo on flagellomeres 1, 5, 6 (Greenlee County, AZ).



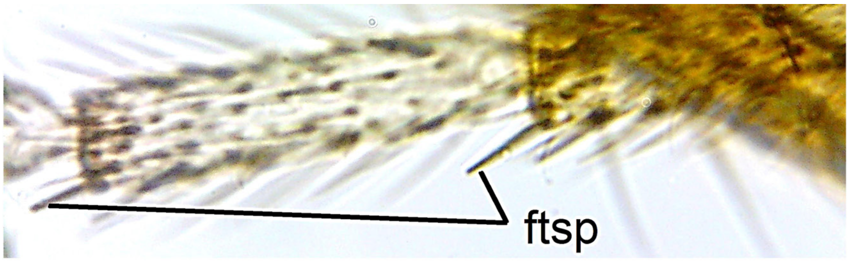
281 *C. denningi* ♀

282 *C. sierrensis* ♀

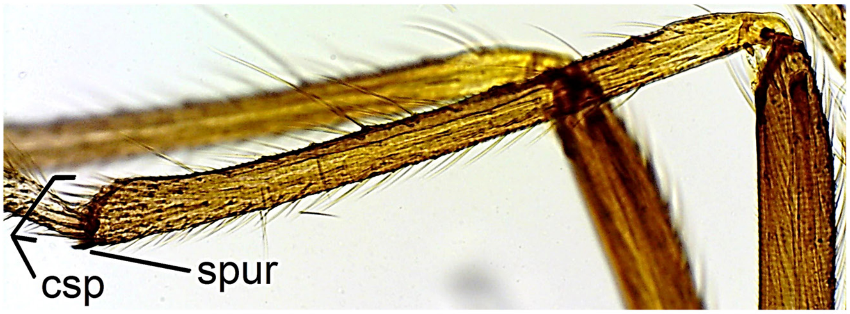
283 *C. palmerae* ♂

284 Sp. F ♀

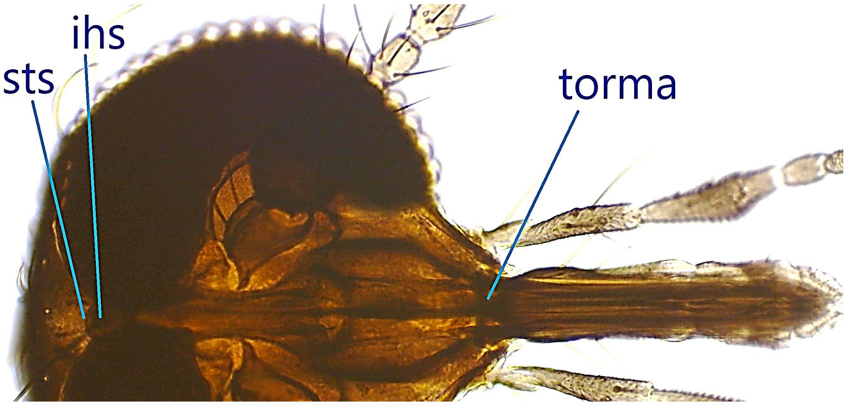
Figures 281–284. Hind tarsomere spines (htsp) on *Culicoides*. **281)** *C. denningi* (Custer County, ID). **282)** *C. sierrensis* (Blaine County, ID). **283)** *C. palmerae*. **284)** Unplaced species F, tibial comb spines (csp) (Bonneville County, ID).



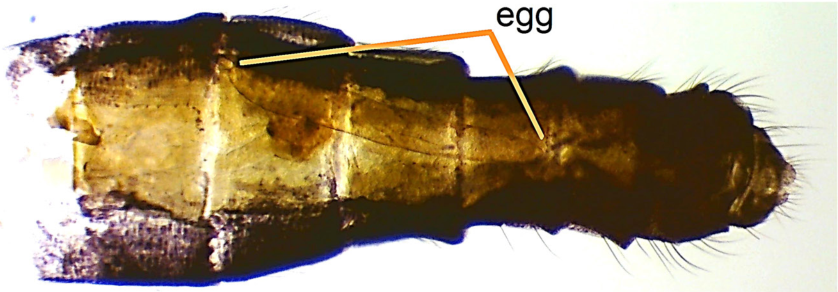
285 *C. calexicanus* ♀



286 *C. sierrensis* ♀

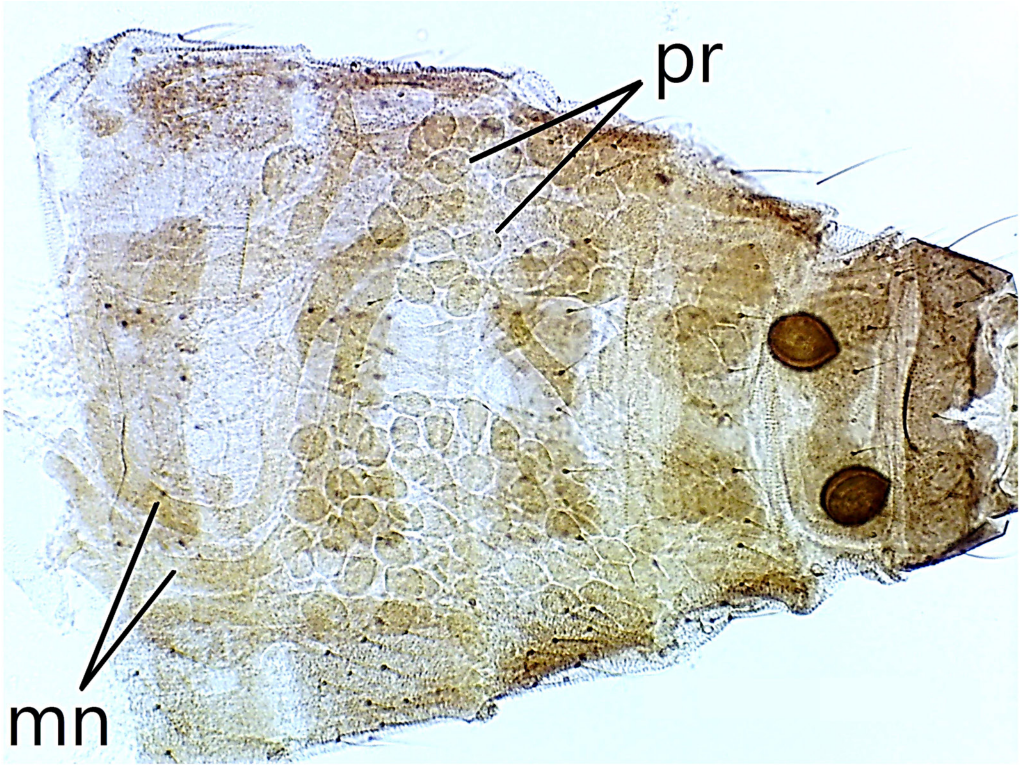


287 *C. cockerellii* ♀

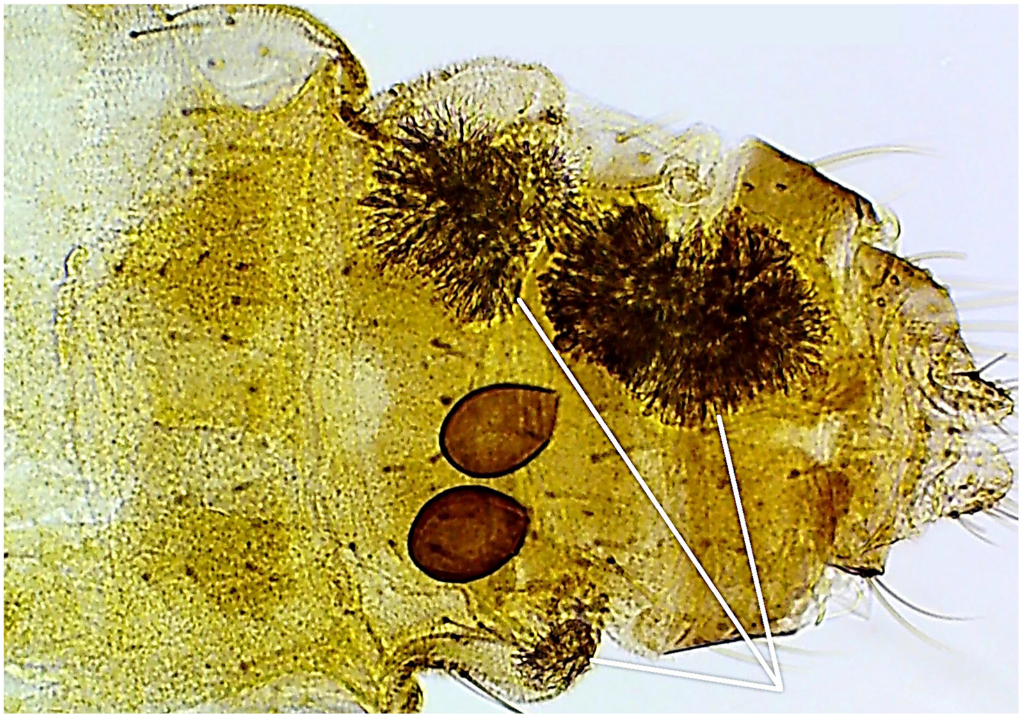


288 *C. neomontanus*

Figures 285–288. 285) *Culicoides calexicanus*, spines on fore tarsomeres 1–2 (ftsp). **286)** *C. sierrensis* hind tibia showing basal pale band, comb spines (csp), apical spur (spur) (Blaine County, ID). **287)** *C. cockerellii* head, superior transverse suture (sts), interocular hair socket (ihs), torma. **288)** *C. neomontanus* female abdomen, ventral view, showing 617 µm × 80 µm egg within abdominal segments 3–5 and the purple-burgundy color on the lateral portions of the abdomen common in parous females but absent from nullipars (Montrose County, CO).



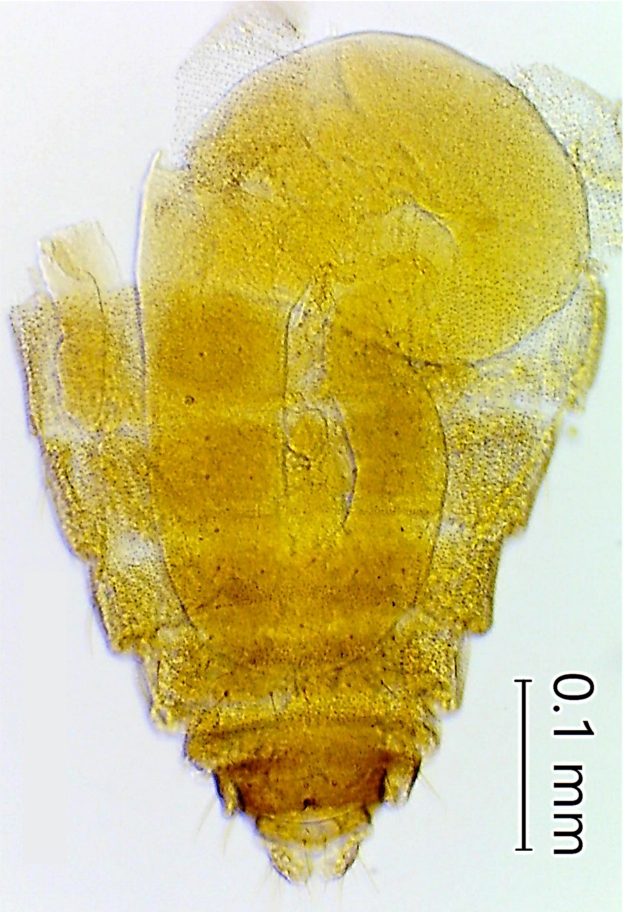
289 *C. mortivallis*



290 *C. mortivallis-owyheensis*

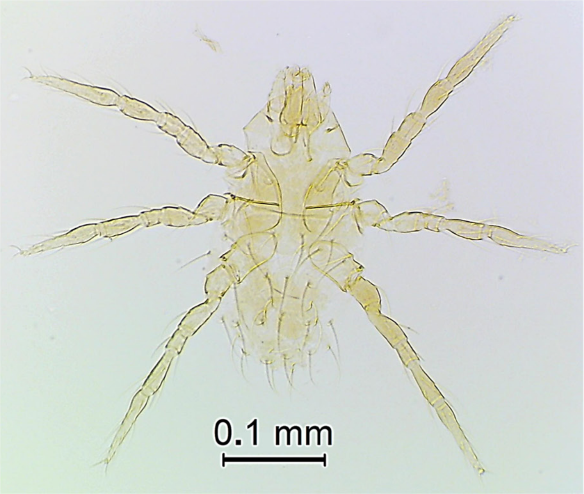
Figures 289–290. 289) *Culicoides mortivallis* abdominal segments 3–8, ventral view, with ciliate protozoan (pr) (*Tetrahymena* sp.?) and mermithid nematodes (mn) parasites. **290)** *C. mortivallis-owyheensis* abdominal segments 5–9, ventral view, starburst infections indicated.

291 *C. californiensis*



292 *C. reevesi*

293 *C. bottimeri* ♀



294 mite larva

Figures 291–294. 291) *Culicoides californiensis* male terminalia, ventral view, showing widely disseminated infuscation that may be an infection. **292)** *C. reevesi* female abdomen, ventral view, with mermithid nematode parasite. **293)** *C. bottimeri* females, dorsal habitus, nulliparous on left, parous on right, showing the burgundy abdominal coloration common in parous *Culicoides* females (in alcohol, Butte County, CA [Bradley Mullens, with permission]). **294)** Mite larva collected from a female *C. mortivallis* collected with CO_2-baited trap 23 June 2004.

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